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SIGNAL DESIGN AND PERCEPTION IN *HYPOCNEMIS* ANTBIRDS: EVIDENCE FOR CONVERGENT EVOLUTION VIA SOCIAL SELECTION

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Natural selection is known to produce convergent phenotypes through mimicry or ecological adaptation. It has also been proposed that social selection—i.e., selection exerted by social competition—may drive convergent evolution in signals mediating interspecific communication, yet this idea remains controversial. Here, we use color spectrophotometry, acoustic analyses, and playback experiments to assess the hypothesis of adaptive signal convergence in two competing nonsister taxa, *Hypocnemis peruviana* and *H. subflava* (Aves: Thamnophilidae). We show that the structure of territorial songs in males overlaps in sympatry, with some evidence of convergent character displacement. Conversely, nonterritorial vocal and visual signals in males are strikingly diagnostic, in line with 6.8% divergence in mtDNA sequences. The same pattern of variation applies to females. Finally, we show that songs in both sexes elicit strong territorial responses within and between species, whereas songs of a third, allopatric and more closely related species (*H. striata*) are structurally divergent and elicit weaker responses. Taken together, our results provide compelling evidence that social selection can act across species boundaries to drive convergent or parallel evolution in taxa competing for space and resources.

KEY WORDS: Character displacement, convergent evolution, interspecific competition, signal evolution, species recognition, suboscine birds, territorial signals.

Species specificity is a hallmark of animal signaling (Marler 1957; Konishi 1970; West-Eberhard 1983). It is widely viewed as the inevitable product of divergent selection acting on sexual and social signals to minimize confusion between sympatric species (Dobzhansky 1951; Brown and Wilson 1956; Blair 1964; Miller 1982; West-Eberhard 1983; Butlin 1987; Nelson 1989; Nelson and Marler 1990; Sætre et al. 1997; Servedio and Noor 2003; Hoskin et al. 2005; Lukhtanov et al. 2005). Divergence is the likely outcome, it is argued, because shared signals impose a range of costs, including maladaptive hybridization and wasteful interaction. However, despite a broad agreement on these predictions, the ubiquity of divergence or even species specificity has been questioned. Some studies find evidence of nondivergent forms of character displacement, namely parallelism or convergence, but the role of these processes in signal evolution remains controversial (Grant 1972; Cody 1973; Murray 1976; Scott and Foster 2000).

Biologists have long been fascinated by character convergence, perhaps because it offers tangible evidence of evolution and the forces of selection by which it operates (Darwin 1859; Grinnell 1924; Grant 1972; Abrams 1996). Convergent ecological selection is widespread, both in allopatric forms occupying

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equivalent niches, or sympatric forms adapted to similar environments (Losos 1992; Losos et al. 1998; Harmon et al. 2005; Langerhans et al. 2006; Rosenblum 2006; Buckley et al. 2008; Fleischer et al. 2008). Other sources of natural selection, such as predation pressure, may cause phenotypic convergence in the form of visual or acoustic mimicry (Jiggins et al. 2006; Wang and Shaffer 2008; Barbero et al. 2009). An alternative and rarely examined possibility is that social selection—that is, selection imposed by social competition (West-Eberhard 1983)—can drive convergence or parallelism in the signals of species competing for space and resources.

The concept of convergent social selection recurs periodically in biological literature, generally in the form of loosely formulated mechanisms. One is "social mimicry," whereby signals converge to increase the efficiency of communication between species foraging collectively (Moynihan 1968, 1981). Another is adaptive interspecific aggression (Cody 1969; Cody and Brown 1970; Hagen et al. 1980; Arthur 1982), in which signals converge to align the competitive behavior of species with overlapping niches, such that they "divide space as a single species" (Cody 1973). However, whether character convergence can be driven by these mechanisms remains essentially unknown. The mechanism underlying social mimicry, for example, is difficult to disentangle from alternative explanations, such as Batesian and Müllerian mimicry (Barnard 1979), "interspecific exploitation" (Barnard 1982; Diamond 1982), or ecological selection on signal transmission (Burtt and Gatz 1982).

Similarly, the idea of convergent competitors was challenged by Murray (1971, 1976, 1981, 1988) on the grounds that published evidence (Cody 1969; Cody and Brown 1970; Cody 1973, 1978) failed to eliminate alternative possibilities. Until recently, the main textbook example of convergent social signals involved the stickleback, *Gasterosteus aculeatus*, which was thought to evolve a convergent color patch to enhance its ability to hold territories against *Novumbra hubbsi* (Hagen et al. 1980). This conclusion was weakened, however, when further research failed to demonstrate competition between these species, and revealed instead that they establish territories early in life, before the key trait develops (Scott and Foster 2000). Nonetheless, a growing number of studies report that interspecific territoriality may be adaptive (Ebersole 1977; Connell 1983; Schoener 1983; Martin 1996; Bourski and Forstmeier 2000; Martin and Martin 2001b) and mediated by interspecific territorial signals (Catchpole 1978; Garcia 1983; Catchpole and Leisler 1986; Prescott 1987; Martin et al. 1996; Gil 1997; Martin and Martin 2001a; Matyjasiak 2005), suggesting that the logic of Cody's (1969) hypothesis may be valid in certain contexts.

One of the most likely signals to yield insight into mechanisms promoting adaptive convergence or parallelism is birdsong. Avian acoustic signals are intensively studied, and known to function in territoriality and mate choice (Catchpole and Slater 1995; Kroodsma and Miller 1996). It is therefore often assumed that differences in song will evolve in sympatry to minimize hybridization and unnecessary territorial aggression (Miller 1982; Wallin 1985; Doutrelant et al. 2000). This view is supported by widespread species specificity in birdsong design, leading to the assertion that "all species have songs recognizably different from those of other species" (Baptista and Kroodsma 2001). Rare exceptions to the rule have been proposed as evidence of convergent social selection (e.g., Cody 1969, 1973; Cody and Brown 1970), but the data in each case have been shown to be misleading, or else unable to discount important proximate factors (Rohwer 1972; Murray 1976; Murray and Hardy 1981).

Perhaps the most pervasive of these factors is hybridization. Interbreeding in birds often produces hybrids with intermediate vocal characters (Grant 1972), and this explains apparent signal convergence in some avian contact zones, particularly those involving sister species. Vocally intermediate hybrids routinely occur in clades with genetically determined songs (de Kort et al. 2002; Gee 2005; Isler et al. 2005; Cadena et al. 2007; den Hartog et al. 2007), and even in species with learnt vocalizations, including oscine passerines (e.g., Robbins et al. 1986; Secondi et al. 2003). In all cases, hybridization is characterized by a mix of normal song types and intermediate song types, or a gradual shift of character states (i.e., a cline).

The second proximate factor is song learning, which is most prevalent in oscine passerines, parrots, and hummingbirds. In these three clades, vocal signals develop via an imprinting-like process that generates geographical and individual variation, and in many cases dialects and extensive repertoires (Jarvis 2004; Kroodsma 2004; Beecher and Brenowitz 2005). Song learning can lead to the transfer of vocal characters from one species to another, a process that generates convergent song types in several oscine contact zones (Sorjonen 1986; Secondi et al. 2003; Haavie et al. 2004). This form of heterospecific copying is a confounding factor in many studies of character convergence (Cody 1969, 1973; Helb et al. 1985; Grant and Grant 1997). As with hybridization, copying is reflected at the population level by a combination of normal song types and mixed song types, the latter containing elements or phrases of heterospecific song.

A third factor leading to apparent convergence is phylogenetic conservatism. Under this scenario, adaptive interspecific territoriality can be reinterpreted as nonadaptive territoriality (i.e., "misdirected intraspecific territoriality") stimulated by shared signaling traits in closely related taxa (Murray 1971, 1976, 1981). This is most likely to occur when species are parapatric, with only a small proportion of individuals in contact with heterospecifics (Murray 1981), or when range overlap is recent and signals have yet to diverge (de Kort et al. 2002). Phylogenetic conservatism is a powerful argument for nondivergence, but it does not explain

convergence across geographical space or evolutionary time. It is also less convincing if nondivergence is restricted to territorial signals and offset by wide divergence in nonterritorial signals. To test ideas about adaptive convergence it is therefore useful to quantify spatial and temporal variation, as well as variation across different signal functions and modalities.

In this study, we assess whether signals have converged in two Neotropical antbirds, *Hypocnemis peruviana* and *H. subflava* (Thamnophilidae), and if so whether convergence can be explained by stochastic or deterministic processes. These species provide an excellent system because they overlap in range, and yet have territorial songs that are reported to be "not distinguishable" by a detailed acoustic analysis (Isler et al. 2007). Moreover, they are not sister species (Tobias et al. 2008), and therefore the design and content of their songs can be compared with allopatric in-groups. The *Hypocnemis* system is also illuminating because both sexes are aggressive in defense of territories (Seddon and Tobias 2006; Tobias and Seddon 2009), thereby exposing sex-specific patterns of trait divergence and perception. Finally, heterospecific copying is unlikely in antbirds because they are tracheophone suboscine passerines (Irestedt et al. 2002) and thus their songs are probably innate (Zimmer and Isler 2003).

The main aims of this study are to ask whether *H. peruviana* and *H. subflava* have territorial signals that are (1) more similar than nonterritorial signals; (2) more similar in sympatry than allopatry; and (3) more similar than predicted by the evolutionary age of the lineages in question. We use acoustic analyses and color spectrophotometry to compare the structure of vocal and visual signals of both sexes, and we use playback experiments to quantify receiver perception of conspecific and heterospecific signals in sympatry and allopatry. In addition, we use an experimental approach to assess how receivers perceive the territorial signals of two other related antbird species. The results allow us to examine whether territorial signals in *Hypocnemis* antbirds are shaped by proximate factors or socially mediated adaptation.

Materials and Methods

STUDY TAXA

Hypocnemis antbirds are small (11–12 cm, 10–14 g) socially monogamous passerine birds in the Neotropical suboscine clade (Zimmer and Isler 2003). Until recently, most *Hypocnemis* taxa were grouped in a widespread polytypic species, *H. cantator* (Zimmer and Isler 2003), but this has now been separated into six species (Isler et al. 2007). Our study focuses on two of these species, *H. peruviana* and *H. subflava*. Their ranges overlap in south Peru, west Brazil, and north Bolivia (Isler et al. 2007), with the region of sympatry spanning ~1100 km at its widest known point and covering at least 150,000 km^2 (Fig. 1).

Molecular analyses indicate that *H. peruviana* and *H. subflava* are separated by 6.8% mtDNA sequence divergence (ATPase 6, ND2 and ND3) and are not sister taxa (Tobias et al. 2008). The extent of genetic divergence suggests that they split from a

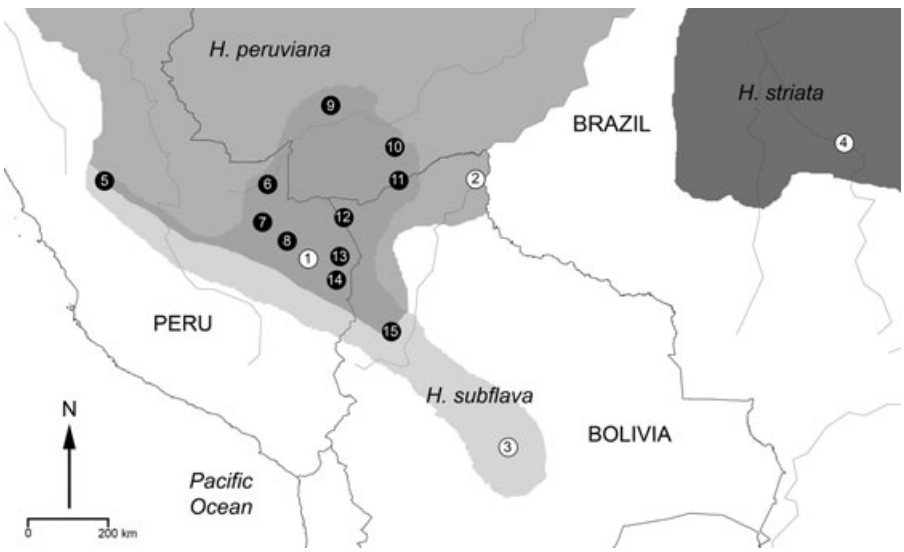

Figure 1. Global ranges of *Hypocnemis peruviana* and *H. subflava*, and the positions of study/recording sites (open circles): (1) CICRA, Río Los Amigos (Madre de Díos, Peru); (2) Los Indios (Pando, Bolivia); (3) Sajta (Cochabamba, Bolivia); and (4) Rio Cristalino (Mato Grosso, Brazil). Closed circles denote sites of known sympatry/parapatry: (5) Pozuso (Pasco, Peru), (6) upper Río Purus (Ucayali, Peru), (7) Cocha Cashu (Madre de Díos, Peru), (8) Manu Wildlife Center (Madre de Díos, Peru), (9) upper Rio Pauini (Amazonas, Brazil), (10) Rio Branco (Acre, Brazil), (11) Reserva Catuaba (Acre, Brazil), (12) Cusco Amazonica, (13) Río Tahuamanu (Pando, Bolivia), (14) Tambopata (Madre de Díos, Peru), and (15) Lago Chalalan (La Paz, Bolivia) (Isler et al. 2007; M. Cohn-Haft, pers. comm.; F. R. Lambert, pers. comm.).

common ancestor 3.4 million year ago (mya), assuming a 2% molecular clock (Weir and Schluter 2008). Despite the lengthy isolation of these lineages, they appear very similar in general behavior, foraging strata, foraging techniques and diet, and are near-identical in six standard mensural characters (bill length, bill depth, bill width, tarsus length, wing-chord, and weight) (J. A. Tobias, unpubl. ms). However, they are easily diagnosed by plumage characters: male *H. subflava* has a yellow chest and buff flanks (Fig. S1, A–D); male *H. peruviana* has a white chest and rufous flanks (Fig. S1, E–H); females are more similar, but again differ in ventral plumage color (Fig. S2, A–H).

In *Hypocnemis*, as with other antbirds (Willis 1967; Stutchbury and Morton 2001; Bard et al. 2002), the primary vocalization is a complex long-range signal functioning mainly in intrasexual competition and territoriality; other vocalizations are relatively simple short-range signals not used in territorial interactions (Seddon and Tobias 2006). By way of shorthand, we refer to these vocalizations as 'songs' and 'calls,' respectively. All vocalizations are highly stereotyped within sexes, but male songs can easily be distinguished from female songs (Isler et al. 2007; Tobias and Seddon 2009). See Figures 2 and 3 for spectrograms of songs and calls; corresponding sound files are available in Supporting information.

STUDY POPULATIONS

From 2004 to 2007 (September–December), we studied races *H. peruviana peruviana* and *H. subflava collinsi* at three sites in southwestern Amazonia (Fig. 1): (1) Centro de Investigación y Conservación de Río Los Amigos (CICRA; 12°34′07″S, 70°05′57″W), Madre de Dios, Perú; (2) Los Indios, Pando, Bolivia

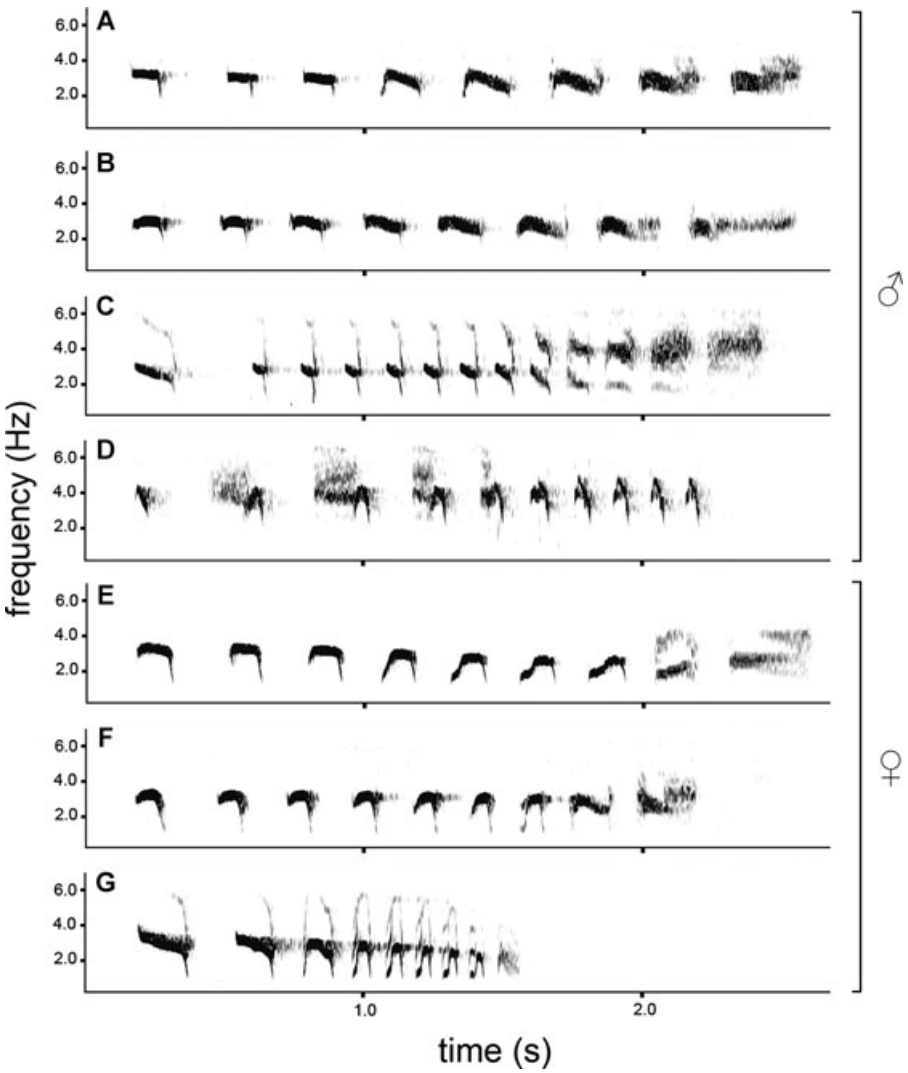

Figure 2. Spectrograms of male territorial songs given by *Hypocnemis peruviana* (*A*, sound file 1), *H. subflava* (*B*, sound file 2), *H. striata* (C, sound file 3) and *Drymophila devillei* (*D*, sound file 4); and of female territorial songs given by *Hypocnemis peruviana* (*E*, sound file 5), *H. subflava* (*F*, sound file 6), and *H. striata* (*G*, sound file 7).

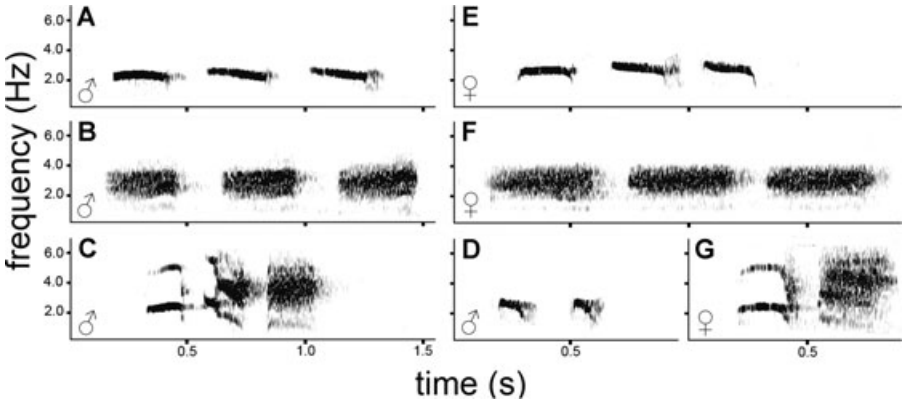

Figure 3. Spectrograms of male nonterritorial calls given by *Hypocnemis peruviana* (A, sound file 8); *H. subflava* (B, sound file 9), *H. striata* (C, sound file 10), and *Drymophila devillei* (D, sound file 11); and of female nonterritorial calls given by *H. peruviana* (E, sound file 12); *H. subflava* (F, sound file 13), and *H. striata* (G, sound file 14).

(10°32′00′S, 65°35′48″W); and (3) Sajta, Cochabamba, Bolivia (17°09′25″S, 64°50′31″W). At CICRA, *H. peruviana* and *H. subflava* co-occur at high population densities (∼3 pairs of each species per square kilometer), and defend mutually exclusive territories (J. A. Tobias, unpubl. ms). In allopatry, we studied populations of *H. peruviana* at Los Indios, and *H. subflava* at Sajta, ∼400 km and ∼800 km from the sympatric zone, respectively. Sample sizes for all populations are given in Table 1; at least one member of all study pairs was caught in 12 × 4 m mist-nets and marked with a unique combination of colored polyvinyl chloride bands.

Vocalizations were also recorded from 10 male striated antbirds (*Drymophila devillei*) at CICRA, and (in May–July 2004) from 15 male and 12 female Spix's warbling-antbird (*Hypocnemis striata*) at Rio Cristalino (Mato Grosso, Brazil, 9°41′S, 55°54′W). We selected these species as comparisons because *D. devillei* is the closest sympatric relative of *H. peruviana* and *H. subflava* (Bates et al. 1999), and *H. striata* is an allopatric species belonging to a clade that includes *H. peruviana* but excludes *H. subflava* (Tobias et al. 2008).

INTERACTION AND COMPETITION

Some ideas tested in this study rest on the assumption that *H. peruviana* and *H. subflava* interact in sympatry. The extent of their interaction is the subject of a parallel paper (J. A. Tobias, unpubl. ms), but the salient facts are reported here. These species are partially segregated by habitat, with *H. peruviana* occurring mainly in terra firme forest around dense understory vegetation, and *H. subflava* occurring mainly in patches of *Guadua* bamboo. However, habitat preferences broadly overlap, with *H. peruviana* sometimes occupying *Guadua* bamboo patches, and *H. subflava* often occurring outside bamboo. Despite overlapping niches, we found minimal overlap between territories at CICRA either within or between species, even though territories of ∼15% of pairs in both species shared one or more boundaries with heterospecific territories. We conclude that these species are interspecifically territorial

Table 1. Location and sample sizes for all territorial songs, nonterritorial calls, and plumage analyzed in this study; samples are given as number of individuals (with total number of songs in brackets).

Trait/sex	*Hypocnemis peruviana*		*Hypocnemis subflava*		Total
	Los Indios	CICRA	Sajta	CICRA	
Song					
Male	16 (57)	28 (106)	14 (41)	27 (104)	85 (308)
Female	12 (40)	22 (78)	12 (23)	19 (55)	65 (196)
Call					
Male	–	14	–	13	27
Female	–	11	–	8	19
Plumage					
Male	–	19	–	26	45
Female	–	24	–	20	44

and compete for space and resources, a view supported by the regular occurrence of aggressive contests with heterospecifics over shared territory boundaries.

As the structure of antbird songs can be shaped to some extent by the transmission properties of habitats (Seddon 2005), acoustic data need to be interpreted in the light of ecological information. Thus, it is worth noting that *H. striata* is an ecological replacement of *H. peruviana*, occurring in very similar habitat in allopatry. Meanwhile, sympatric *D. devillei* is a *Guadua* bamboo specialist (Kratter 1997), and shares many bamboo patches with *H. subflava* without evidence of interspecific competition. All four species sing in the understory (~1–5 m above ground level).

QUANTIFICATION AND ANALYSIS OF SIGNAL DESIGN

Focusing on the sympatric zone of *H. peruviana* and *H. subflava*, we quantified variation in three types of signal: a territorial vocalization (the song), a nonterritorial vocalization (the call), and two plumage signals (chest and flank patches). These visual signals were selected because they account for most visible variation in *Hypocnemis* antbirds (see Figs. S1 and S2); they are therefore candidate signals for mate choice and species recognition but play no part in long-range territorial signaling.

We used a ME67-K3U directional gun microphone (Sennheiser Electronic Corporation, Old Lyme, CT) and a 722 portable digital recorder (Sound Devices, Reedsburg, WI) to record all vocalizations onto compact flash cards as 24 bit wav mono files at a sampling frequency of 44.1 kHz. We then used Avisoft SASLabPro Version 4.15 (R. Specht, Berlin, Germany) to reduce low- and high-frequency background noise (FIR bandpass filter set at 1–8 kHz). Using techniques described in Isler et al. (1998) and Seddon and Tobias (2006), we generated spectrograms from sound files, and measured 20 standard temporal and frequency parameters for each vocalization (see Fig. S3). From these we calculated a mean value for each parameter per individual.

We analyzed 343 songs given by 96 individuals in sympatry (mean ± SD = 3.3 ± 1.1 songs per individual; see Table 1 for sample sizes). Between-individual variation (as defined by PC1; see Table S1A) greatly exceeded within-individual variation (males: $F_{83,307} = 80.0$, $P < 0.0001$; females: $F_{64,195} = 38.9$, $P < 0.0001$). To test for skew, we doubled sample sizes from three to six songs for a subset of individuals. This had no significant effect on mean values generated for any parameter (Wilcoxon signed-rank tests: $0.316 < P < 1.00$; $n = 9$), suggesting that our vocal data are normally distributed and adequately sampled. Further recordings were made at CICRA of 290 calls from a total of 45 *Hypocnemis* individuals (mean ± SD = 6.3 ± 2.0 calls per individual; see Table 1 for sample sizes). To place sympatric data in context, we also quantified song structure of *H. peruviana* and *H. subflava* at allopatric localities, allowing a comparison of overall song structure between allopatric and sympatric populations. We also compared sympatric songs with those of a close relative in allopatry (*H. striata*), and the closest relative in sympatry (*D. devillei*).

To measure plumage variation, we collected three feathers each from the center of chest and flank patches of 43 *H. peruviana* and 46 *H. subflava* captured in mistnets (Table 1). These feathers were laid on top of one another, and mounted onto black velvet to eliminate background reflections. We then took three measures of spectral reflectance from the top feather using an Ocean Optics (Dunedin, FL) USB4000 spectrometer (range: 200–1100 nm), a DH2000-FHS pulsed xenon lamp (190–1700 nm), and a bifurcated 400 μm fiber-optic reflection probe (QR400–7-UV/BX) mounted in a matte black holder (RPH-1). The latter excluded external light and kept the probe perpendicular to the measurement surface at a fixed distance of 5 mm. Data were collected in SpectraSuite and expressed as the proportion of reflectance relative to an Ocean Optics WS-1 white standard, which reflects 97–98% of incident light. For analysis, we averaged raw spectral data into 10-nm bins across the avian-visible wavelength range (300–700 nm). This produced 40 reflectance values per measurement, from which we calculated a single mean reflectance curve for each individual's chest and flank feathers. These were used to produce mean reflectance curves per sex and species (Fig. 4).

We analyzed reflectance curves by first dividing them into the UV (very short-wave, 300–430 nm), blue (short-wave, 430–500 nm), and yellow (long-wave, 500–700 nm) parts of the spectrum, three categories corresponding to the spectral sensitivities of the three cone types in the passerine retina (Hart et al. 2000). Following MacDougall and Montgomerie (2003), we then calculated the intensity of yellow on the chest feathers using three variables: yellow amplitude, UV amplitude, and blue chroma. Yellow amplitude was the difference in percentage reflectance (R) between the blue minimum ($blue_{min}$) and the yellow maximum ($yellow_{max}$); UV amplitude was the difference in R between $blue_{min}$ and the UV maximum (UV_{max}); and blue chroma was the proportion of total R occurring in the blue segment (i.e., R430–500/R300–700). We adapted this method to quantify intensity of rufous on flank feathers, based on yellow chroma (proportion of total R occurring in the yellow segment, i.e., R500–700/R300–700); blue absorbance ($yellow_{max}$ minus $blue_{min}$); and UV absorbance ($yellow_{max}$ minus UV_{min}). As these variables were correlated, we used principle components (PC) analysis to calculate color scores (see Statistical analyses).

TESTS OF RECEIVER PERCEPTION

Previous studies show that acoustic analyses may be misleading if measurements fail to capture subtle acoustic cues used by receivers (e.g., Ryan and Rand 2003), or if most divergence

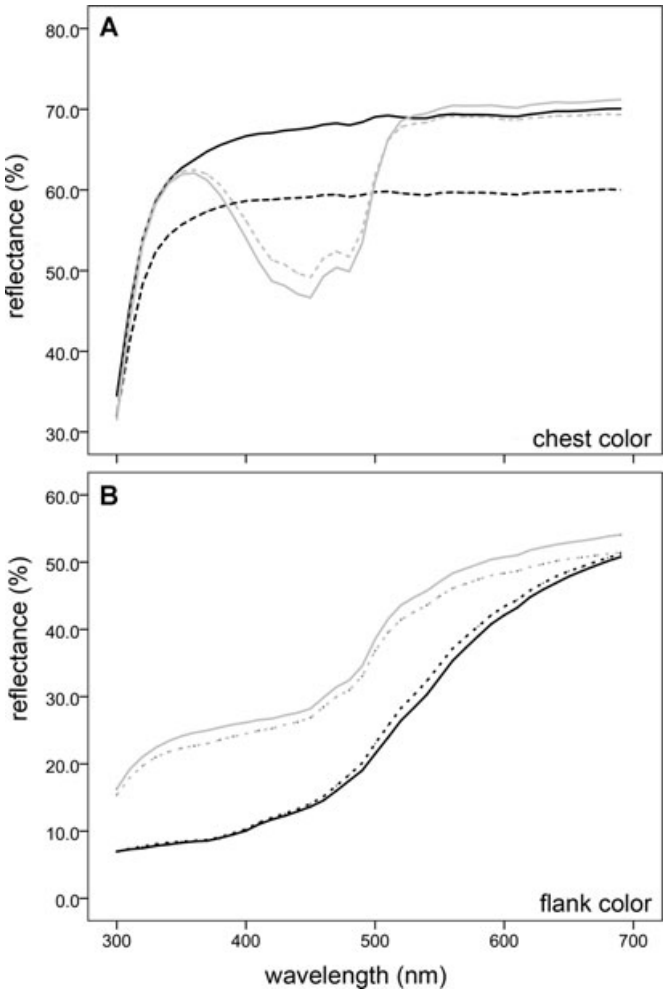

Figure 4. Mean reflectance curves across avian-visible wavelengths generated from (A) chest and (B) flank feathers of *Hypocnemis peruviana* (black line, $n = 43$) and *H. subflava* (gray line, $n = 46$). Data are presented for males (solid line) and females (dashed line). Resolution = 91 × 136 mm (600 × 600 DPI).

occurs not in signals but in receiver discrimination (e.g., Jang and Gerhardt 2006). Thus, we used playback experiments in sympatry to test whether overlapping signal structure in *H. peruviana* and *H. subflava* generated strong interspecific responses to same-sex songs (Bard et al. 2002; Seddon and Tobias 2006). We assumed that phenotypic convergence would be reflected in lower responses to heterospecific song by allopatric birds, and thus we assessed receiver preferences of *H. peruviana* at Los Indios. The equivalent tests on allopatric *H. subflava* were not possible due to logistical difficulties. Heterospecific responses are sometimes learnt in sympatry (e.g., Emlen et al. 1975; Matyjasiak 2005; den Hartog et al. 2008), providing a possible alternative explanation for muted responses in allopatry. We therefore assessed the role of learning by comparing (1) the response of naïve *H. peruviana* at Los Indios to *H. subflava* with (2) the response of naïve *H. peruviana* at CICRA to *H. striata*. Finally, work on frogs has shown that heterospecific responses may relate to ancestral or phylogenetically conserved receiver biases (Ryan and Rand 1995, 2003; Ryan et al. 2001, 2003), and we therefore used playback of songs of two other antbirds, *H. striata* and *D. devillei*, to test whether receiver preferences were better predicted by evolutionary relationships or signal design.

Five different experiments were conducted on resident pairs, consisting of the following treatments: (1) conspecific versus heterospecific male songs, (2) conspecific versus heterospecific female songs, (3) heterospecific versus *H. striata* male songs, (4) heterospecific versus *H. striata* female songs, and (5) male songs of *D. devillei*. We conducted a total of 169 experiments on the following individuals: 19 *H. peruviana* males and 20 *H. subflava* males at CICRA, and 13 *H. peruviana* males at Los Indios (treatment 1); 18 *H. peruviana* females and 20 *H. subflava* females at CICRA, and 10 *H. peruviana* females at Los Indios (treatment 2); 15 males of each species at CICRA (treatment 3); 15 *H. peruviana* females and 14 *H. subflava* females at CICRA (treatment 4); and 10 males of each species at CICRA (treatment 5). Experiments (1) and (2) were carried out in 2006, and (3)–(5) in 2007.

Audio files for playbacks were prepared using Avisoft to filter recordings of high-quality songs (low background noise) and to create PCM wav files consisting of a single song with four repetitions per minute (the mean rate under natural conditions). To avoid pseudoreplication, each experiment involved a unique song recorded from a different individual. Experiments took place at 0600–0900 h, after subjects had been silent for at least 5 min. In experiments (1)–(4), pairs of treatments were separated by 15–30 min, and given from the same location close to the center of territories. Treatment order was randomized. In each experiment, we selected stimulus files recorded from nonneighbors, to minimize the influence of neighbor-stranger recognition. Pairs on adjacent territories were not tested on the same day to ensure independence. Songs were played as uncompressed wav files with an Arcos G-mini mp3 player connected to a SME-AFS field speaker (Saul Mineroff Electronics, Elmont, New York). This was placed within the territory, at least 20 m from the territory boundary, ~0.2 m above the ground, facing subjects 20–40 m away. Peak sound pressure level was adjusted to approximate that of natural songs (65 dB at 10 m).

Seasonal effects are thought to be minor because all four study species hold permanent territories and breed year round (N. Seddon, unpubl. ms). However, there is some seasonal variation and we attempted to control for this effect by conducting all playbacks during the period of peak vocal and breeding activity in southeast Peru. It should be noted that the timing of peak activity in Bolivia is not yet known, and therefore it is possible that our experiments in Pando and Cochabamba were slightly off-peak.

Previous playback studies of *Hypocnemis* antbirds (Seddon and Tobias 2006; Tobias and Seddon 2009) revealed that

territorial individuals approached and sang within 10 min of playback of a conspecific intruder. Therefore, trials lasted 10 min from start of first playback song (1 min of playback, followed by 9 min of silence). During each 10-min trial, we noted three simple behavioral responses that were likely assays of aggression and conspecific recognition (Seddon and Tobias 2007; Uy et al. 2009): (1) closest distance to loudspeaker (to nearest meters), (2) time spent <5 m from loudspeaker (to nearest 10 s), and (3) number of songs during first 5 min from the start of the first song given after playback. To ensure consistency, all experiments were conducted by the same researchers, one making behavioral observations, another transcribing data. As playback response variables were correlated, we used PC analysis to reduce our dataset to a single principal component that reflected the overall strength of territorial aggression ($PC1_{aggression}$; see below for details). $PC1_{aggression}$ scores for each individual in each playback trial were entered as the dependent variable in further analyses.

STATISTICAL ANALYSES

Signal variation in sympatry

To compare song structure of *Hypocnemis* antbirds in sympatry, we first used univariate general linear mixed models (GLMMs) on separate acoustic variables, with individual identity fitted as a random term, and species fitted as a fixed effect. We then conducted a principal components analysis (PCA) on the correlation matrices of individual mean values (log-transformed). This reduced the dimensionality of the song dataset and allowed us to quantify how the overall structure of songs in sympatry varied within and between species and sexes.

To compare sex- and species-specificity of songs with that found in other nonterritorial signals, we also conducted PCAs on the call, chest and flank color datasets (see Table S1 for all factor loadings). This was followed by a series of discriminant function analyses (DFA) to quantify the extent to which individuals could be assigned to the correct species and sex on the basis of signal structure. However, it was not possible to conduct DFAs using raw data, as numerous variables in the acoustic and plumage datasets were strongly correlated with one another (Pearson's correlation >0.8). Multicollinearity violates a key assumption of DFA, resulting in near-zero determinants and producing an unstable inverted matrix (Tabachnick and Fidell 2006). Following numerous studies (e.g., Radford and du Plessis 2003; Hollén and Manser 2007; Podos 2007; Turner et al. 2007), we therefore used PC scores rather than raw variables as predictors.

We first generated PC scores and conducted DFAs for each signal in sympatry by including data from both species and both sexes (Table S1A–B). This procedure revealed that songs are strongly sex-specific but only weakly species-specific. Because strong between-sex differences in signal structure might mask between-species differences, we then conducted a PCA–DFA separately for each species and sex (Table S1C–E). In all DFAs, we used (1) *F* tests (Wilks' Lambda) to examine whether the overall discriminant models were significant, and (2) cross-validation to estimate error rates (see Bard et al. 2002; Seddon and Tobias 2007). This method generates a discriminant function by withholding one observation at a time and then classifying that observation, thus controlling for the bias involved in constructing discriminant functions with the same observations that they are then used to classify.

Geographic variation in signal design and perception

To quantify geographic variation in song structure, we conducted a PCA on song data collected from sympatric (CICRA) and allopatric (Los Indios and Sajta) populations (Fig. 1). This produced five PCs accounting for 82.6% of the variation in the original dataset (Table S1F). We compared PC scores between allopatric and sympatric populations using Mann–Whitney *U*-tests, and we compared the response of *H. peruviana* to conspecific versus *H. subflava* song in sympatry and allopatry using Wilcoxon signed-rank tests. A nonparametric approach was necessary in these cases because of small sample sizes for allopatric songs and playback experiments (Table 1).

Phylogenetic variation in signal design and perception

Variation in song structure was examined by extracting five PCs from acoustic data for the songs of *H. peruviana*, *H. subflava*, and *D. devillei* in sympatry, and *H. striata* in allopatry (see Table S1G for factor loadings). We then carried out a cross-validated DFA with simultaneous inclusion of all five PCs to determine the extent to which the four antbird species included in this study had species-specific songs.

To test for phylogenetic variation in song perception, we conducted paired playback experiments (see above). We modeled the strength of territorial aggression using a GLMM approach. GLMMs were run for each sex separately; $PC1_{aggression}$ was included as the dependent variable, playback treatment as the fixed effect, and identity of the resident male/female as the random effect. We conducted Tukey's pairwise post hoc tests to explore patterns among treatment groups. To determine whether territorial aggression in sympatry is driven by the similarity of the playback treatment to conspecific song or the evolutionary relatedness of the simulated intruder, we ran a GLMM with restricted maximum-likelihood estimation (REML) in which we included species, genetic distance, and song similarity as fixed effects. For conspecific playbacks, the genetic distance was set at zero. Song similarity was calculated as the Euclidean distance between the group (i.e., species) centroids derived from a DFA of the acoustic structure of the cuts used in playback treatments (Table S1G). Genetic distance was calculated as the uncorrected percentage sequence divergence for a combined dataset of three mitochondrial

genes (data taken from Bates et al. 1999; Tobias et al. 2008). The significance of fixed effects was assessed using Wald statistics.

GLMMs with REML estimation were implemented in Genstat (2006); all other statistical tests were carried out using SPSS (2007). All positively skewed data were log-transformed prior to parametric analyses. *P*-values are two-tailed and corrected for ties where appropriate.

Results

SIGNAL VARIATION IN SYMPATRY

In sympatry, the structure of male songs overlapped in *H. peruviana* and *H. subflava* (Fig. 5A). Further analyses showed that the songs of sympatric females were even more similar than those of males (Fig. 5A). There were significant differences between species in only 40% (8/20) of acoustic measures for male songs, and 15% (3/20) of acoustic measures for female songs (see Table 2). Moreover, there was overlap in all measures, meaning that species were not diagnosable (sensu Isler et al. 1998) by any song character. Accordingly, DFA revealed overlap in the overall structure of male songs in both species, and female songs in both species, with cross-validation assigning 18.2% (10/55) of male songs and 19.5% (8/41) of female songs to the incorrect species; three *H. peruviana* males and seven *H. subflava*, and three *H. peruviana* and five *H. subflava* females, produced songs that were incorrectly classified to species. On the basis of song characters alone, individuals were difficult to assign to species, but easily assigned to sex. There was no overlap in overall structure of male and female songs in *H. peruviana*, and only a slight overlap in *H. subflava* (Fig. 5A). Cross-validated DFA assigned only 2.0% (1/50) of *H. peruviana* individuals and 6.5% (3/46) of *H. subflava* individuals to the incorrect sex.

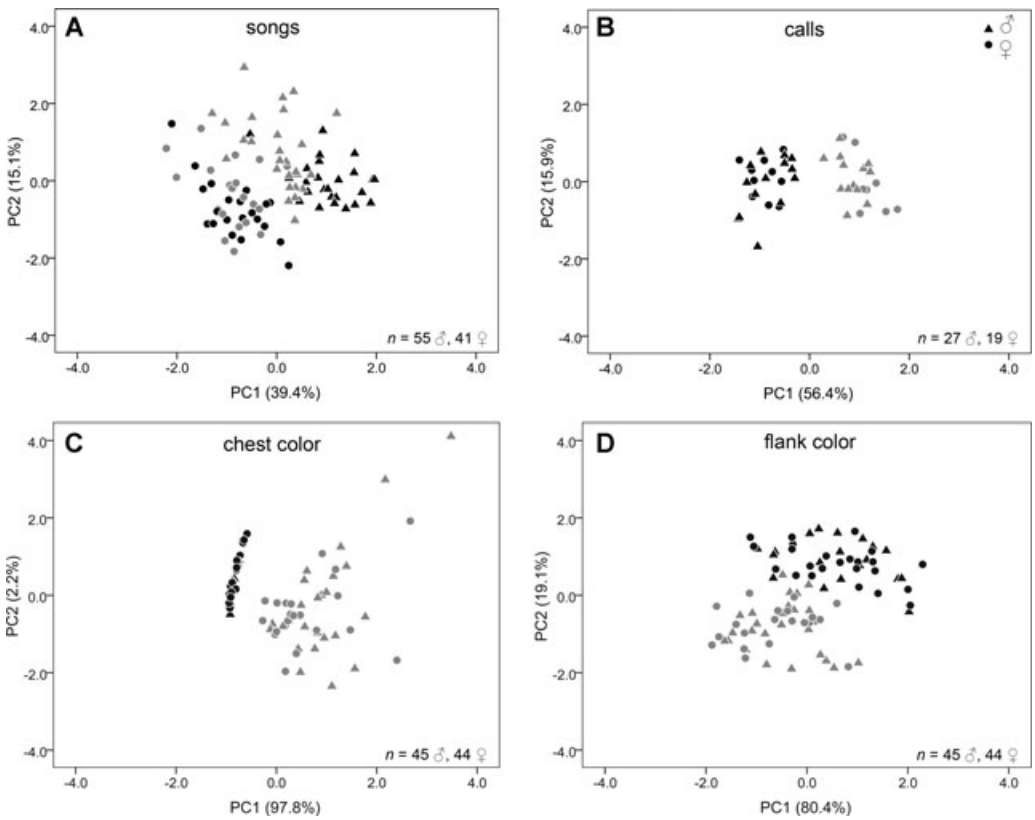

Figure 5. Signal design in sympatry for *Hypocnemis peruviana* (black) and *H. subflava* (gray). Scatterplots show species and sex-specific variation in (A) territorial song structure, (B) nonterritorial call structure, (C) chest color, and (D) flank color, as defined by the first two principal components (PCs). The percentage of variance in the original vocal and plumage datasets explained by each PC is given in parentheses (see Table S1 for factor loadings). Axes are standardized across different signaling modalities to facilitate interpretation of relative trait divergence. In (A), PC1 reflects the temporal patterning of songs and is positively related to note duration, song duration, and internote interval; and negatively related to note pace and pace change; PC2 reflects the spectral properties of song and is positively related to note bandwidth and maximum frequency (Table S1A). In (B), PC1 is positively related to call and note duration, bandwidth, and maximum frequency; and negatively related to note pace; PC2 is positively related to internote interval (Table S1A). In (C), PC1 is positively related to UV amplitude and negatively related to blue chroma; PC2 is positively related to yellow amplitude (Table S1B). In (D), PC1 is strongly positively related to UV absorbance, blue absorbance, and yellow chroma; PC2 is positively related to yellow chroma (Table S1B).

Table 2. Acoustic structure of songs of *Hypocnemis peruviana* and *H. subflava* in sympatry.

	Males			Females		
	H. peruviana	*H. subflava*	P^2	*H. peruviana*	*H. subflava*	P^2
Acoustic trait[1]:						
Note number	8.07±1.28	9.16±2.12	*	7.23±1.15	9.23±1.85	*
Number raspy notes	2.96±1.06	3.12±1.57		1.14±0.35	1.23±0.68	
Song duration	2.83±0.54	3.01±0.81		1.93±0.34	2.45±0.50	*
Duration of notes 1–4	1.16±0.09	1.05±0.06	*	0.97±0.08	1.03±0.07	
Duration of final four notes	1.49±0.20	1.45±0.31	*	1.01±0.13	0.99±0.22	
Duration of first note	0.11±0.01	0.13±0.02	*	0.11±0.02	0.131±0.02	*
Duration of first interval	0.25±0.02	0.23±0.02	*	0.21±0.03	0.19±0.03	
Duration of fourth note	0.19±0.03	0.15±0.02	*	0.12±0.02	0.12±0.01	
Max frequency of first note	3.31±0.26	3.16±0.23		3.29±0.20	3.32±0.21	
Min frequency of first note	1.98±0.26	1.77±0.30		1.94±.23	1.79±.28	
Max frequency of fourth note	3.49±0.19	3.21±0.25	*	2.97±0.18	3.07±0.24	
Min frequency of fourth note	2.04±0.20	1.92±0.27		1.77±0.19	1.71±0.28	
Bandwidth of first note	1.32±0.37	1.36±0.29		1.35±0.22	1.50±0.36	
Bandwidth of fourth note	1.44±0.28	1.26±0.35		1.20±0.16	1.31±0.35	
Peak frequency	2.89±0.16	2.80±0.19		2.80±0.21	2.85±0.31	
Change in frequency	1.06±0.06	1.02±0.05		0.90±0.04	0.93±0.04	
Overall pace of notes	2.88±0.29	3.09±0.32	*	3.78±0.33	3.80±0.42	
Note pace in first segment	3.49±0.30	3.83±0.22	*	4.16±0.36	3.92±0.29	
Note pace in second segment	2.73±0.34	2.87±0.54		4.01±0.52	4.23±0.88	
Pace change	0.78±0.09	0.75±0.13		0.97±0.15	1.08±0.21	

[1]Values show are mean ± SD. Temporal measures are in seconds (s) and frequency measures in kiloHertz (kHz).
[2]Statistics derive from univariate GLMMs, with individual identity as a random effect, and species as a fixed effect; asterisks denote significant differences after Bonferroni correction ($P<0.0025$).

The pattern of variation found in calls was opposite to that in songs. Calls were highly diagnostic in sympatry (Fig. 3) with no evidence of hybrid phenotypes (see Fig. 5B), and they were only weakly sex specific. Cross-validated DFA correctly identified all 45 individuals by species, but only 27 (60.0%) by sex. To test for bias in our song sample, we compared the songs of individuals for which calls were analyzed ($n = 41$) with those from a sample of individuals for which we had no call data ($n = 55$). There were no significant differences between these samples in song structure as defined by PC1 and PC2 (Mann–Whitney U-tests: $0.074 < P < 0.794$; Table S2), confirming that our results were not affected by hybrid individuals for which we did not have call samples.

Flank and chest color was also highly diagnostic in sympatry (Fig. 4; Figs. S1 and S2) with no indication of intermediate phenotypes in chest plumage and only slight overlap in flank plumage (Fig. 5C,D). For chest coloration, cross-validated DFA correctly identified all 89 individuals by species, but only 53 (59.6%) by sex (Fig. 5C). For flank feathers, 86 (96.6%) individuals were correctly identified by species, but only 33 (37.1%) by sex (Fig. 5D). These results suggest that plumage signals in *H. peruviana* and *H. subflava* are species-specific but only weakly sex-specific. In other words, patterns of variation are similar in calls and plumage, but the reverse pattern is found in songs.

When we conducted a PCA–DFA for each sex separately, all individuals were assigned to the correct species by calls and chest color, 85 (95.5%) by flank color, 50 (90.9%) by male song, and 34 (82.9%) by female song. In other words, even when correcting for sex differences in signal structure, we found that interspecific differences in signal structure were greater for calls, chest plumage, and flank plumage than for songs (Fig. S4). In line with these findings, individuals from the zone of sympatry were easily assigned to species by human observers on the basis of calls and plumage, but not by songs (Figs. 2–4; Figs. S1 and S2).

GEOGRAPHICAL VARIATION IN SIGNAL DESIGN AND PERCEPTION

We found a significant variation between allopatric and sympatric populations in song structure as defined by five principal components (Fig. 6; see Table S1F for factor loadings). In males, allopatric songs differed significantly from sympatric songs in PC3 (which mainly reflects bandwidth) for *H. peruviana* (Fig. 6C; $P = 0.018$), and in both PC3 ($P = 0.004$) and PC4 (maximum and peak frequency; $P < 0.0001$) for *H. subflava* (Fig. 6D). In females,

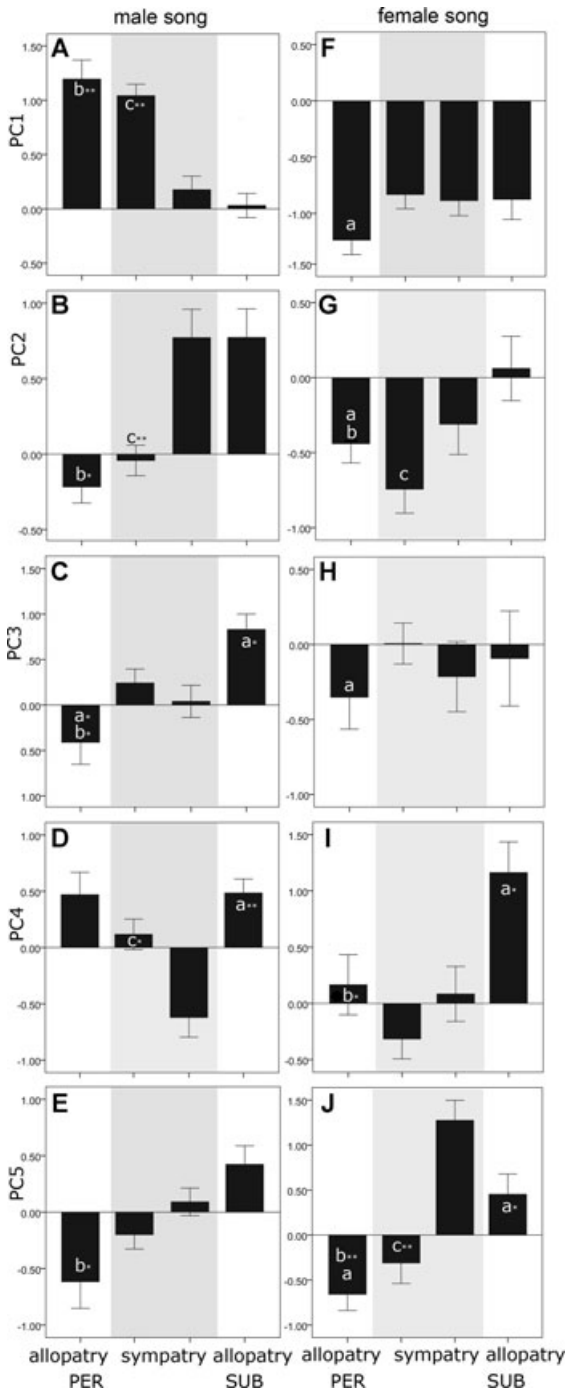

Figure 6. Variation in the acoustic structure of *Hypocnemis peruviana* (PER) and *H. subflava* (SUB) songs between allopatric (Los Indios and Sajta) and sympatric (CICRA, shaded gray) populations, as defined by five principal components (see Table S1F for factor loadings). Left-hand column (A–E) shows results for males; right-hand column (F–J) shows results for females. Statistics are from Mann–Whitney U tests comparing mean PC scores between allopatric and sympatric populations of the same species (a), as well as across populations of both species in allopatry (b) and sympatry (c); no asterisk $P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.0001$. Bars show mean (±SE) PC scores; see Table 1 for sample sizes.

allopatric and sympatric songs tended to differ in all PCs except PC4 (Fig. 6I; $0.066 < P < 0.097$) for *H. peruviana*, and differed significantly in both PC4 ($P = 0.007$, Fig. 6I) and PC5 (duration of first note; $P = 0.023$, Fig. 6J) for *H. subflava.* There were greater interspecific differences in song structure among allopatric than sympatric populations for PC3 ($P = 0.001$ vs. 0.418) and PC5 ($P = 0.002$ vs. 0.152) in males, and for PC4 ($P = 0.011$ vs. 0.308) in females, consistent with character convergence. Meanwhile, in males PC4 was more divergent in sympatry ($P = 0.004$) than in allopatry ($P = 0.792$), consistent with divergent character displacement. In summary, we found mixed support for convergence in vocal traits of both sexes: there was relatively little difference between sympatry and allopatry, with more traits showing significant convergence than divergence.

Playback experiments revealed that *H. peruviana* males and females responded aggressively to conspecific and heterospecific song in both allopatry and sympatry (Fig. 7). However, the strength of response varied between populations. In particular, we found that resident *H. peruviana* males in sympatry did not discriminate between local conspecific and heterospecific songs ($z = -0.926$, $P = 0.355$), whereas in allopatry they responded significantly more strongly to local conspecific song than to *H. subflava* songs ($z = -2.97$, $P = 0.003$; Fig. 7A). Female *H. peruviana* responded equally to conspecific and heterospecific songs in allopatry and sympatry ($0.267 < P < 0.641$), although there was evidence of weaker overall responses to playback in allopatry (Fig. 7B), perhaps due to seasonal effects.

PHYLOGENETIC VARIATION IN SIGNAL DESIGN AND PERCEPTION

Acoustic data from the closest relative in sympatry (*D. devillei*) and allopatry (*H. striata*) reveal that songs in these species are divergent from *H. peruviana/H. subflava*, and from each other. Cross-validated DFA on the structure of male songs of all four species used in the playback experiments assigned all *D. devillei* and *H. striata* songs to the correct species, in a sharp contrast with the situation in *H. peruviana* and *H. subflava* where 8 of 39 (20.5%) songs were incorrectly assigned (Fig. 8A). Similarly, an analysis of female song structure assigned all *H. striata* songs to the correct species, but incorrectly assigned 6 of 37 (16.2%) of *H. peruviana* and *H. subflava* songs (Fig. 8B). The key result is that songs in both sexes of *H. peruviana* are more similar to songs in a sympatric species than to those of a more closely related allopatric species.

Paired playback experiments revealed that this anomalous pattern of variation was reflected in receiver perception. We found a strong significant overall effect of playback treatment on levels of territorial aggression by males (Table 3, Fig. 8C) and females (Table 4, Fig. 8D). Post hoc pairwise tests showed that resident male antbirds ignored the *D. devillei* control, and responded most

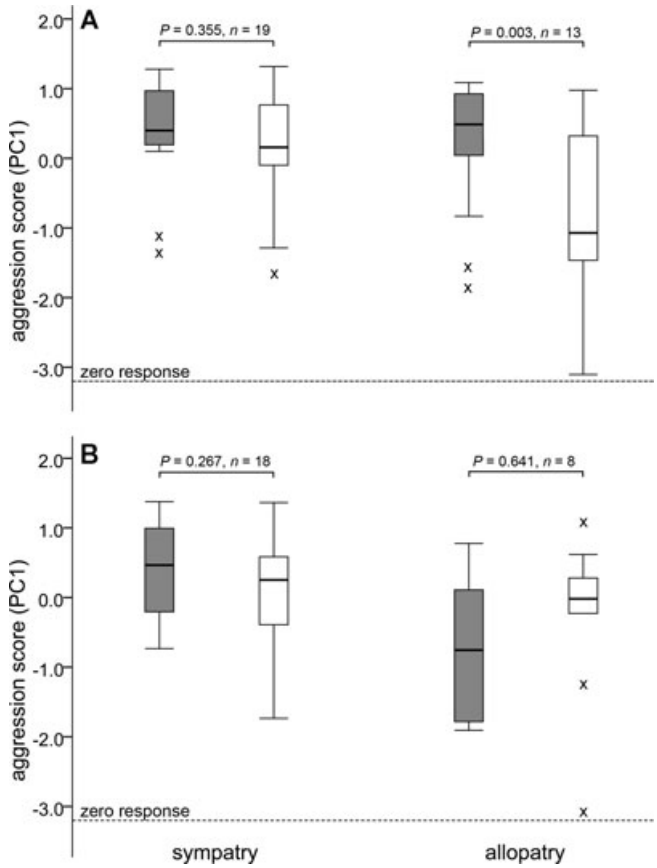

Figure 7. **Box plots showing the overall strength of response by (A) male and (B) female *Hypocnemis peruviana* to playback of conspecific (gray) versus *H. subflava* (white) songs in sympatry (CICRA) and allopatry (Los Indios). The aggression score (PC1) accounts for 63.1% of variation in response strength (eigenvalue = 1.95), and is negatively correlated with closest distance (−0.895), and positively correlated with time spent <5 m from the loudspeaker (0.868) and number of songs given after playback (0.583). Zero response to playback (PC1 = −3.15) is denoted by a dashed line. Boxes indicate the 25th and 75th percentiles, the line in the box marks the median, and the whiskers denote 10th and 90th percentiles; extreme values are also shown. Statistics are Wilcoxon signed-rank tests. Note that low responses by females to conspecific song in allopatry compared to sympatry are unexpected and may reflect modest sample sizes.**

aggressively (i.e., highest $PC1_{aggression}$ scores) to conspecific song and least aggressively to heterospecific *H. striata* song (Fig. 8C). In *H. peruviana*, males did not discriminate between conspecific songs and heterospecific *H. subflava* songs (Figs. 7A and 8C). In *H. subflava*, males responded significantly more aggressively to conspecific song than to heterospecific *H. peruviana* songs, but responded with more aggression to *H. peruviana* songs than to *H. striata* songs. Similar patterns emerged from our experiments on resident female antbirds (Figs. 7B and 8D): conspecific female songs elicited the most aggressive responses, heterospecific *H. peruviana*/*H. subflava* songs produced slightly less aggressive responses, and heterospecific *H. striata* elicited the weakest responses. Note that the order in which a treatment was played did not affect $PC1_{aggression}$ scores (GLMM; males: $F_{2,102} = 0.568$, $P = 0.569$; females: $F_{1,78} = 2.062$, $P = 0.155$), and so this factor was not included in the final models (Tables 3 and 4).

The design of playback experiments allowed a direct test of the relative influence of evolutionary relatedness and song similarity in determining levels of territorial aggression. We found that, for males, song similarity was a strong predictor of territorial aggression ($PC1_{aggression}$) but genetic relatedness had no effect (REML; song similarity: $\chi^2_1 = 162.40$, $P < 0.001$; genetic distance: $\chi^2_1 = 0.98$, $P = 0.322$). In females, both song similarity and genetic distance predicted territorial aggression, although song similarity had the strongest effect (song similarity: $\chi^2_1 = 70.39$, $P < 0.001$; genetic distance: $\chi^2_1 = 34.24$, $P =< 0.001$). We conclude that the strength of receiver responses is driven largely by signal design rather than phylogenetic relationships (see Table S3 for full model).

A decline in response of male *H. peruviana* to *H. subflava* in allopatry could be interpreted as evidence that allopatric individuals simply have not learnt to respond aggressively to congeneric competitors. However, it should be emphasized that naïve males and females at Los Indios (i.e., in allopatry) still responded aggressively to *H. subflava* (Fig. 7). This is underscored by the observation that *H. peruviana* at Los Indios responded significantly more strongly to *H. subflava* than did *H. peruviana* at CICRA to *H. striata* in both males (Mann-Whitney *U*-test: $U = 46.0$, $n_1 = 13$, $n_2 = 15$, $P = 0.016$) and females ($U = 18.0$, $n_1 = 10$, $n_2 = 14$, $P = 0.004$). In other words, naive *H. peruviana* perceived the song of *H. subflava* as a more threatening signal than the song of their closer relative, *H. striata*.

Discussion

Our results demonstrate that long-range territorial songs of *H. peruviana* and *H. subflava* are more or less interchangeable in design and perception. They also suggest that songs are convergent in both sexes from a functional standpoint (i.e., territorial signals are more similar than nonterritorial signals), and an evolutionary standpoint (i.e., songs are less divergent than those of a more closely related taxon). In addition, our findings are consistent with convergence, or at least nondivergence, from a geographical perspective (i.e., some aspects of song structure are more similar in sympatry than allopatry). Why does traditional signal evolution theory, which predicts that divergence generates species-specific signals, not apply in this system? To answer this question, we begin by weighing the evidence from observational and experimental approaches.

In a study based largely on data collected from allopatric localities, Isler et al. (2007) concluded that male songs in *H.*

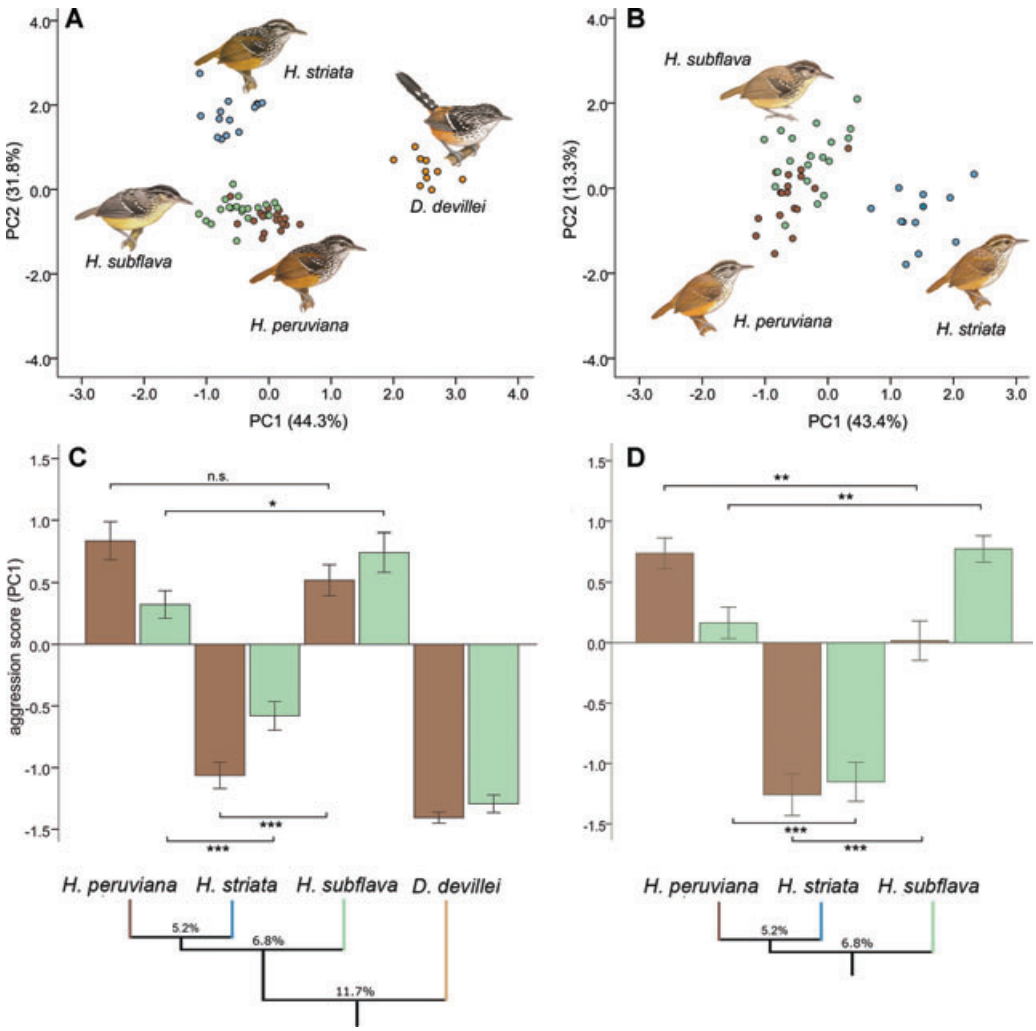

Figure 8. Song structure for all male (A) and female (B) *H. peruviana* (brown), *H. subflava* (green), *H. striata* (blue) and *D. devillei* (orange) used as treatments in playback experiments in sympatry, along with mean (±SE) aggression scores ($PC1_{aggression}$) for males (C) and females (D) receiving these treatments. Song structure is presented as 16 acoustic characters collapsed into two discriminant functions (DFs; see Supporting Table S1 for factor loadings); $PC1_{aggression}$ accounts for 68.0% of the variation in response strength (eigenvalue = 2.04), and is strongly negatively correlated with closest distance (−0.896), and strongly positively correlated with time spent < 5 m from the loudspeaker (0.903) and number of songs (0.649). Negative scores indicate low response. In (C) and (D), the x-axis labels are annotated with a phylogenetic tree showing mtDNA sequence divergence of all taxa used as playback treatments (Bates et al. 1999; Tobias et al. 2008). Asterisks denote significant effects of playback treatment on aggression, as determined from Tukey post hoc tests (*$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$). Note that in (C) and (D), sample sizes are pooled from all playback experiments, and are therefore greater than those presented in Fig. 7. It was not possible to quantify responses to female *D. devillei* song as our sample of recordings was too small to avoid pseudoreplication. Illustrations are reproduced and adapted from Handbook of the Birds of the World with the permission of Lynx Edicions.

peruviana and *H. subflava* were not safely assigned to species based on acoustic analyses. Our results confirm that these songs are not diagnosable even when restricting the analysis to sympatric localities. A similar finding, with even greater structural overlap in sympatry, was evident in female songs. This may reflect higher fitness costs associated with misidentification of males by females (Searcy and Brenowitz 1988), and thus stronger selection on male songs to be species specific. The similarity of songs in these two species stands in a stark contrast to variation in three short-range nonterritorial signals, all of which were highly divergent in both sexes and easily assigned to species. We take this as evidence that different selective forces may be shaping territorial versus nonterritorial signals.

Comparison with data from allopatry revealed subtle but complex variation in male and female songs of both species, with some structural features converging toward the sympatric zone,

Table 3. General linear mixed model (GLMM) of aggressive response ($PC1_{aggression}$) to playback of male song by resident male *Hypocnemis* antbirds in sympatry (adjusted R^2 for full *H. peruviana* model=0.79, and for full *H. subflava* model=0.69).

Species/factor	Type III sum of squares	df	Mean square	*F*	*P*	Effect size[1]
H. peruviana						
Model	82.158	35	2.347	9.415	<0.0001	0.880
Intercept	2.831	1	2.831	11.355	0.002	0.201
Playback treatment	30.942	3	10.314	41.367	<0.0001	0.734
Individual identity	17.068	32	0.533	2.139	0.009	0.603
Residual	11.220	45	0.249			
H. subflava						
Model	55.951	30	1.865	7.099	<0.0001	0.804
Intercept	3.118	1	3.118	11.870	0.001	0.186
Playback treatment	27.469	3	9.156	34.853	<0.0001	0.668
Individual identity	14.470	27	0.536	2.040	0.014	0.514
Residual	13.661	52	0.263			

[1]Partial eta squared.

and others appearing to diverge or to remain constant. Overall, we found more evidence for convergence than divergence in sympatry. However, this analysis is weakened because we were only able to collect data from one sympatric and one allopatric locality per species due to logistical constraints. Data from more localities are needed to determine consistent patterns of variation, although even the current simplified format of our results clearly demonstrates that strong divergent character displacement is not a feature of the *Hypocnemis* contact zone (cf. Kirschel et al. 2009).

Why do we find mixed evidence of divergent and convergent character displacement in sympatry? One possibility is that our allopatric sites were not sufficiently far from sympatry to reveal consistent effects. For example, convergence may be difficult to detect without widespread sampling if gene flow from sympatry to allopatry obscures the stepped patterns of trait variation predicted by character displacement (Gerhardt and Huber 2002). Another possibility is that separate components of song structure have different functions, as found in some oscine species (Collins 2004), in which case aspects relating to mate choice may be divergent whereas those relating to intrasexual competition may be convergent. Further investigation of these ideas is warranted, ideally involving experiments at multiple sites in sympatry and allopatry.

Stronger evidence for convergence was obtained by comparison with *H. striata*, a closer relative of *H. peruviana* both ecologically and phylogenetically (Isler et al. 2007; Tobias et al. 2008). In this case, we found the opposite pattern of variation: *H. striata* was strongly divergent from *H. peruviana* in song traits

Table 4. General linear mixed model (GLMM) of aggressive response ($PC1_{aggression}$) to playback of female song by resident female *Hypocnemis* antbirds in sympatry (adjusted R^2 for full *H. peruviana* model=0.55, and for full *H. subflava* model=0.56).

Species/factor	Type III sum of squares	df	Mean square	*F*	*P*	Effect size[1]
H. peruviana						
Model	55.147	30	1.838	3.685	<0.0001	0.760
Intercept	1.362	1	1.362	2.730	0.107	0.072
Playback treatment	9.474	2	4.737	9.497	0.001	0.352
Individual identity	21.888	28	0.782	1.567	0.104	0.556
Residual	17.457	35	0.499			
H. subflava						
Model	43.918	27	1.627	4.135	<0.0001	0.736
Intercept	0.167	1	0.167	0.424	0.519	0.010
Playback treatment	20.921	2	10.460	26.592	<0.0001	0.571
Individual identity	12.757	25	0.510	1.297	0.227	0.448
Residual	15.735	40	0.393			

[1]Partial eta squared.

but only weakly divergent in nonterritorial signals (Fig. 8). Given that these allopatric lineages split an estimated 2.6 mya (Tobias et al. 2008), this finding supports the prediction that divergence occurs by stochastic processes in isolation (Mayr 1963). It also adds weight to the argument that *H. peruviana* and *H. striata* have convergent songs from the perspective of evolutionary history. Moreover, it seems plausible that convergence has shaped the songs of both sexes independently, driven by sex-specific aggression.

SIGNAL DESIGN TRUMPS GENETIC RELATEDNESS: INSIGHTS FROM PLAYBACK EXPERIMENTS

Our experimental data reveal that male and female *H. peruviana* responded aggressively to conspecific and heterospecific (*H. subflava*) song, but showed little aggression in response to songs of *D. devillei*. We also found that both sexes of *H. peruviana* responded far more aggressively to *H. subflava*, a sympatric species with a similar song, than they did to *H. striata*, a more closely related allopatric species with a dissimilar song. Results in *H. subflava* were the same, except that the response to conspecific song was slightly, but significantly, stronger than the response to heterospecific (*H. peruviana*) song. Overall, our playback results exactly match the expected order of receiver preferences based on signal similarity.

These results allow us to draw two conclusions. First, our measures of song similarity adequately capture the way both sexes perceive vocal traits. And second, the strength of responses to heterospecifics is better predicted by signal design than evolutionary history. This finding is opposite to that of Bernal et al. (2007), who showed that the response of túngara frogs *Physalaemus pustulosus* to heterospecifics was correlated with phylogenetic relatedness, not call similarity. Indeed, studies of mating signals in anurans repeatedly conclude that evolutionary history strongly influences receiver bias (Ryan and Rand 1995; Ryan et al. 2001). This association is disrupted in *Hypocnemis*, but it remains plausible that convergent or parallel selection has acted on ancestral traits and preferences, as *H. subflava* is basal to the "*H. cantator*" clade (including *H. peruviana*).

The relatively weak responses of male *H. subflava* to *H. peruviana* suggest that the strength of heterospecific aggression is asymmetric with respect to species. Unequal responses of this kind may reflect behavioral dominance of one species by another, a common finding in sympatric animals (Lawton and Hassell 1981; Connell 1983; Schoener 1983). Competitive asymmetry is generally governed by size differences, and biometric data from sympatry confirm that *H. subflava* is very slightly, but significantly, smaller than *H. peruviana* in mensural characters, including wing length and mass (J. A. Tobias, unpubl. ms). However, competitive asymmetry is also typically matched by skews in local abundance, whereas population data reveal no difference in the size or density of populations of these species at a local scale (J. A. Tobias, unpubl. ms). We emphasize that many *H. subflava* individuals respond extremely aggressively to *H. peruviana* songs, and that the asymmetric response to playbacks may be driven by a minority of weakly responsive individuals at the lower end of the size range. We suspect that *H. subflava* and *H. peruviana* are competitively symmetrical, or very nearly so, but further tests are required to confirm this.

Further playbacks showed that, although sympatric *H. peruviana* males perceived local conspecific and heterospecific songs as equally threatening, allopatric males responded with more aggression to local conspecific songs than to heterospecific songs recorded in sympatry. The most parsimonious explanation for this finding is that territorial songs of *H. peruviana* are more similar to those of *H. subflava* in sympatry than in allopatry. In other words, territorial signals appear to be convergent in sympatry, at least in aspects of structure related to territorial behavior.

An alternative explanation for geographical variation in responses to heterospecifics is that males have simply learned to react aggressively to *H. subflava* songs in sympatry, but not in allopatry. However, the fact that both sexes of *H. peruviana* responded more strongly to *H. subflava* at Los Indios than they did to *H. striata* at CICRA indicates that naïve individuals perceive the most threatening territorial signal to be the song of *H. subflava*, not that of *H. striata*. Thus, although learning may play a role, the results of multispecies playbacks reinforce the conclusion that receiver behavior is essentially innate and shaped by signal design rather than genetic relatedness.

PATTERN OR PROCESS?

Assuming that *H. peruviana* and *H. subflava* speciated in allopatry, their similar songs either represent a lack of divergence because they shared a common ancestor, or convergent character displacement (Grant 1972). Both outcomes are highly unusual. Moreover, they are at odds with two general predictions based on social selection, first that there should be "more rapid divergence (less phylogenetic conservatism) of socially competitive compared to noncompetitive signals" (West-Eberhard 1983), and second that divergence should be most pronounced in long-range signals detected early in species interactions (Marler 1957; West-Eberhard 1983). Similarly, a nondivergent outcome is inconsistent with the idea that conspecific signals must be recognized against a background of heterospecific signals (Nelson 1989), and that divergent songs are therefore favored to minimize the costs of mistaken identity and misdirected aggression, including time, energy, injury, and the increased risk of predation and hybridization (Marler 1957; Orians and Willson 1964; Murray 1971).

Several factors suggest that at least some of these costs apply to the *Hypocnemis* system. First, we have shown that *H. peruviana* and *H. subflava* come into regular contact at territory boundaries,

and they respond energetically and conspicuously to the songs of heterospecific individuals. Second, their songs are transmitted in the dense undergrowth of tropical rainforest, where vocal signals are detected long before visual signals (Sibley 1957). Third, rainforests are characterized by a high ambient noise and severe degradation of sound, and signals should therefore differ by more than the minimum required to prevent ambiguity caused by overlap in acoustic characters (Seddon 2005; Luther and Wiley 2009). It seems inevitable, therefore, that individuals of both species use time and energy responding aggressively to heterospecifics, potentially leading to injury or an increased risk of predation.

If the costs of shared signals are borne by both species, as our data suggest, it follows that selection will drive divergence unless these costs are (1) inescapably imposed by nonadaptive processes, or (2) outweighed by adaptive benefits. As it is all too often assumed on the basis of inadequate evidence that adaptive processes are at work, we first consider a range of alternatives.

Nonadaptive explanations

The first factor to consider is hybridization. We detected no evidence of hybrid calls or morphology in either species, and—more importantly—we demonstrated that a subset of 41 individuals had nondivergent songs but divergent calls and plumage. This suggests that song similarity does not reflect hybridization. Acoustic analyses also revealed low variability in songs and calls of both species, again suggesting that their songs are stereotyped traits within two reproductively isolated populations. Moreover, we never encountered mixed pairs, or individuals with intermediate phenotype. We propose that mating is strictly assortative in sympatry, and that hybridization is not a proximate cause of song convergence in our system. This conclusion is supported by previous studies as no hybrids have been found in *Hypocnemis* antbirds (Zimmer and Isler 2003; McCarthy 2006; Isler et al. 2007), and interbreeding is very rare throughout the suboscine clade (Graves 1992; Cadena et al. 2007).

The second potential factor is heterospecific copying. This may be possible in antbirds as, though vocal learning is rare in suboscines (Kroodsma 1984; Kroodsma and Konishi 1991), it does occur in at least one nontracheophone species (Saranathan et al. 2007). However, our data show that songs of *H. peruviana* and *H. subflava* are stereotyped, with unimodal structure in the contact zone, no switch to species-specificity in allopatry, and no sign of repertoires or dialects. We conclude that heterospecific copying, a confounding factor in numerous studies of oscines (Cody 1969, 1973; Irwin and Price 1999; Secondi et al. 2003; Haavie et al. 2004; Price 2008), does not produce song convergence in *Hypocnemis*. Overall, our results support the view that, although some form of song learning may eventually be demonstrated in tracheophone suboscines (>500 species), its influence on song structure is likely to be trivial (Isler et al. 1998, 2005; Zimmer and Isler 2003).

A third nonadaptive hypothesis—phylogenetic conservatism—states that similar signals in related species are the result of shared ancestry. Although this argument is difficult to refute, it is weakened by several lines of evidence. In general, signals are expected to diverge over long periods of reproductive isolation, if not through adaptation then by stochastic processes such as social selection, random mutation, and genetic drift (West-Eberhard 1983; Martens 1996; Irwin et al. 2008; Lenormand et al. 2008). Antbird songs typically bear the imprint of stochastic evolution: they vary in line with genetic divergence, leading to a relatively strong phylogenetic signal (Whitney 1994; Isler et al. 1998, 2005), and they can build up measurable acoustic differences over relatively short periods of isolation (<0.005 my; Seddon and Tobias 2007). It is not surprising, therefore, that nonterritorial signals have undergone marked divergence in *H. peruviana* and *H. subflava* after an estimated 3.4 million years of reproductive isolation, and that territorial songs of closer relatives have diverged significantly in a shorter time frame (Isler et al. 2007). More remarkable by far is our finding that territorial signals are nondivergent in an extensive region of sympatry. Although shared ancestry has doubtless played a role, we argue that phylogenetic conservatism alone is unlikely to explain this situation.

A final consideration is the influence of history and dispersal. For example, one possibility is that contact between taxa is recent, and that songs are therefore similar because divergent selection has not yet had time to operate (de Kort et al. 2002). However, three facts suggest that the *Hypocnemis* contact zone does not result from recent colonization by one or both species. First, all antbird species are highly sedentary and probably incapable of rapid dispersal (Zimmer and Isler 2003). Second, the zone of overlap is so extensive that the range of one study taxon, *H. s. collinsi*, is largely encompassed by that of the other, *H. p. peruviana* (Isler et al. 2007). And third, bamboo (*Guadua* spp.) has apparently existed in this lowland region for millions of years (Silman et al. 2003), long enough for at least six endemic bamboo-specialist bird species to evolve (Kratter 1997).

We conclude that song convergence is not adequately explained by any nonadaptive process. This is perhaps unsurprising because, owing to the complexity of vocalizations and the costs of shared signals, convergence in songs is much less likely to reflect nonadaptive processes than has been predicted for simple morphological traits (e.g., body size and shape) under models of random evolution (Stayton 2008).

Adaptive explanations

Only two adaptive hypotheses for signal convergence are relevant. One is that songs are similar because they are adapted to a shared signaling environment (Wiley 1991). Support for this idea

is weak, not only because acoustic adaptation is too imprecise to explain acute vocal similarity, but because one of our study species lives mainly in *Guadua* bamboo forest and the other in terra firme forest. These habitats differ in structure and sound transmission properties (N. Seddon et al., unpubl. ms), and therefore signal divergence is predicted to occur via sensory drive (Endler 1992). Indeed, our demonstration of nondiagnosable songs in two sympatric species that mainly occupy divergent habitats suggests that acoustic adaptation is overridden by a competing mechanism.

Perhaps the most plausible candidate mechanism is that songs converge owing to the forces of selection imposed by interspecific competition (Cody 1969). The main counter-argument—that coexistence does not lead to competition or even interaction (Murray 1976, 1981; Littlejohn 1993; Scott and Foster 2000; Gerhardt and Huber 2002)—does not apply in this case. The fact that *H. peruviana* and *H. subflava* are partially segregated by habitat no doubt relaxes competition for space and food (Murray 1971; MacArthur 1972), yet habitat requirements and foraging niches broadly overlap. This is clarified by the observation that pairs of these species regularly occupy adjacent territories in similar habitats, and defend territories previously occupied by heterospecifics (Isler et al. 2007; J. A. Tobias, unpubl. ms; see Materials and Methods). The evidence for competition is further strengthened because antbirds do not migrate or forage outside the territory, two factors that complicate previous studies of signal evolution via interspecific territoriality (Catchpole and Leisler 1986; Murray 1988; Hoi et al. 1991).

Competition appears to be unavoidable in this case, but a question mark remains over the strength of selection it imposes. This depends on the intensity of competition and the frequency of interaction between species. We have shown that interspecific aggression between *H. peruviana* and *H. subflava* is intense, and it is clear that several factors promote frequent interaction. In particular, the bamboo-terra firme ecotone occupied by both species are widespread throughout the zone of sympatry, where *Guadua* bamboo is distributed mainly in dense patches of 0.07–12.6 ha over an area of 120,000–180,000 km^2 (Saatchi et al. 2000; Silman et al. 2003). Moreover, the distribution of these patches fluctuates as they mature, flower, and die in cycles of 28–30 years, after which they may regenerate into terra firme forest (Nelson and Bianchini 2005). Thus, territories of *H. peruviana* and *H. subflava* replace each other in a complex mosaic both spatially and temporally. Overall, a combination of factors suggests that convergent selection on territorial signals is particularly plausible in the *Hypocnemis* system.

DOES CONVERGENCE MAKE SENSE IN THE LIGHT OF SIGNAL EVOLUTION?

If competition drives convergence in territorial signals, what is the mechanism by which convergent selection acts? Perhaps the simplest possibility is that ecologically similar species incur fitness costs when their territories coincide, and that individuals with convergent signals are more successful in deterring intrusions or encroachment by heterospecifics, without the need for escalated contests. If this is the case, convergent signals may lead to an increase in energy, food supply, foraging success, and ultimately reproductive success. They may also reduce the costs associated with escalated contests.

The notion that adaptive benefits can drive song convergence between species is made more credible because the same basic mechanism operates within species. It is well established, for example, that the territorial songs of birds confer advantages because they function as a deterrent to intruders: as signal strength increases, the number of direct contests decreases (Krebs et al. 1978; de Kort et al. 2008). Moreover, territorial signals are under selection not only for strength but for stereotypy, because standardization or ritualization increases the reliability of detection, which can be viewed as an advantage to signalers and receivers alike (Cullen 1966; Wiley 1983; Nelson 1989; Johnstone 1997; Bradbury and Vehrencamp 1998). The conclusion that selection acts to increase stereotypy of territorial signals is further supported by studies of aggressive interactions in birds. These show that song matching—i.e., responding with a similar song—is a conventional signal of aggressive intent in territorial contests, both within (Krebs et al. 1980; Burt et al. 2001; Vehrencamp 2001; Vehrencamp et al. 2007) and between species (Gorissen et al. 2006).

We propose that selection for effective, stereotyped territorial signals may operate across species boundaries, and that this may lead to convergence in signal design and/or perception in competing species. The process can be framed in terms of receiver bias (Endler and Basolo 1998): given that a proportion of the *H. peruviana* population is forced to defend territories from encroachment by *H. subflava*, and vice versa, selection for convergent signals may be driven by the exploitation of perceptual biases in heterospecific receivers. In other words, where fitness optimization depends on the exclusion of heterospecific competitors from territories, the most successful strategy may be to exploit heterospecific signaling systems, leading to convergence.

Previous studies suggest that related mechanisms based on interspecific communication are widespread. The use of shared social signals has been shown to be advantageous for species that compete or consort, providing examples of possible signal convergence driven by social selection (e.g., Leary 2001; Windfelder 2001). Similarly, nestling cuckoos (*Cuculus canorus*) produce convergent vocal displays that resemble begging calls of a normal brood of host-species nestlings, thereby exploiting the sensory predisposition of heterospecific individuals (Kilner et al. 1999). In addition, the plumage patterns of *Ramphastos* toucans (Weckstein 2005) and *Picoides* woodpeckers (Weibel and Moore 2005) are

convergent in pairs of competing taxa, although in these cases it is hard to discount the possibility that subordinate species benefit by mimicking dominant or aggressive species (Diamond 1982; Davies and Welbergen 2008).

Evidence for these related processes lends support to our proposed mechanism, but several outstanding questions remain. For example, is convergence in the *Hypocnemis* system restricted to a single lineage, or is it symmetrical? Are shared signals advantageous for one species and costly for the other, or are benefits distributed more equitably between individuals of both species? Can these benefits be demonstrated in terms of fitness? And is convergence in aggressive signaling traits much more common than we think because it is generally masked by divergence in traits associated with foraging niche and mate attraction? The answers are worth pursuing because they have a bearing on the forces shaping phenotypes in all taxa with sympatric competitors.

Conclusions

Numerous studies conclude that signals in genetically isolated populations diverge gradually in allopatry, and more rapidly in sympatry, through processes such as stochasticity, ecological adaptation and social selection (e.g., Seddon 2005; Braune et al. 2008; Filardi and Smith 2008; Irwin et al. 2008; Kirschel et al. 2009). However, our findings provide strong evidence that signal divergence is only one possible outcome, and that it may be delayed or reversed by other factors. In the case of *H. peruviana* and *H. subflava*, we rule out the possibility that signals have converged via ecological selection, which may produce convergent characteristics in bird songs or alarm calls as a result of mimicry (Kelley et al. 2008), acoustic adaptation (Wiley 1991), or predation pressure (Marler 2004). Instead, the *Hypocnemis* system provides the first compelling evidence that signals of competing species may converge via social selection.

Our results suggest not only that interspecific competition can drive adaptive convergence in signals mediating social interaction, but that signal convergence may be offset by divergence in noncompetitive signals, presumably to promote species recognition and reduce the costs of reproductive interference (Marler 1957; Gröning and Hochkirch 2008). These findings imply that traditional signal evolution theory is oversimplified, and that species interactions may cause both divergent and convergent processes to play out across a suite of display traits of different sensory modalities, and in this case even within the same vocal display. This variation between divergent and convergent outcomes may help to explain a range of biological phenomena, such as cases of unexpected phylogenetic conservatism in animal signals (e.g., Littlejohn 1993; Gerhardt and Huber 2002), and widespread disparity in rates of signal evolution (e.g., Price 2008).

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Supporting Information

The following supporting information is available for this article:

Figure S1. Photographs of male antbirds (A–D: *Hypocnemis subflava*; E–H: *Hypocnemis peruviana*) showing variation in plumage coloration within and between species in the zone of sympatry.

Figure S2. Photographs of female antbirds (A–D: *Hypocnemis subflava*; E–H: *Hypocnemis peruviana*) showing variation in plumage coloration within and between species in the zone of sympatry.

Figure S3. Demonstration of parameters measured in acoustic analyses, using an example of male song (*Hypocnemis peruviana*).

Figure S4. Overall structure of male (A) and female (B) signals in sympatry for *Hypocnemis peruviana* (black) and *H. subflava* (gray), presented as mean (±SD) DF1 scores generated for each sex separately (see Table S1 for factor loadings).

Soundfiles S1. All territorial songs of male (SM005–SM008) and female (SM009–SM011) antbirds shown as spectrograms in Figure 2 (i.e. soundfiles 1–7).

Soundfiles S2. All nonterritorial calls of male (SM012–SM015) and female (SM016–SM018) antbirds shown as spectrograms in Figure 3 (i.e. soundfiles 8–14).

Table S1. Factor loadings on principal components for measurements taken from acoustic and visual signals of *Hypocnemis peruviana* and *H. subflava* in sympatry and allopatry.

Table S2. Results of statistical tests investigating differences in overall structure between the songs produced by individuals for which calls were sampled, and those for which no calls were sampled.

Table S3. Full linear mixed model (REML) of aggressive response ($PC1_{aggression}$) to playback by resident *Hypocnemis* antbirds in the contact zone, in which species, song distance, and genetic distance are included as fixed effects, and individual identity as a random effect; statistics are from Wald tests.

Supporting Information may be found in the online version of this article.
(This link will take you to the article abstract).

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