Sexual selection and ecological generalism are correlated in antbirds

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Abstract

Sexual selection is thought to counteract natural selection on the grounds that secondary sexual traits are inherently costly and evolve at the expense of naturally selected traits. It is therefore commonly predicted that increased sexual selection is associated with decreased physiological tolerance or ecological plasticity. Using phylogenetic comparative methods, we test this prediction by exploring relationships between traits assumed to be sexually selected (plumage dichromatism and song structure) and traits assumed to be naturally selected (altitudinal range and habitat range) in a diverse family of tropical birds. Contrary to expectations, we find that taxa with higher levels of dichromatism, and lower song pitch, occupy a wider variety of habitats and elevations. In other words, indices of sexual selection are positively related to two standard measures of ecological generalism. One interpretation of this pattern is that sexual selection combines synergistically with natural selection, thereby increasing physiological tolerance or the propensity to adapt to novel environments. An alternative possibility is that ecological generalism increases population density, which in turn promotes sexual selection in the form of greater competition for mates. Overall, our results suggest that a synergism between natural selection and sexual selection may be widespread, but the processes underlying this pattern remain to be investigated.

Introduction

A widespread and influential assumption in evolutionary biology is that sexual selection reduces population mean fitness (Fisher, 1930; Haldane, 1932; Lande, 1980; Grafen, 1990; Kirkpatrick & Ryan, 1991; Gavrilets *et al.* 2001; Houle & Kondrashov, 2001). This is based on the prevailing view that elaborate secondary sexual traits and associated preferences are costly (Fisher, 1915, 1930; Zahavi, 1975; Rohwer, 1982; West-Eberhard, 1983) and therefore deleterious to nonsexual fitness (all aspects of fitness apart from the quantity and fitness of mates; Andersson, 1994). In accordance, previous studies hypothesize that species subject to high levels of sexual selection are likely to have lower competitive ability,

narrower physiological tolerance and increased vulnerability to predators and parasites, because energy allocated towards sexual ornamentation is unavailable for traits associated with survival (McLain, 1993; McLain *et al.*, 1995; Badyaev & Ghalambor, 1998). For similar reasons, it has repeatedly been proposed that sexual selection may ultimately lead to reduced survival of individuals, and therefore to the extinction of populations and species (Møller, 1989; Promislow *et al.*, 1992, 1994; Tanaka, 1996; Sorci *et al.*, 1998; McLain *et al.*, 1999; Brooks, 2000; Doherty *et al.*, 2003; Kokko & Brooks, 2003; Morrow & Pitcher, 2003; Liker & Székely, 2005). On the basis of these assorted costs, it is often concluded that sexual selection counteracts natural selection, an idea that can be traced back to Darwin (1859, 1871).

A contrasting possibility is that sexual selection acts in tandem with natural selection. This may occur, for example, if sexual selection and natural selection both

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favour high-quality individuals, in line with the logic of good genes models of mate choice. The central assumption of these models is that costly ornaments are honest indicators of genetic quality, such that females choosing ornamented males gain indirect benefits by producing higher quality offspring (Zahavi, 1975; Hamilton & Zuk, 1982; Kirkpatrick & Ryan, 1991; Iwasa & Pomiankowski, 1994, 1999). Theoretical studies suggest that, when the attractiveness and condition of individuals is genetically correlated in this way, sexual selection can enhance nonsexual fitness by promoting the fixation of beneficial alleles (Proulx, 1999). From this perspective, the interaction between sexual selection and population mean fitness is positive rather than negative, potentially leading to broader ecological niches (Proulx, 2002), accelerated rates of adaptation (Lorch et al., 2003) and a reduced likelihood of extinction (Whitlock, 2000).

These opposing viewpoints suggest that the interaction between sexual selection and natural selection is complex and poorly understood. To date, it has been studied largely at the level of population or individual using laboratory experiments or theoretical models. It has rarely been examined across multiple species using comparative methods. Birds, as one of the most intensively studied animal groups, provide the most promising template for this approach. They offer two well-supported sexual traits – plumage dichromatism and song complexity – both of which covary with the strength of sexual selection (see Materials and methods). In conjunction, they offer two quantifiable ecological traits – altitudinal range and habitat range – which are likely to capture variation in physiological tolerance, as well as the ability to adapt to novel environments and to compete with related species (see Materials and methods). Thus, the interaction between sexual and ecological traits can be compared across avian taxa to test for predicted correlations.

The only previous study to capitalize on this opportunity found a positive association between dichromatism and altitudinal range in cardueline finches (Badyaev & Ghalambor, 1998). This outcome is intriguing because it is opposite to the relationship predicted if a trade-off exists between sexual selection and ecological generalism (McLain, 1993). However, Badyaev & Ghalambor (1998) pointed out that trade-offs operating within species are unlikely to be evident across species if related taxa differ in behaviour, ecology or physiology. Cardueline finches, in particular, vary widely in pigmentation (melanin-based vs. carotenoid-based), migratory behaviour (sedentary vs. migratory), breeding behaviour (female-only vs. biparental incubation), habitat (dense vs. open), latitudinal distribution (tropical vs. temperate) and biogeography (continental vs. insular) (Clement et al., 1993; Cramp & Perrins, 1994; Badyaev, 1997). All these variables may influence the elaboration of ornaments and reduce the extent to which dichromatism can be viewed as a reliable measure of sexual selection (Martin

& Badyaev, 1996; Badyaev & Hill, 2000; Price, 2008). In birds with female-only incubation, for example, the risk of predation to adults, eggs or nestlings may select for drab plumage in females alone, such that ecological selection on female plumage (rather than sexual selection on male plumage) drives the evolution of dichromatism (Wallace, 1889; Burns, 1998). Likewise, song complexity tends to increase in open habitats or in migratory species (Morton, 1975; Handford & Lougheed, 1991; Wiley, 1991; Read & Weary, 1992) and either increases or decreases when continental species are compared with insular relatives (Hamao & Ueda, 2000; Baker et al., 2006; Price, 2008). Variation in diet and the pigments underlying plumage colour are particularly problematic in cardueline finches, suggesting that this avian subfamily is not ideally suited to comparative studies of dichromatism (Badyaev & Hill, 2000). Thus, although the study by Badyaev & Ghalambor (1998) hints at a counter-intuitive positive relationship between sexual selection and ecological generalism, it is difficult to draw firm conclusions because of potentially confounding interspecific variation.

Here, we use phylogenetic comparative methods to re-examine the interaction between two traits assumed to be sexually selected (song structure and sexual dichromatism) and two traits assumed to be naturally selected (altitudinal range and habitat range) across a diverse family of suboscine passerines, the antbirds. The antbird clade offers a model system for this study for four reasons. First, interspecific variation is unusually low in ecological attributes: all species are nonmigratory insectivores with continental distributions in the tropics and all inhabit dense vegetation such as scrub or forest (Zimmer & Isler, 2003). Second, underlying pigmentation is also relatively invariable: antbird plumage is dominated by black, grey, rufous and white, whereas yellows and reds are absent or rare (Zimmer & Isler, 2003; Olson & Owens, 2005). Sexual dichromatism therefore appears to be mediated almost entirely by melanin-based coloration, which is less closely linked to food intake than carotenoid-based coloration (Fox & Vevers, 1960; Brush, 1978; Gray, 1996). Third, the dimorphic elements of antbird plumage tend to involve conspicuous signals on the crown, throat, chest or wings, many of them exaggerated during inter- or intrasexual displays (see Fig. 1). This suggests that dichromatism evolves through social selection (including sexual selection) rather than by ecological selection for camouflage. Fourth, the possibility that dichromatism is a by-product of sexual biases in behavioural roles can be discounted because 231 antbird species (99%) breed in socially monogamous pairs and incubation duties are shared in all 90 species for which data exist (Zimmer & Isler, 2003). Hence, there is no reason to expect selection for camouflage to be stronger in one sex than the other. The prevalence of social monogamy does not undermine our assumption that variable levels of sexual selection are

Fig. 1 Examples of melanin-based plumage dichromatism in three species of antbirds (*Thamnophilidae*). Males of many species in this family are characterized by conspicuous black plumage patches on body regions associated with inter- or intrasexual signaling, such as the crown, throat and chest; females typically lack these patches and are therefore relatively subdued in pattern. In this study, dichromatism was quantified by comparing males (left) with females (right) and scoring differences in five body regions (see Materials and methods). The stripe-backed antbird *Myrmorchilus strigilatus* (a) shows major differences between the sexes in one body region (underside), whereas the rufous-tailed antbird *Drymophila genei* (b) differs in three body regions, and the scale-backed antbird *Hylophylax poecilinotus nigrigula* (c) in all five body regions. These three forms were therefore given dichromatism scores of 2, 6 and 10, respectively. Note that *H. poecilinotus* is now reassigned to a separate genus, *Willisornis*. Illustrations are reproduced from the *Handbook of the Birds of the World* with the permission of Lynx Edicions.
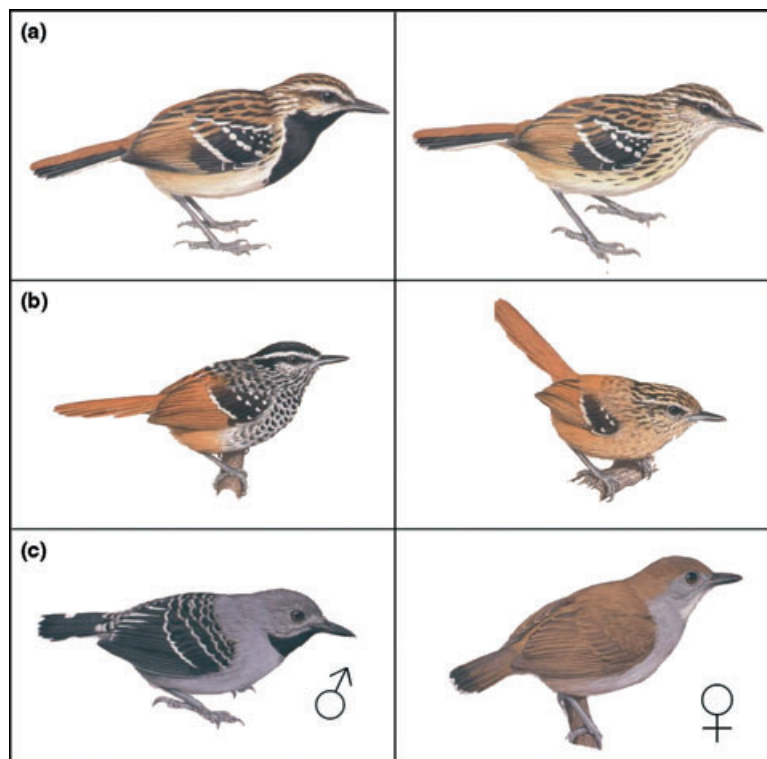
exerted by factors such as mating competition, mating costs and sex ratios (Kvarnemo & Ahnesjö, 1996; Kokko & Johnston, 2002). Indeed, field studies in some antbird species clearly demonstrate that operational sex ratios are skewed, mate switching is regular and mating competition is intense (e.g. Morton *et al.*, 2000; Fedy & Stutchbury, 2004). Overall, by restricting our analysis to the antbird family, we hold a large number of confounding variables relatively constant, whereas interspecific variation remains high in terms of dichromatism and song structure (Seddon *et al.*, 2008).

The aim of this study was to use an expanded set of predictors to assess the sign and magnitude of the relationship between sexual selection and ecological generalism in antbirds. Specifically, we test the prediction that, if sexual selection inhibits ecological generalism (McLain, 1993), a negative correlation will exist between the elaboration of secondary sexual characters and indices of niche width. Conversely, we assume that if sexual selection causes local populations to adapt more rapidly or more readily (Lorch *et al.*, 2003), then this will lead to species that are more ecologically plastic across their global ranges. By way of definition, we treat the terms 'ecological plasticity' and 'ecological generalism' as almost interchangeable, but for the fact that plasticity implies adaptability (i.e. the ability of individuals to adapt from one environment to another or to switch from one diet to another), whereas generalism may simply refer to a broad niche (i.e. the ability of individuals to exploit a range of environments simultaneously). Although subtly different, adaptability and niche width are jointly relevant to the hypothesis under examination.

Materials and methods

Study species

Antbirds are small- to medium-sized insectivorous passerines occurring from 0 to 3000 m a.s.l. in the continental Neotropics (e.g. Stotz *et al.*, 1996; Zimmer & Isler, 2003). The antbird family (Thamnophilidae) is diverse and unambiguously monophyletic (Irestedt *et al.*, 2002, 2004; Zimmer & Isler, 2003). For the purposes of this study, species limits were assigned following Remsen *et al.* (2006) and genera were assigned following Zimmer & Isler (2003), incorporating recent modifications (Braun *et al.*, 2005; Brumfield & Edwards, 2007; Isler *et al.*, 2007a, b, c). Most antbird taxa with distinctive songs are likely to be cryptic species (Isler *et al.*, 1998; Remsen, 2005) and therefore we also included in our sample all taxa identified as vocally distinct by Isler & Whitney (2002). The published totals of 209 species, 46 genera and 503 subspecies (Zimmer & Isler, 2003; Remsen *et al.*, 2006) are thus increased to 233 species, 53 genera and 503 subspecies. The final classification and assignment of species to genera is presented in Table S1.

Antbirds lend themselves to the compilation of standardized indices because comprehensive vocal and

ecological information has recently been published for all species in standardized format (Isler & Whitney, 2002; Zimmer & Isler, 2003). The level of detail is roughly constant across species and, as there are otherwise few detailed ecological studies published for this Neotropical family, variation in research effort is unlikely to influence our results. This contrasts with the situation in the Nearctic, or Western Palearctic, where there is great variation in research effort across passerine species, and where, consequently, it is necessary to statistically control for publication bias when conducting comparative studies (e.g. Garamszegi et al., 2007). Similarly, the need to correct for sampling error and within-species variation (Felsenstein, 2008) is less pressing when generating means for antbirds because vocal and plumage traits are relatively stereotyped in this family (see below).

Indices of ecological generalism

We used two ecological indices: (i) the ability to tolerate a range of environmental conditions (altitudinal range) and (ii) the ability to exploit a variety of habitats and foraging niches (habitat range). These indices were positively correlated ($r = 0.39$, $P < 0.0001$, $N = 233$ species). Both altitudinal range and habitat range are here assumed to represent a measure of competitive ability, propensity to adapt to novel environments and ability to tolerate environmental variability. They are regularly used as surrogates for both ecological plasticity or ecological generalism (Badyaev & Ghalambor, 1998; Sorci et al., 1998; Bennett & Owens, 2002; Phillimore et al., 2006). Altitudinal range was calculated by subtracting minimum elevation from maximum elevation for each species. Habitat range was scored as the number of discrete habitat types, including major microhabitats, used by each species across its geographical range. We subdivided Neotropical habitats into 19 types following Parker et al. (1996) plus three key microhabitats (2–4), following Zimmer & Isler (2003): (1) tropical lowland evergreen forest interior, (2) bamboo (*Guadua/ Merostachys/Chusquea*), (3) light gaps in forest (tree falls/landslides/natural clearings), (4) vine tangles (including lianas and arboreal leaf litter), (5) flooded tropical evergreen forest interior (*igapó* and *várzea*), (6) montane evergreen forest interior, (7) tropical deciduous forest interior (including *caatinga*), (8) forest edge (including river edge, lake edge and ecotone), (9) gallery forest, (10) white-sand forest (*campinarana*, *restinga*, *varillal* and other forest types growing on nutrient-poor soils), (11) palm forest (including *Mauritia flexuosa* swamp and montane palm forest), (12) mangrove, (13) secondary forest, (14) pastures and agricultural lands (including gardens), (15) arid lowland scrub, (16) semi-humid/ humid montane scrub, (17) *cerrado* (shrubby grasslands), (18) riparian thickets (including Amazonian riverine succession: *Tessaria–Gynerium–Cecropia*), (19) river-island scrub, (20) second-growth scrub, (21) freshwater marshes and (22) forested streams. Two observers unfamiliar with the hypotheses tested assigned species to these categories. Their scores showed high repeatability (intraclass correlation coefficient, $r = 0.86$, $P < 0.0001$) and the mean of their scores was used. Species were omitted if it was not clear which habitats they occupied. Most species exploit more than one habitat or microhabitat (mean ± SD 3.5 ± 1.8 habitats/microhabitats per species), but in no case does the use of one invariably involve use of another (i.e. redundancy is low). Categories are thus effectively discrete and a simple count can be used as a measure of ecological generalism.

Indices of sexual selection

Plumage dichromatism has long been assumed to arise from female choice or male competition (Darwin, 1871), thus providing a metric by which sexual selection can be assessed (Barraclough et al., 1995; Dunn et al., 2001; Bennett & Owens, 2002; Badyaev & Hill, 2003; Morrow et al., 2003; Price, 2007). Similarly, the use of vocal traits as indicators of inter- and intrasexual selection is buttressed by the results of numerous studies in birds (reviewed in Searcy & Andersson, 1986; Catchpole & Slater, 1995; Searcy & Yasukawa, 1996; Collins, 2004; Kroodsma, 2004), including antbirds (Wikelski et al., 1999; Bard et al., 2002; Fedy & Stutchbury, 2005). In general, previous work has demonstrated that bright plumages and complex songs are costly condition-dependent indicators of genetic and phenotypic quality and their elaboration is positively correlated with mating success (Bennett et al., 1997; Doucet et al., 2005; Reid et al., 2005; Spencer et al., 2005; Garamszegi et al., 2006). Comparative studies have also revealed that both dichromatism and song complexity correlate positively with three other powerful indices of sexual selection: testis size, degree of polygyny and level of extra-pair paternity (Read & Weary, 1992; Owens & Bennett, 1994; Møller, 1997; Dunn et al., 2001). Thus, we assume that variation in plumage dichromatism and song complexity reflects variation in sexual selection.

Plumage dichromatism

Following standard methodology (e.g. Owens & Bennett, 1994; Dunn et al., 2001; Morrow et al., 2003), dichromatism was scored on a scale of 0 (monomorphic) to 10 (maximum dichromatism) from colour illustrations of all known antbird species and all distinctive subspecies (Zimmer & Isler, 2003; see Fig. 1). All illustrations were produced by a single artist. We recognized five body regions: head (forecrown, crown and nape), upperside (mantle and rump), underside (throat, breast and belly), wings and tail. To each, we allocated a score of 0 (=no difference between the sexes), 1 (=difference in shade or intensity) or 2 (= *z*difference in colour or pattern). The mean of subspecies values was calculated to produce a composite dichromatism score for each species and the

mean value for each genus was generated from these species values. Scores for dichromatism were produced by an independent observer with no knowledge of the hypotheses being tested.

Because most birds are able to see ultraviolet (UV) light (Cuthill *et al.*, 2000) these methods will overlook dichromatism restricted to UV wavelengths (Eaton, 2005). However, we do not believe that this undermines our results because a parallel study demonstrated that cryptic dichromatism strongly positively correlated with visible dichromatism across 71 species ($r^2 = 0.40$) from 43 (79%) of the genera recognized in this study (Seddon *et al.*, unpublished data). This result is not unexpected because UV reflectance is a relatively minor feature in birds of the dimly lit forest understorey, including antbirds (Gomez & Théry, 2007). Moreover, molecular sequencing of the short-wave-sensitive SWS1 opsin gene indicates that antbirds are relatively insensitive to UV wavelengths (Seddon *et al.*, unpublished data).

Song structure

We assume that song structure (i.e. reduced pitch and increased complexity) is a signal of quality used in mate choice and/or intrasexual competition, following numerous authors (reviewed in Catchpole & Slater, 1995; Collins, 2004; Kroodsma, 2004). We quantified song structure by analysing spectrograms of high-quality recordings of male antbird songs obtained from a commercially available CD (Isler & Whitney, 2002) and private archives (for details, see Seddon, 2005). Songs were digitized at 44.1 kHz using Avisoft SASLabPro Version 4.1c (Specht, 2006) and spectrograms were produced using broadband filter settings (bandwidth 323 Hz; FFT 1024; frame 50%; window FlatTop; overlap 88%). We recorded eight basic song variables thought to be targeted by sexual selection because of their energetic and/or neurophysiological costs (Gil & Gahr, 2002; Collins, 2004): number of different note types (NnTypes), song duration (Dur), maximum (MaxFreq) and minimum frequency (MinFreq), bandwidth (BW), peak frequency (Peak), number of notes (Nn) and number of notes per second (Pace). All variables were measured using on-screen cursors, except for peak frequency which was automatically measured from amplitude spectra (for examples of annotated spectrograms and amplitude spectra of antbird songs see Fig. S1 in the Supporting Information available online). Because our analyses were focused on among-genus variation, we averaged data for each genus across all samples and locations (mean ± SD songs per species 3.4 ± 2.4; range 2–11; individuals per species 1.65 ± 1.17; range 1–5). These samples are adequate for the calculation of species and genus mean values because antbird songs are simple in structure (for examples, see Seddon 2005) and characterized by high within-species stereotypy and low geographic variation (e.g. Isler *et al.*, 1999, 2001, 2002, 2005; Zimmer & Isler, 2003; Seddon & Tobias, 2007).

Body mass covaries with the acoustic structure of male antbird songs (Seddon, 2005); so, we included this variable in our analyses, using data from Dunning (1993) and Zimmer & Isler (2003). Antbirds show minimal sexual size dimorphism, but males tend to be slightly larger than females (Zimmer & Isler, 2003). We therefore chose the maximum value whenever a range of body mass values was given.

Data handling

Mean values of dichromatism, song structure, body mass, altitudinal range and habitat range were calculated for each species and genus. To meet parametric assumptions, all data were log transformed prior to analyses, apart from a subset of acoustic variables (number of note types, song duration, number of notes and minimum frequency) which were square-root transformed (see Table S2). Because song measures strongly correlated (see Table S3), we employed principal components analysis to generate two uncorrelated synthetic variables. The first (PC1) accounted for 37.8% of total variation in song variables (eigenvalue 3.02) and an increase in PC1 scores was associated with an increase in maximum frequency (factor loading 0.979), minimum frequency (0.762), peak frequency (0.938) and bandwidth (0.678). 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 the number of note types (factor loading: 0.568), pace (0.734) and note number (0.746). Thus, an increase in PC1 score was associated with an increase in song pitch, whereas an increase in PC2 score was associated with an increase in song complexity (number of note types, pace and note number).

Phylogeny and phylogenetic signal

We constructed a phylogenetic tree at the genus level because a comprehensive species-level phylogeny is not yet available for antbirds. Our tree (Fig. S2) comprised 53 genera, of which 45 were positioned according to Irestedt *et al.*'s (2004) phylogeny, two (*Myrmeciza* E and *Cymbilaimus*) were positioned according to other phylogenetic data (Brumfield *et al.*, 2007) and six (*Clytoctantes, Stymphalornis, Skutchia, Rhopornis, Schistocichla* and *Biatas*) were positioned according to recent morphological and behavioural analyses (Zimmer & Isler, 2003; Braun *et al.*, 2005; Isler *et al.*, 2007b). The assignment of species to genera is given in Table S1.

We used a generalized least squares (GLS) approach to assess the phylogenetic signal of our variables at the genus level (Martins & Hansen, 1997; Pagel, 1999). A simple multiplier, λ (Pagel, 1999), captures the degree to which traits vary/covary across a tree in line with the Brownian motion model of evolutionary change (Freckleton *et al.*, 2002). Applied to internal branches, λ can

vary the strength of a signal from phylogenetically independent (0) to phylogenetically conserved (1); a value of $\lambda = 0$ is consistent with traits evolving independently in a star phylogeny (or a loss of evolutionary history), whereas a value of $\lambda = 1$ is consistent with a gradual Brownian model along the branches of a given phylogeny. We calculated confidence intervals for λ using likelihood ratio tests, with values obtained from the likelihood surface (following Freckleton *et al.*, 2002). The phylogenetic signal (λ) was low for all variables except altitudinal range (Table 1). However, the confidence intervals of λ for dichromatism, song complexity (PC2) and habitat range were broad suggesting that the evolution of these traits may have been influenced by shared ancestry.

Comparative analyses and statistics

We used general linear models (GLMs) to evaluate relationships between traits and our two measures of ecological generalism. We first analysed raw species values and raw genus values without phylogenetic correction (equivalent to assuming $\lambda = 0$). However, as cross-taxa analyses may be confounded by statistical nonindependence among samples, we also constructed GLMs with phylogenetic correction at the genus level (equivalent to assuming $\lambda = 1$).

To produce phylogenetically independent data under a particular evolutionary model, we calculated standardized linear contrasts (Felsenstein, 1985; Harvey & Pagel, 1991) using the CRUNCH procedure implemented by the computer package COMPARATIVE ANALYSIS OF INDEPENDENT CONTRASTS (CAIC; Purvis & Rambaut, 1995). CAIC generates linear contrasts that are standardized differences in traits at evolutionarily independent nodes in phylogenies. Contrasts were standardized assuming either that branches in our phylogeny were of equal length – representing a punctuated model of evolution – or that they were proportional to the number of taxa in each clade – similar to a gradual model of evolution (Grafen, 1989). Because these two evolutionary models produced slightly different outcomes in our study, we present both sets of results. Relationships between traits

Table 1 Phylogenetic signal of the six variables considered in this study.

Trait	Phylogenetic signal
Dichromatism	0.00 (0.00–0.63)
PC1	0.00 (0.00–0.38)
PC2	0.00 (0.00–0.92)
Body mass	0.00 (0.00–0.52)
Altitudinal range	0.71 (0.00–1.00)
Habitat range	0.00 (0–0.76)

The maximum likelihood values of λ are given (with approximate 95% confidence intervals).
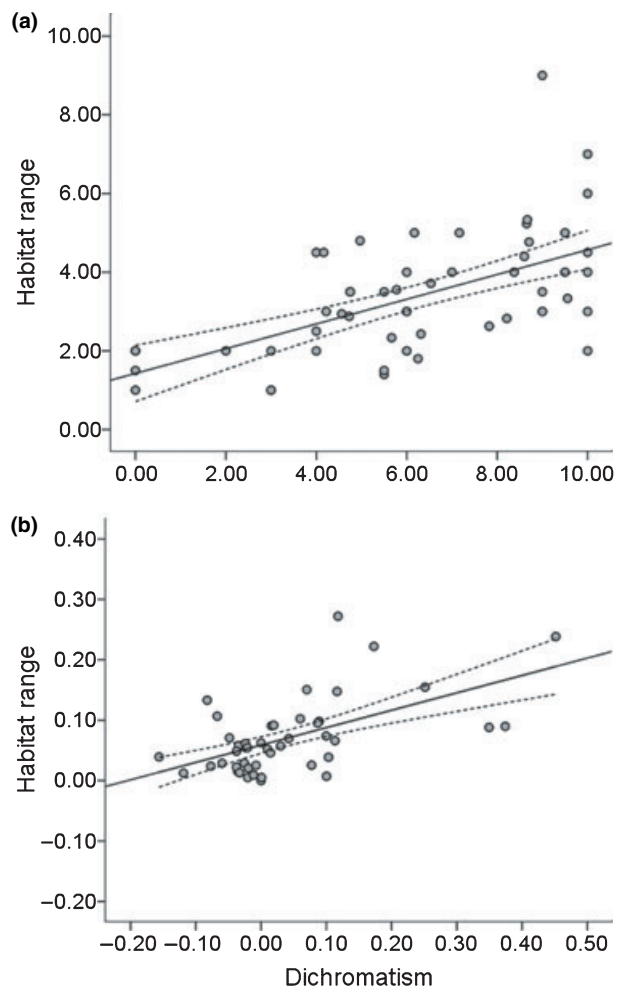

Fig. 2 Relationship between habitat range and dichromatism for all antbird genera, using (a) raw values without phylogenetic correction and (b) independent linear contrasts generated under a punctuated model of evolution. Strong correlations were found by both nonphylogenetic and phylogenetic analyses. Lines are regressions (solid) with mean confidence intervals (dashed); $r^2 = 0.33$ in (a) and 0.32 in (b); $N = 53$ genera, 45 contrasts.

were then analysed by regressing contrasts of one trait against contrasts of another trait, with regression forced through the origin (Felsenstein, 1985; Harvey & Pagel, 1991; Garland *et al.*, 1992).

The PIC method implemented in CAIC assumes that continuous characters evolve following a Brownian motion (i.e. random walk) model of evolution (Felsenstein, 1985). Following Purvis & Rambaut (1995), we tested this assumption by regressing the absolute values of standardized contrasts of each trait against the estimated values of the trait for ancestral taxa at corresponding nodes in the phylogeny. We found a strong slope for altitudinal range ($P < 0.0001$, $r^2 > 0.3$), but all other characters had nonsignificant slopes,

confirming that the assumptions of PIC were generally met. To test whether the significant slope produced any confounding heterogeneity of variance, we looked for outliers in the altitudinal range model with studentized residuals > 3 (see Jones & Purvis, 1997). However, deletion of the only outlier increased the strength of the model, suggesting that the unexpected phylogenetic signal of altitudinal range does not affect our conclusions. Nonetheless, as a precaution, we generated raw correlations along with contrast correlations, which allows us to test whether relationships persist at extreme scenarios ($\lambda = 0/1$). We retain both sets of correlations because differences between them may be biologically informative (Harvey & Rambaut, 2000; Price, 2007).

Adopting an information theoretic approach, we employed the small-sample version of the Akaike information criterion (AIC), AIC_c, to identify the simplest models with the best explanatory power (Burnham & Anderson, 2004). To test the robustness of our conclusions, we reran analyses excluding contrasts with residuals > 1.96 or < 1.96. The phylogenetic signal of traits was estimated in the R environment (R Development Core Team, 2004) using the APE package (Paradis et al., 2004). All other statistical tests were carried out in SPSS version 16.0 (SPSS, 2007).

Results

Species-level analyses

We found strong associations between indices of sexual selection and ecological generalism at the level of species (Table 2). Nonphylogenetic GLMs explained 6% of the variation in altitudinal range and 13% of the variation in habitat range across antbird species. The best AIC_c altitude range model included dichromatism, PC1 (a measure of song pitch) and body mass; the best AIC_c habitat range model only included dichromatism and PC1. In other words, species with higher values for sexually selected traits – particularly the extent of dichromatism – occupied a wider altitudinal range and occurred in a greater number of habitat types.

Genus-level analyses

Nonphylogenetic models explained 30% of the variation in altitudinal range and 38% of the variation in habitat range across 53 antbird genera (Table 3). The best AIC_c altitude range model included all three sexual traits plus body mass; the best AIC_c habitat range model included dichromatism and PC2 only. When we accounted for phylogeny using independent contrasts, we found that dichromatism, PC1 and body mass were all retained in the altitude model, but that only dichromatism was retained in the habitat range model (Table 3). In other words, genera with higher mean values for sexual selected traits occupied a wider altitudinal range and

Table 2 Results of multivariate models exploring relationships between sexually selected traits and ecological generalism among antbird species.

Trait	Slope ± SE	t	P
(a) Altitudinal range			
Dichromatism	0.405 ± 0.160	2.54	**0.012**
PC1	0.075 ± 0.029	2.57	**0.011**
PC2	0.019 ± 0.028	0.68	0.499
Body mass	0.221 ± 0.124	1.79	**0.076**
Final model	$F_{3,167} = 4.79$, $r^2 = 0.06$, $P = 0.003$		
(b) Habitat range			
Dichromatism	0.340 ± 0.091	3.72	**< 0.0001**
PC1	−0.046 ± 0.017	−2.77	**0.006**
PC2	0.027 ± 0.018	1.45	0.149
Body mass	0.078 ± 0.082	0.95	0.342
Final model	$F_{2,203} = 14.71$, $r^2 = 0.13$, $P < 0.0001$		

Values refer to final output from a general linear model, with linear regression of independent contrasts forced through the origin in the models marked with an asterisk. Each nonsignificant trait is tested when included with all other significant traits. Traits included in the AIC_c best models are highlighted in bold.

occurred in a greater number of habitat types (Fig. 2). The exclusion of high standardized residuals generated qualitatively similar results for the altitude range models (Table S5a) and increased the explanatory power of the habitat range models (Table S5b).

Discussion

Our results indicate that plumage dichromatism and, to a lesser extent, song structure are positively associated with two indices of ecological generalism. A similar relationship was previously reported in cardueline finches, but in that case it was not possible to rule out food intake and diet as drivers of interspecific variation in carotenoid-based plumage signals (Badyaev & Ghalambor, 1998). Focusing on antbirds, we find stronger evidence that taxa with higher levels of sexual selection occupy a wider variety of elevations and, especially, habitats than those with lower sexual selection. This conclusion remained qualitatively unchanged whether we conducted the analysis at the level of species or genus, and whether or not we controlled for phylogeny. In identifying an apparent synergism between sexual selection and ecological generalism, our findings contradict the prevailing view that sexual selection opposes natural selection (e.g. McLain, 1993). Broadly speaking, a synergism of this kind might arise in one of two ways: by sexual selection promoting ecological generalism or vice versa.

Does sexual selection promote ecological generalism?

The relationship between sexual selection and natural selection has been the subject for much recent debate (e.g. Lorch et al., 2003; Rundle et al., 2006; Candolin &

Table 3 Results of multivariate models exploring relationships between sexually selected traits and ecological generalism among antbird genera with and without phylogenetic correction.

Trait	Genus values			Gradual model*			Punctuated model*		
	Slope ± SE	t	P	Slope ± SE	t	P	Slope ± SE	t	P
(a) Altitudinal model									
Dichromatism	0.265 ± 0.123	2.16	**0.036**	0.371 ± 0.152	2.44	**0.019**	0.292 ± 140	2.09	**0.043**
PC1	0.063 ± 0.035	1.82	**0.076**	0.136 ± 0.050	2.70	**0.010**	0.114 ± 0.045	2.52	**0.015**
PC2	0.054 ± 0.032	1.69	**0.098**	0.038 ± 0.038	1.02	0.314	0.038 ± 0.035	1.09	0.283
Body mass	0.344 ± 0.113	3.03	**0.004**	0.457 ± 0.26	1.78	**0.082**	0.377 ± 0.202	1.87	**0.069**
Final model	$F_{4,45} = 4.84, r^2 = 0.30, P = 0.002$			$F_{3,42} = 3.67, r^2 = 0.21, P = 0.020$			$F_{3,42} = 3.27, r^2 = 0.19, P = 0.030$		
(b) Habitat model									
Dichromatism	0.409 ± 0.081	4.19	**< 0.0001**	0.412 ± 0.088	4.68	**< 0.0001**	0.431 ± 0.088	4.90	**< 0.0001**
PC1	−0.023 ± 0.026	−0.88	0.382	−0.001 ± 0.028	−0.05	0.958	−0.013 ± 0.027	−0.47	0.640
PC2	0.038 ± 0.03	1.44	**0.156**	0.023 ± 0.022	1.05	0.301	0.021 ± 0.022	0.93	0.360
Body mass	0.095 ± 0.087	1.10	0.279	−0.028 ± 0.141	−0.20	0.846	0.032 ± 0.121	0.26	0.795
Final model	$F_{2,49} = 14.97, r^2 = 0.38, P < 0.0001$			$F_{1,44} = 21.89, r^2 = 0.33, P < 0.0001$			$F_{2,49} = 23.95, r^2 = 0.35, P < 0.0001$		

Values refer to final output from a general linear model, with linear regression of independent contrasts forced through the origin in the models marked with an asterisk. Each nonsignificant trait is tested when included with all other significant traits. Traits included in the AIC_c best models are highlighted in bold. Parameter estimates for full models are given in Table S4 in the electronic Supporting information.

Heuschele, 2008). One line of thinking suggests that, if condition-dependent sexual selection increases nonsexual fitness via the spread of advantageous alleles and/or the purging of genetic load, sexual selection may have a positive effect on survival and rates of adaptation at the individual level, thereby driving an increase in the ability to expand niches and adapt to novel environments at the population level (Proulx, 1999, 2002; Whitlock, 2000; Lorch *et al.*, 2003). These theoretical predictions have received little empirical support, although it is worth pointing out that they are relatively difficult to assess experimentally (Promislow *et al.*, 1998; Holland, 2002; Rundle *et al.*, 2006; Fricke & Arnqvist, 2007). Moreover, most experimental tests have been conducted in laboratory populations of *Drosophila* species, and their results are open to alternative interpretations. In particular, the benefits of sexual selection might be counterbalanced or reversed by male-induced harm to females, a direct cost which is known to affect *Drosophila* systems under elevated sexual selection (Holland & Rice, 1999; Orteiza *et al.*, 2005; Rundle *et al.*, 2006). The present study approaches this question from a different angle by using comparative methods to assess interactions between sexual selection and natural selection across a diverse clade of territorial birds.

Our results demonstrate strong positive interspecific correlations. Although these findings are consistent with the hypothesis that sexual selection promotes ecological generalism at the population level, they appear to contradict the assertion that sexual selection increases mortality and extinction risk (Promislow *et al.*, 1992, 1994; McLain *et al.*, 1995; Doherty *et al.*, 2003; Morrow & Pitcher, 2003). However, increased ecological generalism and reduced survival are not mutually exclusive. It is possible, for example, that sexual

selection may favour one outcome over the other depending on the strength of mating preferences, and the burden of costs that they impose (Kirkpatrick & Ryan, 1991; Brooks, 2000). When sexual selection is intense and mating preferences extreme, the balance between reproductive success and survival is produced by highly elaborate and costly traits. When sexual selection is less pronounced, both the degree of ornamentation and the burden of cost are reduced, such that individuals are more capable of accommodating further energetic demands, including those imposed by novel or variable environments. Thus, we might expect any positive effects of sexual selection to be most evident in the absence of: (1) direct costs of mating interactions and (2) highly elaborate ornamentation. All antbirds meet these criteria and it is therefore possible that the positive relationship between sexual and ecological traits detected in this study is driven by the intrinsic fitness benefits of sexual selection.

Does ecological generalism promote sexual selection?

Having discussed our results from the perspective of one causal pathway, we now consider the reverse possibility. Ecological generalism may be positively related to sexual selection if, for example, a broad niche increases population density, which in turn leads to more intense mating competition. Both these processes are intuitively plausible. An interaction between ecological generalism and population density has been shown or suggested in other studies (e.g. Svardson, 1949; Svanback & Persson, 2004) and appears to operate in antbirds because the number of habitats occupied by a species is

positively related to its relative per-area abundance (Parker *et al.*, 1996; raw genus values: $F_{1,51} = 8.47$, $r^2 = 0.14$, $P = 0.005$; gradual model: $F_{1,43} = 4.27$, $r^2 = 0.09$, $P = 0.045$; punctuated model: $F_{1,43} = 8.52$, $r^2 = 0.17$, $P = 0.006$). A further interaction between population density and sexual selection is often proposed (reviewed in Parker, 1979; Sharp & Agrawal, 2008) and seems especially likely in territorial systems. In the context of antbirds, most of which are strictly territorial, greater population density represents an increase in the number and proximity of immediate neighbours. This suggests an ecological mechanism whereby antbird species occupying a wider diversity of habitat types share territory boundaries with more conspecifics than do specialists, both across habitat boundaries and within given habitats and microhabitats. Overall, this increased contact with conspecifics may elevate the intensity of sexual selection, either overtly, by increasing direct competition for mates, or covertly, via increased opportunities for extra-pair fertilizations (e.g. Eshel, 1979; West-Eberhard, 1983; Westneat & Sherman, 2004). Under this scenario, generalism promotes sexual selection rather than vice versa.

This interpretation of our findings brings to light a potentially important and rarely considered mechanism by which ecological generalism or population density may influence interspecific variation in social signals, including secondary sexual characters. It also underscores the need to consider a highly complex network of intrinsic and extrinsic factors when addressing phenotypic evolution in general, and the elaboration of ornaments in particular. This serves as a reminder that laboratory experiments, much as they can be uniquely informative about sexual selection, cannot capture the spatial component typical of vertebrate ecology (e.g. home ranges and territoriality). Nonetheless, the extent to which ecological generalism shapes variation in sexual selection remains an open question. To address this issue, one potentially fruitful approach would be to quantify and compare geographic variation in ecology and phenotype within widespread polytype species; another would be to conduct comparative analyses exploring relationships between habitat use, population density and sexual selection, using direct measures where possible. In all cases, it would appear essential to consider underlying biology. In particular, pooling together territorial with nonterritorial systems, or social monogamy with polygamy, might contribute to the mixed results reported by previous studies (e.g. Sharp & Agrawal, 2008).

Strengths and limitations of this study

The results described here provide support for a positive relationship between sexual selection and ecological generalism. However, they must be interpreted cautiously as this study is limited in several ways. Perhaps the main weakness of our analysis, and of the compar-

ative method in general, is that it is not informative about the direction of causality. In effect, the observed correlation may be driven by sexual selection or ecological generalism, or else by both factors in combination. Equally, the comparative method does not allow us to identify the mechanisms underlying correlations, nor can we safely predict that synergisms and trade-offs operating within species will be evident between species. These limitations are offset by the main strengths of the comparative method, namely its insulation from the peculiarities of single-species systems, and its ability to detect large-scale patterns that generate hypotheses and predictions for empirical testing. The taxonomic scope of a comparative analysis brings its own costs and benefits: restricting our study to a single avian family reduces our ability to generalize, but in this case it allows us to hold numerous variables relatively constant and thus perhaps to escape the muddle of conflicting outcomes reported in broader reviews (e.g. Candolin & Heuschele, 2008; Sharp & Agrawal, 2008). Overall, the relationship detected by our analysis is compelling because it exists across a diverse clade wherein potentially confounding variation is minimized.

The most important limitations specific to this study concern the scale of variation in sexual selection and the validity of indices by which it is measured. Sexual selection is presumably less costly and less variable in antbirds than in groups with higher incidence of polygyny, elaborate ornaments or extensive carotenoid pigmentation. In addition, although a large body of empirical work supports the assumption that dichromatism and song complexity are accurate proxies of sexual selection in many avian families (see Materials and methods), this has not been directly tested in antbirds. However, we do not believe that these factors weaken our results for three main reasons. First, the previously contentious idea that melanin-based plumage may function as a costly, condition-dependent signal used in mate choice has received broad support from recent empirical studies (Veiga & Puetra, 1996; Thusius *et al.*, 2001; Parker *et al.*, 2003; Tarof *et al.*, 2005; Nadeau *et al.*, 2007; Pogány & Székely, 2007; Kingma *et al.*, 2008), reinforcing the conclusion that melanin-based signals, such as those used by antbirds, are signals of attractiveness exaggerated by sexual selection (Jawor & Breitwisch, 2003; Griffith *et al.*, 2006; McGraw, 2006, 2008; Bókony *et al.*, 2008). Second, increases in song duration, note number, pace and note diversity are very likely to involve energetic, physiological and neurological costs (Gil & Gahr, 2002; Collins, 2004; Podos *et al.*, 2004). And third, even if future work reveals that antbird signals are only weakly linked to intersexual selection, there is no doubt that they are strongly shaped by intrasexual selection as both male–male and female–female competition for mates and territories is prominent in this family (e.g. Seddon & Tobias, 2006).

A final potential drawback is that our indices of ecological generalism may reflect local adaptation, rather

than ecological plasticity *per se*. In other words, if higher scores are driven by regional variation in habitat occupancy or elevational range, it is possible that generalist species are composed of specialist individuals. However, even if this is true, it does not alter our conclusions. This is because the hypotheses being tested do not focus on individual generalism but the ability of separate individuals to tolerate variations in elevation or habitat. Thus, population-wide or range-wide indices are appropriate. Moreover, we should also emphasize that habitat selection by antbirds appears to be fairly consistent across global distributions (Zimmer & Isler, 2003). Tropical forests and woodlands are highly heterogeneous environments and the habitat ranges presented in this paper usually reflect the use of multiple habitat types within antbird populations or even within territories.

Conclusions

Our finding that secondary sexual traits and indices of ecological generalism are positively correlated across a diverse clade runs counter to the predictions of a hypothetical trade-off between sexual selection and ecological plasticity (McLain, 1993). Instead, this correlation supports a recent spate of theoretical models concluding that sexual selection promotes adaptation and increases niche width (Proulx, 1999, 2002; Lorch *et al.*, 2003). Although the direction of causality and the exact mechanisms involved remain to be clarified, our results suggest that a synergism between sexual selection and ecological plasticity may be widespread, particularly in the absence of costly interactions or highly exaggerated sexual ornaments. This synergism may disrupt the trade-offs between naturally selected and sexually selected traits predicted by classic sexual selection theory and could therefore play a fundamental role in shaping phenotypic evolution. It may also help to explain the positive association reported between sexual selection and species richness (e.g. Seddon *et al.*, 2008) because habitat generalists are often considered more likely to colonize new regions or to experience population subdivision through vicariance events, both of which may lead to increased speciation (Simpson, 1953; Mayr, 1963; Rosenzweig, 1995). Further studies are needed to investigate the ecological correlates of sexual selection in a variety of clades and to test the idea that ecological generalism may promote sexual (or social) selection.

Acknowledgments

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Supporting information

Additional supporting information may be found in the online version of this article:

Figure S1 Annotated spectrograms with associated waveforms and power spectra illustrating structural simplicity of typical antbird songs. (a) Shows the song of white-bearded antshrike *Biatas nigropectus* which consists of the same note repeated eight times; and (b) shows the relatively complex song of Imeri warbling-antbird *Hypocnemis flavescens* which consists of four different note types. Annotations show acoustic parameters taken: song duration (DurLS), maximum (MaxFreq) and minimum frequency (MinFreq), bandwidth (BW) and peak frequency (Peak). Sound files used to generate spectrograms are from Isler & Whitney (2002).

Figure S2 Evolutionary relationships amongst antbird genera, based on the phylogeny of Irestedt *et al.* (2004), a combined majority rule consensus tree with generic relationships established via Bayesian inference analysis of two nuclear introns and mitochondrial cytochrome *b*. Asterisks denote genera not covered by Irestedt *et al.* (2004) and therefore positioned according to recent analyses of morphology and vocalizations (Table S1) as well as additional molecular data (Brumfield *et al.*, 2007).

Table S1 Typical antbirds (Thamnophilidae) – classification and assignment of species.

Table S2 Mean genus values for body mass, altitudinal range, habitat range, plumage dichromatism and song structure (separate acoustic measures and the two principal components derived from these measures).

Table S3 Correlations (Spearman's rho) among eight measures of antbird song structure ($N = 53$ antbird genera).

Table S4 Results of full multivariate models exploring relationships between sexually selected traits and ecological generalism among antbird genera with and without phylogenetic correction.

Table S5 Results of full multivariate models exploring relationships between sexually selected traits and ecological generalism among antbird genera with and without phylogenetic correction, excluding high standardized residuals (i.e. > 1.96 or < -1.96).

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