

# Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments

J. A. TOBIAS\*, V. GAMARRA-TOLEDO†‡, D. GARCÍA-OLAECHEA§, P. C. PULGARÍN¶ & N. SEDDON\*

\*Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, UK

†Laboratorio de Biología Evolutiva de Vertebrados, Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá, Colombia

‡Museo de Historia Natural, Universidad de San Agustín, Arequipa, Peru

§Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru

¶Instituto de Biología, Universidad de Antioquia, Medellín, Colombia

## Keywords:

antbirds;  
armament–ornament model;  
duetting;  
female ornaments;  
female song;  
intrasexual competition;  
mutual ornaments;  
signal evolution;  
social selection.

## Abstract

The evolution of sexually monomorphic (i.e. mutual) ornamentation has attracted growing attention as a ‘blind-spot’ in evolutionary biology. The popular consensus is that female ornaments are subject to the same modes of sexual selection as males: intrasexual competition and mate choice. However, it remains unclear how these forces interact within and between sexes, or whether they fully capture selection on female traits. One possibility is that the ‘armament–ornament’ model – which proposes that traits used primarily in male-male contests are also co-opted by females as indicators of male quality – can be extended to explain signal evolution in both sexes. We examine this idea by testing the function of acoustic signals in two species of duetting antbirds. Behavioural observations and playback experiments suggest that male and female songs function primarily as armaments in competitive interactions. Removal experiments reveal that song is also a classic ornament used by unpaired males and females to advertise for mates. These results indicate that ‘armament–ornament’ processes may operate in reciprocal format, potentially explaining widespread mutual ornamentation in species with elevated intrasexual competition for resources. In addition, given that songs mediate competition between species outside the breeding season, our findings suggest that processes shaping monomorphic ornaments extend beyond the traditional definitions of sexual selection and are best understood in the broader framework of social selection.

## Introduction

The observation that male animals are typically more conspicuously armed or elaborately ornamented than females inspired Darwin’s (1871) theory of sexual selection. He proposed that costly weapons and ornaments were the result of competition amongst males for access to mates and mating opportunities, a view subsequently supported by studies in a wide array of taxa (Andersson,

1994). Nonetheless, many organisms appear to contradict the traditional narrative because their ornaments are mutual – i.e. expressed in both sexes – and this has brought two questions to the forefront of evolutionary biology: how does mutual ornamentation evolve, and does it challenge general assumptions about mechanisms of selection in both sexes (Kraaijeveld *et al.*, 2007; Clutton-Brock, 2009, 2010; Rubenstein & Lovette, 2009)?

It seems possible that a fundamental rethink is necessary if mutual ornamentation and weaponry are unlikely to be explained by sexual selection theory alone. But what are the alternatives? The most widely acknowledged argument is that costly traits in both sexes, and

Correspondence: Joseph A. Tobias, Department of Zoology, Edward Grey Institute, University of Oxford, Oxford OX1 3PS, UK.  
Tel.: +44 1865 271244; fax: +44 1865 271168;  
e-mail: joseph.tobias@zoo.ox.ac.uk

particularly in females, often appear to be under selection via competition for ecological resources (West-Eberhard, 1983; LeBas, 2006; Kraaijeveld *et al.*, 2007). For example, it has long been noted that plumage signals in female birds are used in female–female competition over food and territories (Beletsky, 1983; Bleiweiss, 1985) and often predict female dominance in these interactions (Johnson, 1988; Senar, 2006; Pryke, 2007; Murphy *et al.*, 2009). Similarly, female song functions in territorial competition (Fedy & Stutchbury, 2005; Vondrasek, 2006; Geberzhan *et al.*, 2009), even in species where females only defend solitary nonbreeding territories (Tobias, 1997a). These observations suggest that the selective advantage of costly traits is mediated at least partly by competition for nonsexual resources, in which case the processes shaping the evolution of costly traits extend beyond sexual selection. This point was originally raised by West-Eberhard (1979, 1983), who concluded that a more inclusive framework was required to capture the full spectrum of competitive interactions underlying costly traits in males and females. The framework she proposed was social selection, a catch-all term encompassing all competitive interactions between individuals (with sexual selection being limited to the subset of competitive interactions targeting sexual resources).

Although the concept of social selection represented a paradigm shift, it has not been widely adopted, perhaps because of a long-standing research bias towards systems with strong sexual selection (Kraaijeveld *et al.*, 2007). Instead, the dominant view remains that costly traits in both males and females can be fully explained by the two primary modes of sexual selection (Clutton-Brock, 2007, 2009). On the one hand, mutual ornamentation may arise because both sexes are forced to compete for mates and mating opportunities in a variety of systems, particularly in polygynous or group-living species (Trail, 1990; Amundsen, 2000; Clutton-Brock *et al.*, 2006; Clutton-Brock, 2009; Rubenstein & Lovette, 2009). On the other hand, mutual mate choice may generate sexually monomorphic ornamentation if both sexes are choosy (Huxley, 1914). This process has been the focus of much recent research and is broadly supported by empirical (e.g. Jones & Hunter, 1993; Velando *et al.*, 2001) and theoretical studies (e.g. Kokko & Johnstone, 2002; Hooper & Miller, 2008). Although it seems likely that both these modes of selection may act as drivers in the evolution of sexually monomorphic ornamentation, very little is known about whether and how they interact to produce mutual ornaments.

Three main routes seem plausible. First, intrasexual and intersexual selection may operate in contrasting ways (Moore, 1990; Moore & Moore, 1999). This often leads to partitioning of intrasexual and intersexual functions into different signals, as occurs in some male-ornamented systems (Staicer, 1989; Spector, 1992; Byers, 1995; Grether, 1996). Second, if selection operates differently in males and females, then signal function

may be partitioned unevenly, with traits having different functions in either sex (Clutton-Brock, 2009). A third possibility is that mutual ornaments are functionally symmetrical, with intrasexual and intersexual roles operating in tandem regardless of sex.

The idea that the two modes of sexual selection work together to explain the exaggeration of dual-function male traits is known as the ‘armament–ornament’ model (Berglund *et al.*, 1996). This hypothesis unites intrasexual competition and mate choice into a single conceptual framework, based on the logic that male contests over resources will maintain the cost and therefore honesty of male armaments, which in turn are preferred by females as indicators of male quality (Kodric-Brown & Brown, 1984; Borgia & Coleman, 2000). Although difficult to test directly, it is supported by numerous studies showing that male–male competition and female choice act in concert to shape the evolution of male ornaments, with males generally assumed to be competing for sexual resources (e.g. Jones & Hunter, 1999; Benson & Basolo, 2006; McGhee *et al.*, 2007). Theoretically, a similar combination of processes could drive mutual ornamentation if competition is elevated in both sexes (Griggio *et al.*, 2010). Moreover, such competition may partly target nonsexual resources, in which case the armament–ornament model may need to be rephrased in terms of social selection.

A few studies have considered these possibilities. One controlled for body size but found no evidence that female ornaments in crested auklets (*Aethia cristatella*) predicted the outcome of female–female contests (Jones & Hunter, 1999; see also Al-khairulla *et al.*, 2003 for a similar example in insects). Another showed that ornament expression in female black swans (*Cygnus atratus*) was correlated with winning contests, but could not discount the possibility that contests were settled by other correlates of female signals, such as age or body size (Kraaijeveld *et al.*, 2004). A third study controlling for the effect of body size showed that large yellow chest patches in female rock sparrows (*Petronia petronia*) are not only preferred by males but influence access to food supplies, suggesting that costly traits have dual function in both sexes (Griggio *et al.*, 2010). However, as the focal trait in all cases was a permanent visual ornament, it is possible that receivers adjusted their behaviour during intrasexual contests based on information contained in a primarily intersexual signal. A separate issue is that most experiments were conducted in the breeding season, making it difficult to argue that contested resources were nonsexual. In other words, such cases provide only weak support for the role of armament–ornament mechanisms or social selection in mutually ornamented systems.

Previous studies have mainly focused on temperate species, reflecting a broader research bias towards avian systems with relatively high levels of polygamy, short reproductive seasons and superabundant food resources.

This means that research may over-emphasize mate choice and attraction, and under-emphasize resource competition and defence, particularly in female birds (Morton, 1996; Stutchbury & Morton, 2001). One way of addressing this issue is to focus on tropical passerines. Given that these include many poorly known socially monogamous species with long-term pair-bonds and intrasexual competition for scarce ecological resources, they offer a contrasting perspective on the evolution and function of mutual ornaments (Kraaijeveld *et al.*, 2007).

In this study, we investigated the interplay between intersexual and intrasexual selection in a classic socially monogamous system, the Neotropical antbirds. Most members of this diverse family defend all-purpose territories year-round (Hau *et al.*, 2004; Stutchbury *et al.*, 2005), with both sexes contributing more or less equally to territory defence and parental care (Greenberg & Gradwohl, 1983, 1986; Zimmer & Isler, 2003; Stutchbury *et al.*, 2005). Furthermore, rates of extra-pair copulation are low, and monogamous partnerships prolonged, such that males are rarely forced to advertise for mates (Morton, 1996; Morton *et al.*, 2000). Despite the lack of overt sexual competition, male and female antbirds often share mutual ornaments in the form of vocal or visual signals (see Tobias, 2009; Tobias & Seddon, 2009a; Seddon *et al.*, 2010).

Given that visual signals perform poorly over long distances in dense rainforest vegetation, all long-distance signalling by species inhabiting such environments is likely to be mediated by acoustic traits. We therefore focused on vocalizations in two understory species – *Hypocnemis peruviana* and *H. subflava* – in their region of sympatry in western Amazonia. The advantage of this two-species system is that it provides a novel opportunity to consider the role of signals in competitive interactions between species, which are likely to be motivated by competition for ecological resources rather than competition for mates (Payne & Groschupf, 1984; Doutrelant *et al.*, 2000; Grether *et al.*, 2009). In addition, the *Hypocnemis* system is potentially informative because it is characterized by convergent songs and divergent calls (Tobias & Seddon, 2009b; see Materials and Methods for definitions). This is a counter-intuitive pattern of trait divergence, suggesting that calls may have important functions in mate attraction and courtship because mating signals are costly to misidentify and therefore theoretically more unambiguously species-specific than signals of aggression or dominance (Bradbury & Vehrencamp, 1998). Songs and calls therefore provide a means of assessing a key question: the partitioning of intersexual and intrasexual functions between signals.

Antbirds are also suited to this investigation because their songs appear to function primarily, if not entirely, as armaments. Previous studies clarify that intrasexual competition in both sexes is mediated by vocalizations, both within and between species (Seddon & Tobias, 2006; Tobias & Seddon, 2009b,c). Indeed, several previous authors have concluded that songs of male antbirds

function solely as intrasexual armaments on the grounds that paired individuals use them daily (Willis, 1967; Bard *et al.*, 2002), and unpaired individuals switch to a different vocalization to attract mates (Morton, 1996; Morton *et al.*, 2000). The idea that antbirds therefore use song in a different way to other birds has led to the term ‘loudsong’ being coined (Willis, 1967) and widely adopted (e.g. Zimmer & Isler, 2003; Isler *et al.*, 2007; Seddon & Tobias, 2007) to highlight the perceived uniqueness of songs in all members of the family.

This view of antbird songs as armaments but not ornaments contrasts with the prevailing concept of birdsong as a multipurpose signal used in intrasexual aggression and mate attraction (Collins, 2004; Catchpole & Slater, 2008). It is worth clarifying that this dual role is typically associated with male songs, which are thus often referred to as both armaments and ornaments (e.g. Berglund *et al.*, 1996; Leitão & Riebel, 2003; Hasselquist & Bensch, 2008; Logue & Forstmeier, 2008; Hoeschele *et al.*, 2010). Conversely, female songs that have dual function in both intrasexual aggression and mate attraction are reported rarely, if ever. Moreover, we are not aware of any example where the given ornament can be considered either ‘monomorphic’ or ‘mutual’, either because female songs differ fundamentally from male songs (e.g. Dalziell & Cockburn, 2008; Cockburn *et al.*, 2009), or because sex roles are reversed and males do not sing (Geberzahn *et al.*, 2010).

Our goal in this study is to examine whether the sexually monomorphic songs or sexually dimorphic calls of *Hypocnemis* antbirds function as armaments, ornaments or both. In particular, we aim to determine how function is partitioned between different signals, and whether the dynamics of intrasexual competition and mate choice are symmetrical or skewed between the sexes. Do these evolutionary forces operate in tandem? Does intrasexual selection take precedence over intersexual selection as predicted by the ‘armament–ornament’ model (Berglund *et al.*, 1996)? And can intrasexual selection be driven by competition for non-sexual resources? To address these questions, we take advantage of the fact that vocal signals are switched on or off depending on context, allowing us to make inferences about function on the basis of quantifiable signalling regimes or receiver responses.

## Materials and methods

### Study system

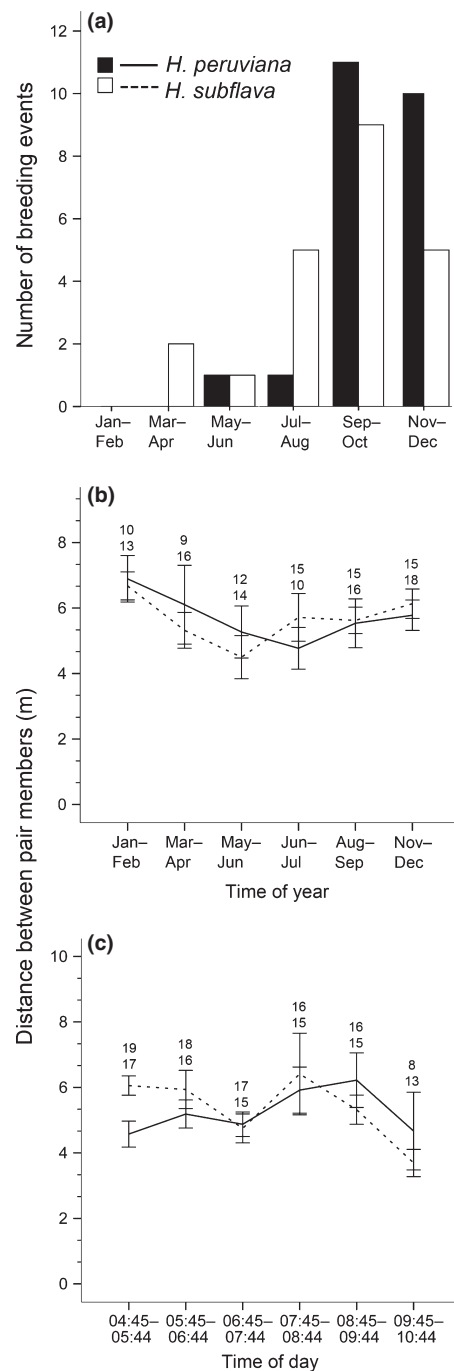
*Hypocnemis* antbirds are small (11–12 cm, 10–14 g) passerine birds of dense understory in the Amazon basin and foothills of the Andes (Zimmer & Isler, 2003). Most taxa in this genus were grouped into a widespread form, *Hypocnemis cantator* (Zimmer & Isler, 2003), which has now been separated into six species on the basis of vocal (Isler *et al.*, 2007) and genetic analyses (Tobias *et al.*,

2008). In 2004–2009, we studied 19 pairs of *H. peruviana* and 20 pairs of *H. subflava* at the Centro de Investigación y Conservación de Río Los Amigos (CICRA; 12°34′07″S, 70°05′57″W), Madre de Dios, Peru. These species are partially segregated into two habitats – *H. peruviana* mainly in *terra firme* forest; *H. subflava* mainly in *Guadua* bamboo – which occur in a complex mosaic at this locality (Tobias *et al.*, 2010). At least one member of all study pairs was tape-lured into a 12 × 4 m mist-net and marked with a unique combination of coloured polyvinyl chloride rings. Depending on context, all individuals were lured using a recording of their own song, their mate’s song, or the song of a same-sex individual from a different pair.

Pairs of both species maintained stable year-round territories for long periods. Of 33 individuals colour-banded in 2006, 11/17 (64.5%) *H. peruviana* and 14/16 (87.5%) *H. subflava* remained on the same territory 3 years later. Moreover, two males (one of each species) from a small sample of individuals ringed in a pilot study in 2004 were still defending the same territory after 5 years. Maximum duration of territory ownership is presumably longer. For 31 pairs in which both pair members were ringed for at least some of the study period (2006–2009), we observed seven definite pairing events (i.e. replacement of one individual by a new pair member). Pair-bonds were relatively prolonged: one pair from 2004 was still together 5 years later, and most pairs remained intact at the end of the study period. Breeding activity in both *H. peruviana* and *H. subflava* was concentrated in the second half of the year, with a peak in September–November (Fig. 1a).

### Potential ornaments

All *Hypocnemis* antbirds use two distinct vocalizations: a simple 2–3 note signal with unknown function, and a relatively complex multinote signal given either as solos or male-led duets (for full descriptions and spectrograms, see Isler *et al.*, 2007; Tobias & Seddon, 2009c). We refer to these vocalizations as ‘calls’ and ‘songs’, respectively. Detailed acoustic analyses have shown that the repertoire of all individuals consists of a single song type (Seddon & Tobias, 2010), and that males and females have similar but identifiably sex-specific songs, with those in males being slightly longer than those in females (Tobias & Seddon, 2009b,c). The greater elaboration of male ornaments fits the general pattern found in species with female ornamentation (Møller, 1993; Regosin & Pruett-Jones, 2001; Veit & Jones, 2003). We follow numerous studies (e.g. Velando *et al.*, 2001; Kraaijeveld *et al.*, 2004; Viera *et al.*, 2008) in treating nonidentical but phenotypically similar ornaments expressed in both sexes as ‘sexually monomorphic’. Note that monomorphism refers to phenotypic expression rather than frequency of use, as is the norm in most studies of ornaments.



**Fig. 1** Breeding events (a) per two-month period for *Hypocnemis peruviana* and *H. subflava*; (b) and (c) show mean ( $\pm$ SE) distance (in metres) between male and female pair members. In (b), male–female distance is averaged by month across pairs and years; in (c), male–female distance is averaged by 1-h observation periods across pairs and years. Data derive from a total of 457-h observation of 19 pairs of *H. peruviana* and 546 h of 20 pairs of *H. subflava* conducted during focal watches at CICRA in 2006–2008. Sample sizes (i.e. number of study pairs) are given above error bars (upper number: *H. peruviana*; lower number: *H. subflava*).

## Assumptions and predictions

The hypotheses considered here are closely intertwined with partially overlapping predictions (see Table 1 for a summary). It is important to note that evidence for Hypothesis 1 is not evidence against social selection, because social selection encompasses all hypotheses. However, evidence for Hypothesis 3 suggests that not all selection exerted on song qualifies as sexual selection. Given that antbird songs and calls potentially play a role in a range of interactions, and because these interactions vary in the strength of evidence they provide for sexual versus nonsexual competition, we used a combination of approaches to build a complete picture of signal function.

First, we focused on seasonal patterns of vocalization. Following previous studies of song in temperate (Merilä & Sorjonen, 1994; Tobias & Seddon, 2000; Dalziell & Cockburn, 2008; Cockburn *et al.*, 2009) and tropical birds (Staicer, 1996; Stutchbury & Morton, 2001; Moore *et al.*, 2004), we assumed that increased rates of signalling in the breeding season reflect sexual competition. This is a common finding because song rates are often associated with greater motivation to defend breeding territories or fertile partners, and advertisement for mates and extra-pair copulations (EPC). Conversely, we assumed that consistent vocalization inside and outside the breeding season is evidence of territory defence or intrapair communication (Stutchbury *et al.*, 2005).

Next, we assessed diel patterns. Previous studies suggest that dawn signalling in paired birds is mainly associated with territory defence (Staicer, 1996; Amrhein *et al.*, 2004; Liu & Nottebohm, 2005; Amrhein &

Erne, 2006; Liu & Kroodsmas, 2007; Foote *et al.*, 2008), but an alternative hypothesis is that dawn singing serves to defend fertile females or attract mates and EPCs. These strategies have been reported in systems with either year-round (Staicer, 1996; Dalziell & Cockburn, 2008) or breeding territoriality (Mace, 1987; Kunc *et al.*, 2005). They are associated with distinctive behaviours, such as solitary singing, elevated polygyny, low proximity between pair members, and frequent territorial incursions and excursions at dawn. We use behavioural observations to assess whether these traits apply to *Hypocnemis* antbirds. We then test a prediction based on the generality that dawn advertising for mates and EPCs is typically absent or reduced in the nonbreeding season, even in species with year-round territoriality (Staicer, 1996; Dalziell & Cockburn, 2008; Cockburn *et al.*, 2009). We assume that a consistent dawn peak in singing throughout breeding and nonbreeding seasons indicates that songs function primarily as territorial armaments. This does not rule out advertising for mates or EPCs, but we would expect to see a pulse of singing during the breeding season if advertising represented the major role.

Another line of evidence relates to neighbourhood effects. An increased rate of signalling in densely populated neighbourhoods during the breeding season is suggestive of territoriality, but does not rule out advertisement for EPCs. A positive association between signalling rate and neighbourhood density in the nonbreeding season provides stronger evidence that signals function in competition with neighbours for space and food resources (Stutchbury & Morton, 2001; Catchpole & Slater, 2008). Overall, if a given acoustic signal functions at least partly in intrasexual competition for ecological resources, we predict that the following patterns will persist through the nonbreeding season in both sexes: (i) high and consistent rates of signalling; (ii) dawn peaks in signalling; and (iii) positive effects of neighbourhood density on signalling rates.

Finally, we conducted a series of experiments to test our hypotheses. We first used playback experiments to compare the responses of territorial individuals to songs and calls of both species. When interpreting the results, we assumed that territorial signals elicit stronger aggressive responses than nonterritorial signals and that mating signals are likely to elicit stronger responses than signals without sexual functions. We then conducted mate-removal experiments to examine the extent to which individuals of both sexes continued to defend solo territories in the absence of mates. Although we do not quantify mate choice preferences, this approach allowed us to test which signals function in mate attraction and courtship. We follow numerous authors (e.g. Krebs *et al.*, 1981; McElroy & Ritchison, 1996; Staicer *et al.*, 2006) in assuming that songs given at higher rates in the absence of mates are sexually selected advertising signals.

**Table 1** Summary of predictions regarding functional significance of vocalizations, indicating whether they support Hypothesis 1 (song functions as an ornament used in mate attraction), Hypothesis 2 (song mediates intrasexual competition for sexual resources) or Hypothesis 3 (song mediates competition for nonsexual resources). Note that these hypotheses are not mutually exclusive. We classify predictions according to the strength of support they provide, based on whether they are unambiguous (bold), or leave some room for ambiguity (not bold).

Evidence (same for both sexes)	Hypotheses supported
No association between vocalization and breeding season	3
Consistent dawn peak in vocalization during breeding and nonbreeding season	<b>2,3</b>
Positive association between vocalization and neighbourhood density in breeding and nonbreeding season	<b>2,3</b>
Elicits aggressive responses from conspecifics	2,3
Elicits aggressive responses from heterospecifics	<b>3</b>
Output increases in absence of female	<b>1</b>
Used during courtship displays	<b>1</b>

### Behavioural observations

To quantify seasonal and diel variation in the use of vocalizations, 1–2 observers followed study pairs from dawn (~04:45 h, with minor seasonal variation) to ~11:00 h. In total, we spent 1673 h on pair territories (mean  $\pm$  SD = 43  $\pm$  25 h per territory), with direct contact (i.e. pairs in view or within earshot) for 457 h in *H. peruviana* (mean  $\pm$  SD = 24  $\pm$  18 h per pair), and 546 h in *H. subflava* (27  $\pm$  15 h per pair). Throughout the observation period, we recorded the number of songs given by each pair member during 10-min observation periods (hereafter 'blocks'), usually starting with the first vocalization of the day. Unlike songs, calls do not appear to be sex-specific (Isler *et al.*, 2007; Tobias & Seddon, 2009b), and thus an overall rate of calling was calculated per pair.

Vocalizations in some species are used to maintain contact between separated pair members or to advertise for EPCs, so we also assessed distances between individuals and rates of territorial incursion and excursion. We noted the distance between pair members at 10-min intervals during all focal watches. We also opened 2–4 mist-nets (12 m each) on study territories before dawn on 1–4 mornings per territory to assess rates of territorial incursion by neighbours and floating individuals; nets were closed at the end of focal watches. To assess the reproductive seasonality, we recorded all evidence of breeding events, including nest-building, chick provisioning or the presence of young (< 1 month old) juveniles.

### Influence of neighbours

To assess whether vocalizations were targeted at partners or neighbours, we investigated the relationship between singing and calling rate and the number of adjoining territories. This required a detailed investigation of the position of territory borders, so we noted coordinates of colour-banded pairs every 10 mins during focal watches (using a Garmin GPS 60csx, accurate to  $\pm$  5 m). We then drew minimum convex polygons (MCP; Southwood, 1966) around these points using ARCVIEW 3.3 (ESRI, 1999). These data confirmed that socially monogamous pairs defend small (1–5 ha) territories year-round (J. A. Tobias, unpublished data). They also revealed that *H. peruviana* lived at lower local population densities than *H. subflava*. In *H. peruviana*, all study pairs were bordered by at least one neighbouring pair, with eight study pairs having one, nine having two, and three having three neighbouring pairs; in *H. subflava*, only one study pair was bordered by a single neighbouring pair, seven had two, eight had three, and four had four neighbouring pairs. Note that because *H. peruviana* and *H. subflava* are interspecifically territorial, we quantified the number of adjoining territories occupied by *Hypocnemis* antbirds of either species. This is the only valid approach given that males and females of both species

treat same-sex conspecifics and heterospecifics virtually interchangeably (Tobias & Seddon, 2009b). Data were then partitioned into breeding (July–December) and nonbreeding (January–June) seasons to assess whether neighbourhood effects depended on seasonal context.

### Playback experiments

Previous work demonstrated that song is used in aggressive interactions between *H. peruviana* and *H. subflava* (Tobias & Seddon, 2009b), yet did not confirm that song is the primary competitive signal in these species, nor whether social and sexual functions are partitioned between songs and calls. We therefore conducted experiments to test the function of species-specific calls in interactions within and between species. We used a Sennheiser ME67-K3U directional microphone and a Sound Devices 722 portable digital recorder to compile a library of calls from our study populations (individuals identified to sex). Recordings were made onto compact flash cards as 24 bit wav mono files at a sampling frequency of 44.1 kHz. Playback audio files were prepared using AVISOFT SASLABPRO Version 4.15 (R. Specht, Berlin, Germany) to filter out low- and high-frequency background noise (FIR bandpass filter set at 1–8 kHz) and to create PCM wav files consisting of calls repeated at eight repetitions per minute (i.e. same rate as song playbacks; Tobias & Seddon, 2009b).

We played conspecific and heterospecific same-sex calls to territorial individuals. To avoid pseudoreplication, each experiment involved a unique call recorded from a different individual. Experiments took place at 06:00–09:00 h, in September–December 2006 and 2007. We used a paired experimental design to assess the relative response of receivers to calls and songs; pairs of treatments were separated by 30 min and given from the same location close to the centre of territories. Treatment order was randomized. In each experiment, we selected stimulus files recorded from non-neighbours, to minimize the influence of neighbour-stranger recognition. Pairs on adjacent territories were not tested on the same day to ensure independence. Further details of methods can be found in Tobias & Seddon (2009b).

During each 10-min trial, we noted three simple behavioural responses that provide robust assays of aggression (Seddon & Tobias, 2007): (i) closest distance to loudspeaker (to nearest m), (ii) time spent < 5 m from loudspeaker (to nearest 10 s), and (iii) number of songs during first 5 mins from the start of the first song given after playback. Note that both species are sexually dimorphic in plumage (compare males Fig. S1 and females Fig. S2 in Tobias & Seddon, 2009b), which facilitates discrimination between the sexes during observations. As playback response variables were correlated, we used principal components analysis (PCA) to reduce our dataset to a single principal component, (PC1<sub>aggression</sub>), which reflected overall response strength.

We conducted the PCA on the correlation matrix of individual means, and we used varimax rotation with Kaiser normalization to extract PC scores.

### Removal experiments

We conducted removal experiments in September–December 2007, September–December 2008, and July–August 2009. During these periods, we temporarily removed 14 resident males (ten *H. subflava* and four *H. peruviana*) and 20 resident females (ten of each species) from their territories. We detected no naturally occurring unpaired females in the study populations, but unpaired males were regularly encountered in small numbers; in all experimental territories, the nearest conspecific unpaired male was situated less than 1 km away. Birds were captured at 05:00–08:00 h in mist-nets, transported in cotton bags to holding cages (60 × 40 × 40 cm), and kept in a room with ambient light and temperature; food and water were provided *ad libitum*. Individuals were released back onto their territories after 08:30 h the following day.

To assess the influence of removals on signalling behaviour, we calculated rates of singing and calling by residents during two focal watches: one during the week prior to removal (when paired), and another on the day after removal (when unpaired). We waited until the day after removal to reduce the chance that individuals were merely trying to locate their own mate; under natural conditions, pair members are rarely separate for longer than 30 min. In the two periods of observation, rates of vocalizing (i.e. mean number of songs or calls per 10-min block) were calculated from dawn until ~08:30 h or the point at which removed birds were released back on their territories. We excluded four male removals from analysis because the resident female could not be located on the first day after the removal (two *H. peruviana* and one *H. subflava* pairs), or new males were present on territory (one *H. subflava* pair). Similarly, we excluded four female removals because new females were already present (two *H. peruviana* and two *H. subflava* pairs).

### Acoustic analysis of mating signals

To determine whether males use a different song type in the context of mate attraction, we compared the acoustic structure of male songs given with and without the resident female. With equipment, software and settings described earlier, we recorded at least six songs from the focal watch prior to and during the removal experiment. Using the techniques described in detail elsewhere (Seddon & Tobias, 2006), we generated broadband spectrograms (bandwidth = 323 Hz, FFT = 1024) from sound files and measured eight standard temporal and spectral parameters: song duration, total number of notes, number of terminal raspy notes, note pace, maximum frequency, minimum frequency, peak fre-

quency and bandwidth. We then calculated mean values for each of these parameters per male before and after female removal. We were not able to conduct the same test on females because solo female song was given less often, making it difficult to record.

### Statistical analyses

Vocalization rates were quantified as number of songs or calls per 10-min block and averaged across all focal watches, months and years. To compare the rates of singing, we calculated a mean overall rate for each pair-member; to compare rates of calling with rates of singing, we calculated a mean overall rate of calling for each study pair. Paired *t*-tests were used to compare male vs. female song rates and song versus call rates (sexes pooled). To assess seasonality in rates of singing and calling, we calculated a mean song rate per pair-member and a mean call rate per pair, averaged first within focal watches, and then by month. We then modelled the effect of season on vocal behaviour using General Linear Mixed Models (GLMM) in which we included male song rate, female song rate or pair call rate as the dependent variable, month as the fixed effect and identity of the study pair as a random effect. To assess the effect of time of day on singing and calling rates, we calculated a mean rate of singing for each pair member, and a mean rate of calling for each pair, for each of six 1-h observation periods, the first starting at dawn (04:45 h), averaged across all months and years. We then compared between 1-h periods using a Friedman test (as data could not be transformed for parametric analyses).

We modelled the strength of territorial aggression in response to playback using a GLMM approach with restricted maximum-likelihood estimation. GLMMs were run for each sex separately;  $PC1_{aggression}$  was included as the dependent variable, playback treatment (song or call), vocal type (conspecific or heterospecific) and species (*H. peruviana* or *H. subflava*) as the fixed effects, and identity of residents as the random effect.

All statistical analyses were conducted using JMP (version 7.0, SAS Institute Inc., Cary, NC, USA, 2007). Prior to parametric analyses, all variables were log-transformed to meet the assumptions of normality and homogeneity of variance. Means are reported  $\pm$  SD, unless stated otherwise. Nonparametric tests were used when the distribution of variables did not meet parametric assumptions. *P*-values are two-tailed and corrected for ties where appropriate; where  $n < 15$ , exact *P*-values are used, otherwise asymptotic *P*-values are given.

## Results

### Behavioural observations

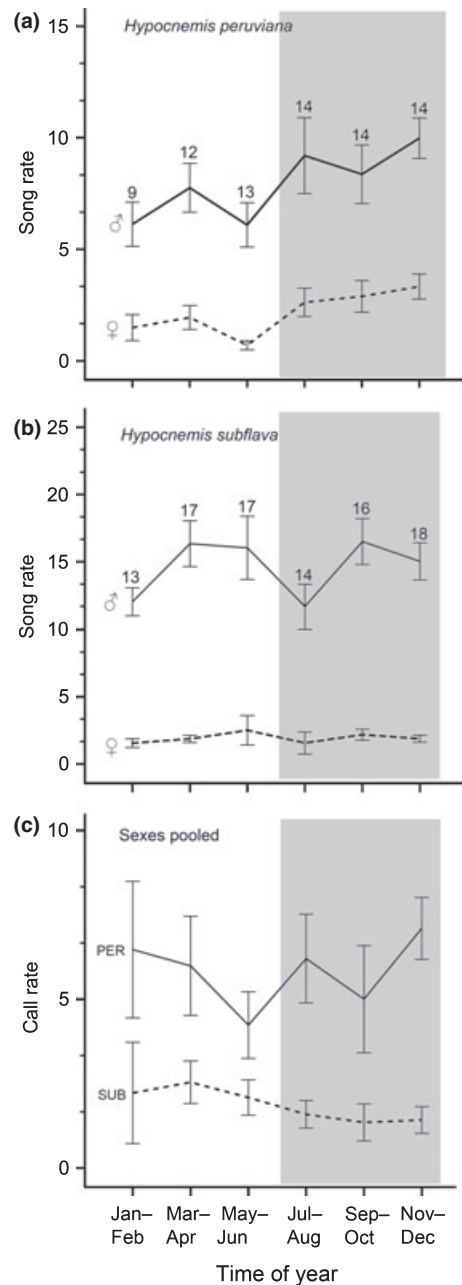
Before considering hypotheses about signal function using seasonal or diel variation, it is important to outline

associated behaviours. In both species, pair members typically foraged and sang in close proximity: there was no difference between intrapair distance in *H. peruviana* ( $5.3 \pm 1.9$  m; range: 2–10 m) and *H. subflava* ( $5.7 \pm 1.8$  m; range: 2–12 m; unpaired *t*-test:  $t = -0.530$ , d.f. = 35,  $P = 0.600$ ). Breaking this down by season (Fig. 1b), we found no significant difference in intrapair distance between the breeding and nonbreeding season for either species (paired *t*-test; *H. peruviana*:  $t = -1.915$ , d.f. = 16,  $P = 0.074$ ; *H. subflava*:  $t = 1.494$ , d.f. = 17,  $P = 0.154$ ). Similarly, when looking at diel patterns (Fig. 1c), we found no significant difference in intrapair distance between early morning (04:45–07:44 h) and late morning (07:45–10:45 h) observation periods (*H. peruviana*:  $t = -1.194$ , d.f. = 18,  $P = 0.248$ ; *H. subflava*:  $t = 0.414$ , d.f. = 19,  $P = 0.684$ ).

The implication that territorial incursions and excursions are either rare or absent in *Hypocnemis* is corroborated by two other observations. First, during hundreds of hours of continuous focal watches or casual observations, we never encountered individuals outside their usual territory or observed individuals departing from or returning to their territory. Second, in 69 mornings of standardized mist-netting on pair territories, one or both pair members were captured on 12 occasions, unringed males on three occasions, and yet no ringed individual was ever detected outside its known territory. We are confident that the unringed males were nonterritorial floaters as all territorial males in a 3-km radius had been trapped and ringed. In summary, paired *Hypocnemis* antbirds sing nonindependently at dawn, with both individuals remaining on territory, and in close proximity, as found in other antbird species (Greenberg & Gradwohl, 1997; Stutchbury & Morton, 2001: 68). Several of these behavioural traits contrast starkly with the behaviour of species such as superb fairy-wren (*Malurus cyaneus*) that use dawn singing to attract mates and EPCs (Dalziell & Cockburn, 2008; Cockburn *et al.*, 2009).

### Vocal behaviour

Males and females produced songs and calls consistently throughout the year, with higher rates of singing in males than females (Fig. 2). There was no significant seasonality in rates of male or female singing or calling in *H. subflava*, and only weakly significant variation between months in rates of calling and female singing in *H. peruviana*, with a slight increase in rate of singing towards the end of the year (Table 2; Fig. 2). In both species, singing rates remain high in the nonbreeding season and are always higher than calling rates (Fig. 2). It remains possible that pairs breed at different times and thus consistent mean singing rates at the population level conceal fluctuating or seasonal individual singing rates. However, plotting monthly song rates per individual reveals that, despite some fluctuations caused by small



**Fig. 2** Seasonal patterns of singing (2006–2008) by male and female (a) *Hypocnemis peruviana* and (b) *H. subflava*, and (c) patterns of calling (sexes pooled) in *H. peruviana* (solid line) and *H. subflava* (dashed line). Shown are mean ( $\pm$ SE) song/call rates (i.e. number of songs per 10-min block) averaged by month across pairs and years. Sample sizes (i.e. number of study pairs) for (a) and (b) are given above the bars; in (c), sample sizes are the same as in (a) for *H. peruviana* and (b) for *H. subflava*. Grey panel indicates the timing of the breeding season (July–December).

sample sizes, singing rates are essentially consistent year-round for individual males and females in *H. peruviana* (Fig. S1) and *H. subflava* (Fig. S2).



**Table 2** Effect of month on signalling behaviour.

Species	$F^*$	d.f.	$P$
<i>Hypocnemis peruviana</i>			
Call rate	1.98	11,85.7	0.040
Male song rate	1.50	11,84.3	0.146
Female song rate	2.09	11,85.7	0.029
<i>Hypocnemis subflava</i>			
Call rate	0.79	11,104	0.651
Male song rate	1.16	11,100.3	0.324
Female song rate	0.94	11,100.3	0.502

\*GLMM comparing singing and calling rates across month; pair identity entered as a random effect.

We found a strong influence of time of day on rates of singing but only a weak effect on rates of calling (Table 3; Fig. 3). Rates of calling showed no dawn peak (Figs 2 and 3). Instead, *H. subflava* called at a low, constant rate throughout the morning, with a peak at ~09:00 h. In *H. peruviana*, call rates varied more widely and increased through the morning, exceeding rates of singing at ~08:00 h and peaking at ~09:00 h. However, in both species and both sexes, rates of singing peaked at dawn (~05:00 h) and declined rapidly thereafter. This dawn peak persisted throughout the breeding and nonbreeding seasons (Fig. 4). Thus, although attraction of mates and EPCs may be a secondary function of dawn singing in paired antbirds, it is unlikely to be the primary function.

### Effect of neighbours

In both species, we found a significant positive relationship between overall singing rate and number of neighbours (Mann–Whitney  $U$ -test; *H. peruviana*:  $U = 17$ ,  $P = 0.026$ ; *H. subflava*:  $U = 21$ ,  $P = 0.039$ ; Fig. 5). Meanwhile, call rate was negatively related to number of neighbours in *H. peruviana* ( $U = 11$ ,  $P = 0.005$ ; Fig. 5a) and unrelated to number of neighbours in *H. subflava* ( $U = 45$ ,  $P = 0.851$ ; Fig. 5b). Pooling the species (valid given lack of discrimination between conspecifics and heterospecifics: Tobias & Seddon, 2009b), we found a strong overall effect of number of neighbours on vocal behaviour in the breeding season, with song rate increasing (Kruskal–Wallis test:  $\chi^2_3 = 14.9$ ,  $P = 0.002$ ) and call rate decreasing ( $\chi^2_3 = 14.5$ ,  $P = 0.002$ ) as local population density increased (Fig. 5c). The same patterns persisted in the nonbreeding season (January–July; Fig. 5d): there was a significant increase in rate of singing and a significant decrease in rate of calling with increasing number of neighbours (song rate:  $\chi^2_3 = 11.8$ ,  $P = 0.008$ ; call rate:  $\chi^2_3 = 11.2$ ,  $P = 0.010$ ).

### Playback experiments

For the male playback experiments, a PCA conducted on response data produced an aggression score ( $PC1_{aggression}$ )

**Table 3** Effect of time of day on vocal signalling behaviour in *Hypocnemis* antbirds during (A) breeding and (B) nonbreeding season.

Species	$\chi^2_5$	$n$	$P^*$
(A) Breeding season			
<i>Hypocnemis peruviana</i>			
Call rate	11.51	14	0.042
Male song rate	58.12	14	< 0.0001
Female song rate	42.89	14	< 0.0001
<i>H. subflava</i>			
Call rate	8.24	18	0.144
Male song rate	68.9	17	< 0.0001
Female song rate	37.7	17	< 0.0001
(B) nonbreeding season			
<i>H. peruviana</i>			
Call rate	15.8	13	0.007
Male song rate	43.6	11	< 0.0001
Female song rate	19.7	8	0.001
<i>H. subflava</i>			
Call rate	8.2	12	0.146
Male song rate	53.2	15	< 0.0001
Female song rate	17.5	15	0.004

\*Friedman tests comparing rates of calling and singing between six 1-hr time periods (for data see Fig. 2). Use of matched tests reduced overall sample sizes.

that accounted for 61.7% of variation in response strength (Eigenvalue = 1.85) and was negatively correlated with closest distance (−0.920) and positively correlated with time spent < 5 m from the loudspeaker (0.930) and number of songs given after playback (0.372). For female playbacks,  $PC1_{aggression}$  accounted for 73.8% of variation in response strength (Eigenvalue = 2.21) and is negatively correlated with closest distance (−0.873) and positively correlated with time spent < 5 m from the loudspeaker (0.941) and number of songs given after playback (0.752). In both sets of experiments, therefore, high positive  $PC1$  scores indicated an aggressive response.

Sexes differed in the degree to which they discriminated between conspecific and heterospecific same-sex calls (Fig. 6). Males responded more strongly to conspecific than heterospecific calls in *H. peruviana* (Wilcoxon signed-rank test:  $z = -2.27$ ,  $P = 0.023$ ; Fig. 6b) and *H. subflava* ( $z = -2.27$ ,  $P = 0.023$ ; Fig. 6d). However, there was no difference in female responses to conspecific and heterospecific calls in *H. peruviana* ( $z = -1.68$ ,  $P = 0.093$ ; Fig. 6a) or *H. subflava* ( $z = -0.05$ ,  $P = 0.959$ ; Fig. 6c). This apparent lack of call discrimination in females reflected weak responses to calls of either type. Regardless of these minor sex differences in responses to calls, we found that male and female territory owners always responded aggressively to playback of same-sex songs (positive  $PC1_{aggression}$  values) and nonaggressively to playback of same-sex calls (negative  $PC1_{aggression}$  values; Fig. 6). We also found that the type of signal

**Table 4** Effect of playback on territorial aggression.

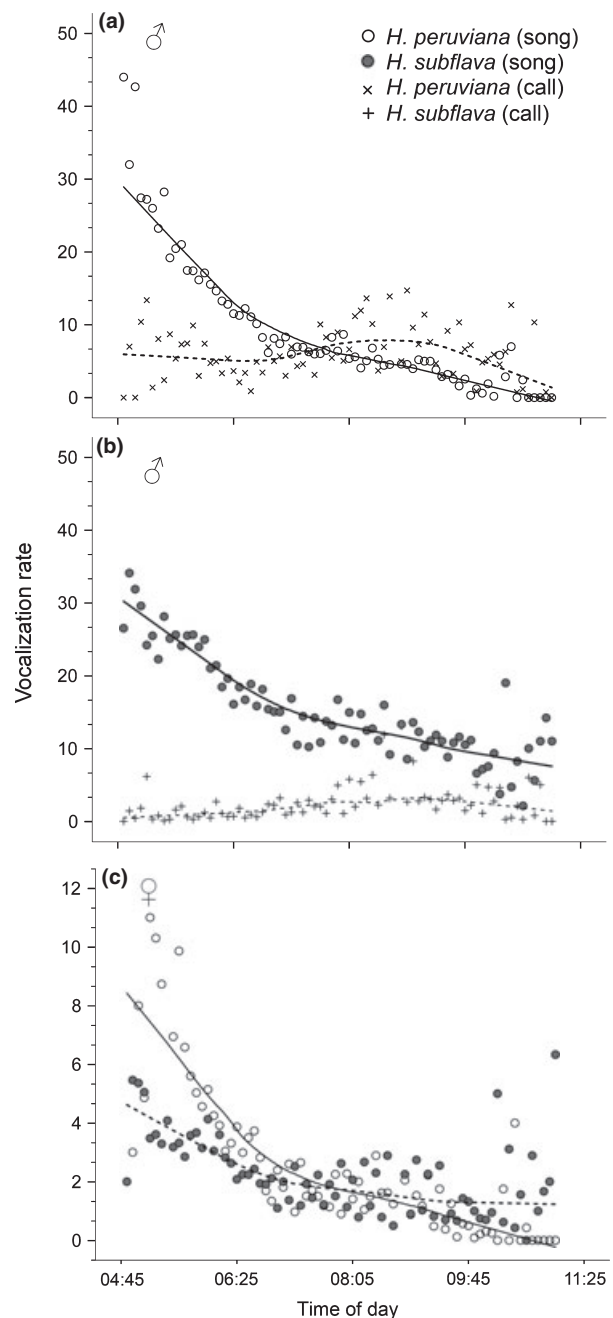
Sex	Main effect	$F^*$	d.f.	$P$
Male	Treatment [song or call]	66.77	1,127.5	< 0.0001
	Vocal type [conspecific or heterospecific]	12.96	1,81.82	0.0005
	Species [ <i>Hypocnemis peruviana</i> or <i>H. subflava</i> ]	1.35	1,42.3	0.252
Female	Treatment [song or call]	215.64	1,119.6	< 0.0001
	Vocal type [conspecific or heterospecific]	9.504	1,72.13	0.003
	Species [ <i>H. peruviana</i> or <i>H. subflava</i> ]	0.429	1,40.52	0.516

\*GLMM testing effect of playback treatment on aggression by resident male and female antbirds; pair identity entered as a random effect. Note that the order in which a treatment was played did not affect  $PC1_{aggression}$  scores (GLMM:  $0.110 < P < 0.663$ ) and so this factor was not included.

(song or call) was a much better predictor of aggression than the species giving the vocalization; this result held true for both sexes and both species (Table 4). Put another way, song retains its importance as a signal of aggression in heterospecific interactions, whereas calls do not: residents were more likely to approach within 5 m of the playback speaker in response to heterospecific songs (64/75 experiments) than heterospecific calls (13/56 experiments; chi-square test:  $\chi^2_1 = 48.5$ ,  $P < 0.0001$ ).

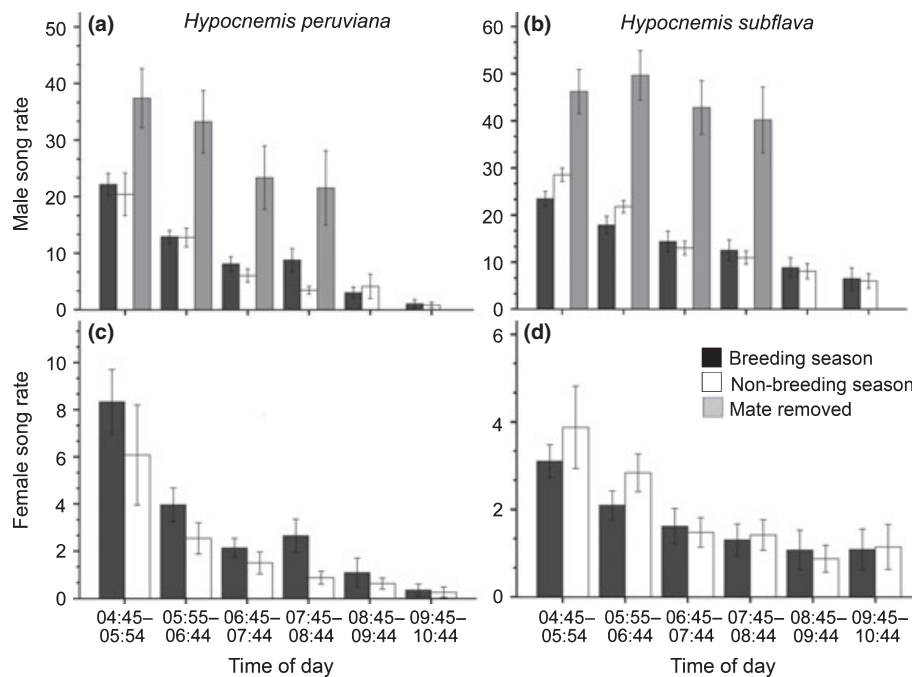
### Removal experiments

After their mates were temporarily removed, resident males of both species continued to defend territories and increased their rate of singing (Wilcoxon signed-rank tests; both species:  $W = 36$ ,  $P = 0.008$ ,  $n = 8$ ; Fig. 7a). Indeed, the rate of male singing after female removal was higher than the combined rate of male and female singing prior to the experiment (*H. peruviana*:  $W = 16$ ,  $P = 0.0234$ ; *H. subflava*:  $W = 18$ ,  $P = 0.0078$ ; Fig. 7a). As this surpasses the amount needed to compensate for the absence of female territorial songs, we assume that continuous singing by solo males does not have a solely territorial function. The alternative possibility that males are singing at high rates to regain contact with their mate can be discounted because behavioural responses were only quantified after a ~24 h period. Once their mates had been removed, solitary males generally spent a few hours producing calls at high rates, whereas song rates only increased dramatically up to a day later. Naturally bereaved males continued to sing at high rates – sometimes for months – until new females settled on the territory. Contrastingly, after 24 h had elapsed, there was no significant effect of female removal on rates of male calling in either species (*H. peruviana*:  $W = 32$ ,  $P = 0.055$ ,  $n = 8$ ; *H. subflava*:  $W = 17$ ,  $P = 0.250$ ,  $n = 8$ ; Fig. 7b). Calls therefore appear to function



**Fig. 3** Diurnal variation in singing and calling rates of *Hypocnemis* antbirds. Data are mean vocalization rates (i.e. number of songs or calls per 10-min block) averaged across pairs and years (2006–2008). In (a) and (b), rates of male singing (solid line) and male and female calling (dashed line) are compared for *H. peruviana* and *H. subflava*, respectively. In (c), rates of female singing are compared between *H. peruviana* (solid line) and *H. subflava* (dashed line). Linear splines estimated with the Epanechnikov kernel function.

in contact between established pair members and songs are the primary advertising signal for attracting mates.



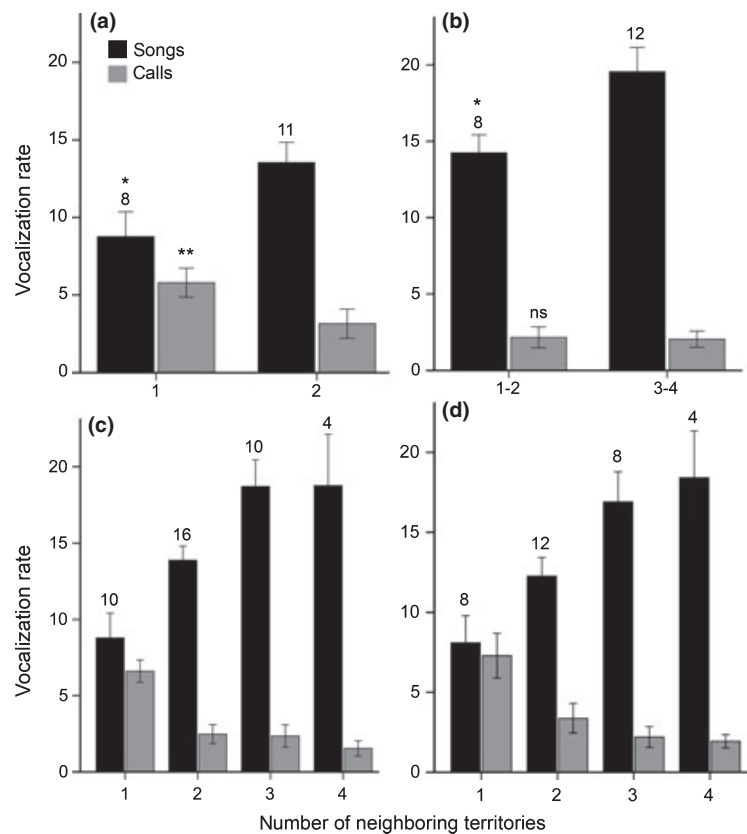
**Fig. 4** Effect of time of day and season on patterns of singing in male (a, b) and female (c, d) *Hypocnemis peruviana* (left panel) and *H. subflava* (right panel). Shown are mean ( $\pm$ SE) number of songs given by both pair members per 10-min block within each of six 1-h periods, averaged by study pair. Note the dawn peak in singing in both species and sexes both the breeding (black) and nonbreeding season (white), contrasting with the lack of dawn peak in singing during temporary removal of resident female (grey; see text). Asterisks denote significant differences between mean breeding season and nonbreeding season song rates within a given 1-h period; Mann-Whitney  $U$ -tests: \*  $P < 0.05$ . Sample sizes per 1-h period: *H. peruviana* 8–17 pairs; *H. subflava* 15–20 pairs.

Mate removals produced two further pieces of evidence that male song functions in mate attraction and courtship. First, pairing success of experimentally ‘bereaved’ males was relatively high as they attracted new females within 24 h in 20% of removals (4/20 experiments). In each case, females were colour-marked birds that abandoned nearby territories and switched mates. Second, during these experimentally induced pairing events, newly formed pairs duetted vigorously using normal songs. When the resident female was returned to her territory, an aggressive contest between females ensued, after which the newcomer was always expelled by the previous resident.

When resident male *H. subflava* were removed, their partners typically remained on the territory for the duration of the experiment. Anecdotal observations confirmed that female *H. subflava* hold territories in the absence of males for a minimum of 2 weeks (C. Salisbury, unpublished data). Sample size was too small to permit standard nonparametric tests. Instead, we grouped songs as ‘normal’ (i.e. between the 5th and 95th percentile of natural singing rates for the entire study population) and ‘extreme’ (i.e. outside those intervals). Prior to the removal of their mate, all eight female subjects gave songs at a ‘normal’ rate (Fig. 8a). After removal of their mates, five females sang at a rate higher than the 95th

percentile (i.e.  $> 4.6$  songs per 10-min block); this difference was significant (Fisher’s exact test: 3/5 vs. 8/0,  $P = 0.026$ ; Fig. 8a). Indeed, when two young females that had held territories for  $< 1$  year were excluded from the analysis, the increase in female song rate in the absence of males was more pronounced ( $P = 0.015$ ; Fig. 8a). We detected no impact of male removal on rates of calling by females (Fig. 8b). Although indirect, these tests demonstrate that female vocal behaviour changed after mate removal, with a significant increase in the number of individuals producing unusually large amounts of song.

Finally, female removal experiments reinforce the suggestion that a dawn peak in singing rate of pairs under natural conditions (see Figs 1 and 2) largely reflects territorial behaviour. When solitary males advertised for mates under experimental conditions, the dawn peak disappeared and there was no effect of time of day on rates of singing (Friedman tests; *H. peruviana*:  $\chi^2_3 = 6.5$ ,  $P = 0.087$ ; *H. subflava*:  $\chi^2_3 = 4.37$ ,  $P = 0.224$ ; Fig. 4). In other words, singing behaviour in resident males is strongly associated with the first hour of the day when they are motivated to defend pair territories, but they continue to sing at a high rate throughout the morning when they are motivated to attract females.



**Fig. 5** The effect of neighbourhood population density (i.e. number of adjoining *Hypocnemis* territories) on mean ( $\pm$ SE) year-round number of songs (black) and calls (grey) per 10-min block in (a) *Hypocnemis peruviana*, (b) *H. subflava*, and (c, d) overall (species pooled). The pooled approach is valid because of strong interspecific aggression and low interspecific discrimination (Tobias & Seddon, 2009b). In (a) and (b), data are taken from throughout the year; in (c), data are from the breeding season, and in (d) data are from outside the breeding season. Asterisks in (a) and (b) are from Mann–Whitney *U*-tests comparing song or call rate between pairs with (a) 1 versus 2 neighbouring *Hypocnemis* territories, and (b) 1–2 versus 3–4 neighbouring *Hypocnemis* territories; \*  $P < 0.05$ , \*\*  $P < 0.01$  (see text). Sample sizes (i.e. number of study pairs) are given above the bars.

### Acoustic analyses

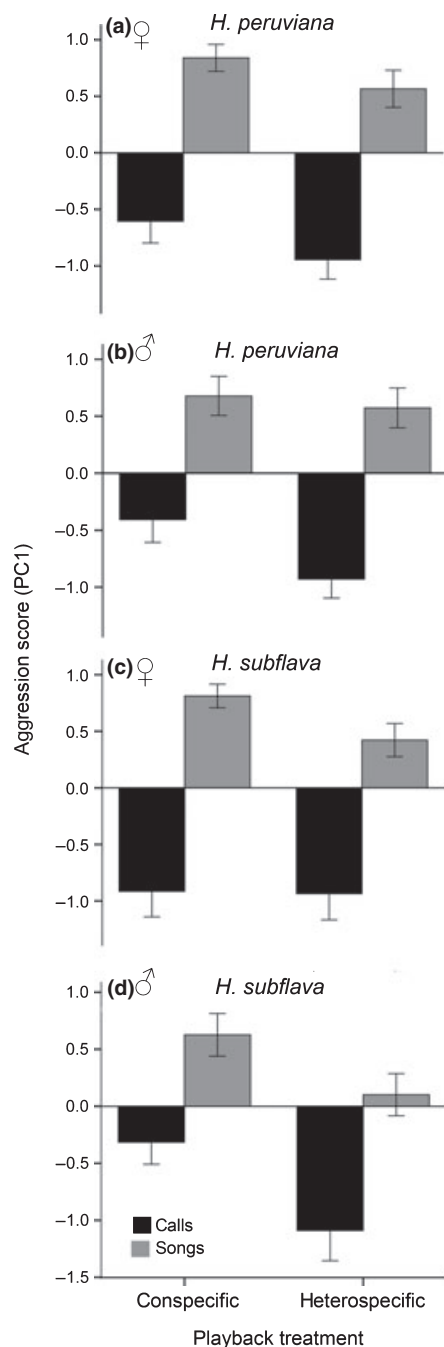
We found no consistent differences in acoustic structure of male songs before and after female removal in *H. peruviana* or *H. subflava*. Songs produced by males when advertising for mates were structurally identical to those produced when accompanied by mates (Table 5). Thus, there is no evidence that male *Hypocnemis* antbirds use different songs in the context of mate attraction and territory defence. We were not able to record enough high-quality female songs before and after male removal to conduct similar statistical tests, but we heard numerous songs from unpaired females in the field and managed to record 10 songs from experimentally ‘bereaved’ females ( $n = 4$ ). We detected no differences by ear, and spectrograms appeared typical in all respects to normal female song.

### Discussion

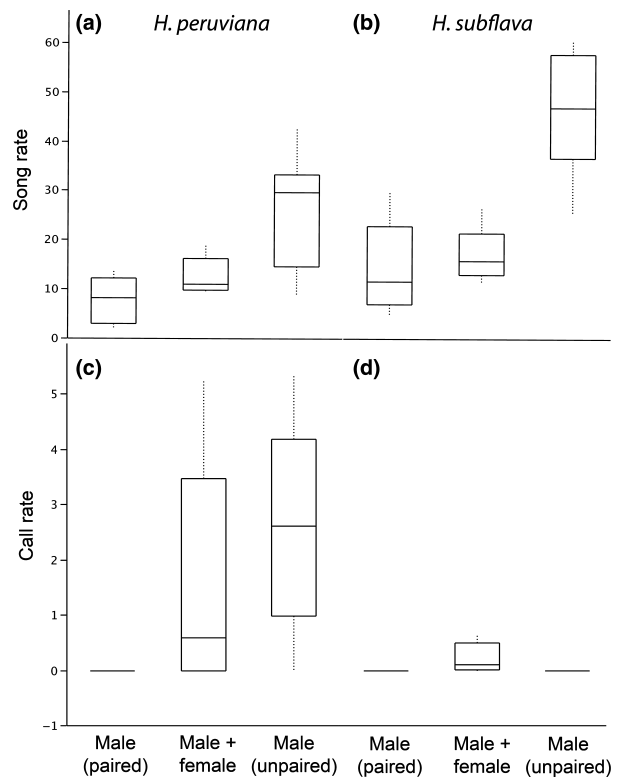
Our results offer the first detailed assessment of the function of sexually monomorphic ornamentation in

species with year-round territoriality. They confirm that song is the primary signal used by males and females to defend territories, whereas the main alternative vocalization – the species-specific call – functions in intrapair communication, perhaps maintaining contact between pair members. Removal experiments also demonstrated that both sexes use convergent songs, rather than divergent calls, to attract mates. In combination, observational and experimental approaches provide strong support for intrasexual and intersexual functions of song, although the emphasis on both these functions appears to be reduced in females (Table 6). In other words, *Hypocnemis* antbirds fit the general pattern of females giving fewer signals and weaker responses than males (e.g. Bretagnolle *et al.*, 1998; Penteriani, 2002; but see Price *et al.*, 2008; Illes & Yunes-Jimenez, 2009). We conclude that selection is stronger in males than females, but that songs of both sexes perform a dual function as armaments and ornaments.

An alternative hypothesis to consider is that monomorphic songs function in intrapair communication,

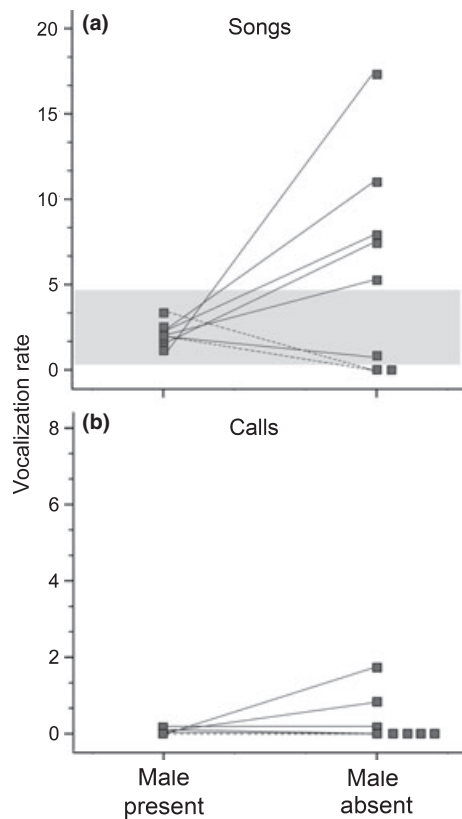


**Fig. 6** The overall strength of response by female and male *Hypocnemis peruviana* (a, b) and *H. subflava* (c, d) to playback of conspecific versus heterospecific calls (black) and songs (grey). Positive values indicate a strong aggressive response; negative values weak or no response. In all species and sexes, song playback elicited significantly more aggression than call playbacks, within and between species (Wilcoxon signed-rank tests:  $P < 0.05$  in all comparisons; see Table 3). Sample sizes for song playbacks are 17 *H. peruviana* and 19 *H. subflava* pairs; sample sizes for call playbacks are 15 *H. peruviana* and 13 *H. subflava* pairs. For factor loadings see Results.



**Fig. 7** Effect of temporary removal of resident female on the vocal behaviour of resident male *Hypocnemis peruviana* (left) and *H. subflava* (right). Shown are boxplots indicating median number of songs (a, b) and calls (c, d) per 10-min block (during the main vocal period, 04:45–08:30 h) given by males in the presence of the resident female, given by both males and females, and given by males in the absence of the resident female. The bars show the 25th and 75th percentiles, and the whiskers denote 10th and 90th percentiles. Asterisks denote the significance of changes in rates of singing and calling on removal of resident female (Wilcoxon signed-rank tests comparing male song rate with and without resident female: \*\*  $P < 0.01$ ;  $n = 8$  pairs per species). No data are presented on rate of calling for unpaired males as it was not possible to assign calls to sex.

particularly as male and female *Hypocnemis* antbirds often sing in duet (Seddon & Tobias, 2006; Tobias & Seddon, 2009c). However, we can discount the argument that they function in synchronizing breeding attempts (Slater & Mann, 2004), as we have shown that songs are produced consistently by both sexes regardless of season. Moreover, three findings suggest that the intended receiver is not the mate. First, pairs foraged and sang loudly in close proximity – typically remaining within sight of each other – throughout the morning at all seasons. Second, both sexes continued to defend solo territories with song after mate removals. And third, singing rates increased in relation to neighbourhood density. Thus, although we cannot rule out the possibility that song maintains contact between pair members or



**Fig. 8** Effect of temporary removal of males on the vocal behaviour of territorial female *Hypocnemis subflava*. Shown are mean rates of singing (a) and calling (b) per 10-min block in the presence and absence of resident males. Data from immature or juvenile females shown in dashed lines. Grey area denotes the interval between the 5th and 95th percentile of female singing rates under natural conditions. The equivalent range for calling rate could not be determined as male and female calls were indistinguishable in the field.

strengthens pair-bonds (Sonnenschein & Reyer, 1983), it is clear that these are not the primary functions.

Previous studies suggested that male antbird songs function only as an armament in intrasexual contests

(Morton, 1996; Morton *et al.*, 2000), leading to the wider generalization that male song in socially monogamous tropical birds has little to do with female mate choice (Stutchbury & Morton, 2001: 82). Although we agree that intersexual functions are far less prominent in the songs of tropical than temperate birds, our findings confirm that both intrasexual aggression and mate attraction are mediated by male song in at least two socially monogamous tropical species. As far as we are aware, this is the first direct evidence that male songs are used as mating signals in the tracheophone suboscine clade (> 500 species). Moreover, opportunistic observations of naturally or experimentally unpaired individuals in > 20 species indicate that male antbirds habitually use the same song to defend territories and attract mates (J. A. Tobias, unpublished data). We propose that male song in many tropical suboscines is shaped by the combined forces of male–male competition and female choice and is thus functionally analogous to song in oscines (Searcy & Nowicki, 2000; Collins, 2004).

#### Interpreting dual functionality in male song

Dual functionality resolves apparent contradictions regarding antbird songs, validating their treatment as both socially selected territorial signals (Morton, 1996; Tobias & Seddon, 2009b) and sexually selected mating signals (Seddon *et al.*, 2008; Tobias & Seddon, 2009a). It also helps to explain the sexual conflict played out in *Hypocnemis* duets (Tobias & Seddon, 2009c). Nonetheless, the result seems counter-intuitive given that near-identical songs mediate interspecific male–male competition in this system (Tobias & Seddon, 2009b). Convergent territorial signals make sense, but convergent mating signals contradict deep-rooted evolutionary ideas about species recognition and character displacement (see Seddon, 2005). This raises a key question: even if convergent territorial signals are adaptive in interspecifically territorial species (Cody, 1969; Grether *et al.*, 2009), why are sexual functions not transferred to a less ambiguous signal to overcome the potentially severe

**Table 5** Comparison of the structure of songs given by male *Hypocnemis* antbirds before and after their mates were removed.

Acoustic character	<i>H. peruviana</i>			<i>H. subflava</i>		
	Before	After	<i>P</i> *	Before	After	<i>P</i> *
No. notes	7.39 ± 0.23	7.83 ± 0.21	0.625	9.65 ± 0.28	9.36 ± 0.34	0.813
No. raspy notes	2.12 ± 0.23	2.29 ± 0.25	0.719	3.16 ± 0.19	2.87 ± 0.31	0.578
Note pace (per s)	2.87 ± 0.03	2.93 ± 0.05	0.438	3.02 ± 0.05	3.21 ± 0.07	0.219
Song duration (s)	2.59 ± 0.09	2.70 ± 0.09	0.563	3.27 ± 0.14	2.30 ± 0.14	0.219
Max freq (kHz)	3.50 ± 0.03	3.53 ± 0.02	0.563	3.35 ± 0.03	3.32 ± 0.04	0.219
Min freq (kHz)	1.78 ± 0.04	1.89 ± 0.04	0.031	2.00 ± 0.02	2.00 ± 0.03	1.000
Peak freq (kHz)	2.90 ± 0.03	2.92 ± 0.03	0.844	2.79 ± 0.024	2.84 ± 0.03	0.578
Bandwidth (kHz)	1.72 ± 0.04	1.64 ± 0.04	0.688	1.35 ± 0.03	1.32 ± 0.03	0.375

\*Wilcoxon signed-rank tests ( $n = 6$  male *H. peruviana*, 7 male *H. subflava*; exact *P*-values). Sample sizes were too small to permit parametric tests. All differences were nonsignificant after correction for multiple comparisons.

**Table 6** Summary of key results. For both sexes, we state whether the result for songs\* supports Hypothesis 1 (trait functions as an ornament used in mate attraction), Hypothesis 2 (trait mediates intrasexual competition for sexual resources) or Hypothesis 3 (trait mediates competition for nonsexual resources). We classify our results according to whether they provide weak negative (–) or positive (+) support, or strong negative (––) or positive evidence (++) . Zeros (0) indicate no support either way.

	H1	H2	H3
<b>Male</b>			
No association between singing rate and breeding season	–	+	+
Consistent dawn peak in singing rate during breeding and nonbreeding season	0	0	+
Positive association between song and neighbourhood density in breeding and nonbreeding season	0	0	+
Same-sex songs elicit aggressive responses from conspecifics	+	+	0
Songs elicit aggressive responses from heterospecifics	–	0	++
Singing increases in absence of female	++	0	0
Song used during courtship displays	++	0	0
<b>Female</b>			
No association between singing rate and breeding season	–	+	+
Consistent dawn peak in singing rate during breeding and nonbreeding season	0	0	+
Positive association between song and neighbourhood density in breeding and nonbreeding season	0	0	+
Same-sex songs elicit aggressive responses from conspecifics	+	+	0
Songs elicit aggressive responses from heterospecifics	–	0	+
Singing increases in absence of male	+	0	0
Song used during courtship displays	++	0	0

\*Results for calls mainly run in the opposite direction: no dawn peak, no association with neighbourhood density, no strong responses from conspecifics or heterospecifics, no increase in absence of mate and no use during courtship displays.

costs of hybridization (Trivers, 1972)? After all, intrasexual and intersexual functions can be partitioned into different vocalizations in antbirds (Morton *et al.*, 2000), much as they are in some oscine families (Spector, 1992).

Our results do not conclusively answer this question, yet they are consistent with the idea that dual functionality arises through ‘armament–ornament’ mechanisms. Theoretically, females should assess the most informative male trait only if the benefits of doing so outweigh the costs of mistaken identity (Gröning & Hochkirch, 2008). It is therefore significant that female *Hypocnemis* antbirds locate and assess males by song, despite near-identical songs in heterospecifics. Moreover, our results also show that a suitable alternative vocal signal – the call – is not co-opted for use in either male–male competition or mate

attraction. In effect, we have demonstrated dual functionality of male songs in the face of elevated risks of hybridization and despite alternative options.

In line with the armament–ornament model, we propose that females in this system benefit from detecting and selecting males on the basis of a socially enforced honest armament (Kodric-Brown & Brown, 1984; Berglund *et al.*, 1996) and that hybridization is averted by other means. For example, a previous study showed that female auditory perception is highly resolved in *Hypocnemis*, allowing discrimination between species and even individuals on the basis of male songs alone (Seddon & Tobias, 2010). Females may also rely on a suite of preferences, such that the divergent calls and colour patches of *H. peruviana* and *H. subflava* (Tobias & Seddon, 2009b) function as close-range ‘back-up’ signals (see Hankison & Morris, 2003). These perceptual and visual safety nets against hybridization bring energetic and developmental costs of their own, suggesting that there must be positive selection on dual functionality in the songs of male antbirds. The original argument for the armament–ornament model was based on the observation that traits functioning in both male–male competition and female choice are commonplace (Berglund *et al.*, 1996), yet this evidence is fairly weak given that dual-function traits can almost always be explained as the products of chance or convenience. However, the convergent mating signals of sympatric *Hypocnemis* antbirds strongly suggest that song functions are yoked together, as proposed by the armament–ornament model.

Further support is provided by the emphasis on competitive functions: antbirds defend territories and partnerships daily, but seek mates only rarely. This shifts the focus from attracting mates to defending territories and partnerships (Stutchbury & Morton, 2001). Accordingly, their songs appear to function primarily as intrasexual armaments and secondarily as intersexual ornaments. The implication is that traits used by females to assess males are fundamentally intrasexual territorial signals, in accordance with the armament–ornament model. Again, the reverse is true in most temperate-zone birds, where the sexual functions of song tend to be more prominent than the territorial functions (Merilä & Sorjonen, 1994; Morton, 1996; Kunc *et al.*, 2005).

### Armaments and ornaments in females

Although females sang less, female song resembled male song in being a loud, long-range signal directed mainly at same-sex rivals. Competition is mainly for territories and partnerships (Seddon & Tobias, 2006), but this study suggests that the highest value is placed on the territory. Unpaired females defended solo territories even though unpaired males were available in the population. This is consistent with evidence from other socially monogamous tropical passerines, suggesting that females tend to be more faithful to territories than partners (Gill &

Stutchbury, 2006) and hold solo territories for up to a year (Morton *et al.*, 2000). Contrastingly, male-removal experiments in temperate-zone species often reveal that females abandon territories to seek unpaired males soon after their mates have been removed, at least before the nesting phase (e.g. Harper, 1985; Klatt & Ritchison, 1994; Tobias, 1997a). The implication is that ecological resources are of greater value to females in stable tropical systems, where resources can be defended year-round.

This is not the only function of female song in antbirds; however, as removal experiments suggested, they also serve to attract mates. At a glance, this seems to support the view that female birds sing for roughly the same reasons as males, i.e. territory defence and mate attraction (Langmore, 1998, 2000; Riebel *et al.*, 2005; Catchpole & Slater, 2008). The difference is that aggressive and attractive functions have not usually been reported in the same species and apparently never in the same female trait. Instead, most previous studies in socially monogamous systems – including antbirds – suggest that female song functions only in intrasexual competition for resources or intrapair contact, rather than mate attraction (Levin, 1996; McElroy & Ritchison, 1996; Fedy & Stutchbury, 2005; Stutchbury *et al.*, 2005; Seddon & Tobias, 2006; Mennill & Vehrencamp, 2008; Tobias & Seddon, 2009c). Meanwhile, a few studies in polygynous systems suggest that females may sing to attract males, but not to defend territories (Langmore *et al.*, 1996). Thus, our results provide a rare demonstration that (i) female songs can have dual function as both armaments and ornaments in socially monogamous species, and (ii) sexually monomorphic songs can function as armament and ornament in both sexes.

Symmetrical functions imply that selection on ornaments is similar in males and females. This contrasts with many systems in which selection appears to act asymmetrically (Clutton-Brock, 2007, 2009). For example, even when intrasexual competition and female choice act on male ornaments, the corresponding traits in females appear to function only in competition for resources (LeBas, 2006; Watson & Simmons, 2010), only in mate attraction (Langmore *et al.*, 1996), or neither (Al-khairulla *et al.*, 2003). Our findings shed new light on the dynamics of selection in animals by suggesting that long-term monogamy and elevated resource competition can lead to both sexes converging towards the same intermediate signalling strategy mediated by dual-function signals.

#### **Double or nothing: the armament–ornament model as a driver of mutual ornamentation**

Drawing together the evidence from males and females, it seems that song in both sexes of *Hypocnemis* antbirds functions largely in intrasexual resource defence, as seems to be the case for many species with communal signals (Hall, 2000; Seddon & Tobias, 2003; Hall &

Magrath, 2007). The emphasis on resource defence may be rooted in one of the key life history traits of *Hypocnemis* antbirds: year-round territoriality. This is perhaps the most common form of avian territoriality, adopted by thousands of tropical and south-temperate species, yet its evolutionary implications remain poorly understood (Stutchbury & Morton, 2001: 74). It is generally associated with low adult mortality, delayed dispersal, and social monogamy with little or no EPC (Greenberg & Gradwohl, 1986, 1997; Fleischer *et al.*, 1997; Russell *et al.*, 2004; Gill & Stutchbury, 2006; Stutchbury *et al.*, 2007). In many systems, including *Hypocnemis* antbirds, the main implications are intense competition for territories and increased value of breeding partnerships (Morton, 1996; Gill *et al.*, 2007). Our results are consistent with two broad predictions arising from these conditions: first, the year-round resource competition is likely to exert positive selection on elaborate traits in both sexes (West-Eberhard, 1983), and second, the long-term monogamy will lead to choosiness and therefore ornamentation in both sexes (Huxley, 1914; Burley, 1986).

This raises the possibility that sexually monomorphic songs evolve by armament–ornament processes acting symmetrically in both sexes. Previously, dual-utility signals have been reported in males of many animals (e.g. Behr *et al.*, 2006; Griggio & Hoi, 2008; Vasconcelos *et al.*, 2010). They have also recently been found to occur in females in sex-role reversed species (Berglund & Rosenqvist, 2008; Geberzahn *et al.*, 2010). However, our study provides the first direct evidence that sexually monomorphic territorial armaments are used in mutual mate attraction: a novel extension of the armament–ornament model in reciprocal format. This finding may help to explain some poorly understood phenomena, including widespread mutual ornamentation in socially monogamous tropical species with year-round territoriality (West-Eberhard, 1983; Slater & Mann, 2004; Kraaijeveld *et al.*, 2007).

#### **The case for social selection**

A common assumption is that armament–ornament mechanisms are driven by sexual selection (e.g. Berglund *et al.*, 1996; Borgia & Coleman, 2000; Leitão & Riebel, 2003), but this is not necessarily the case. West-Eberhard (1983) was amongst the first to note ‘a correlation between monomorphically bright signal coloration and territoriality by both sexes’, ascribing this phenomenon to social competition. However, the idea of mutual ornamentation via social competition has never gained widespread acceptance because of the impression that sexual selection theory can account for the same patterns (e.g. Hooper & Miller, 2008; Clutton-Brock, 2009; Rubenstein & Lovette, 2009).

This issue is worth revisiting because the wider perspective of social selection could help to explain a



range of puzzling patterns in phenotypic evolution. For example, Friedman *et al.* (2009) wondered why migratory lifestyles were often associated with a loss of bright plumage in female birds. Similarly, Price *et al.* (2009) used a phylogenetic approach to show that several factors appeared to select against female song, including brood parasitism and colonial breeding. These observations are not easily explained in the framework of sexual selection, but make sense as indirect relationships driven by the relaxation of social competition. In other words, the de-ornamentation of females along evolutionary pathways may simply reflect the loss of year-round territoriality associated with the evolution of migration, brood parasitism or coloniality.

Social selection has the potential to offer significant insights, but it is only really required if individuals compete for commodities that fall outside the bounds of sexual selection theory. Its relevance therefore depends on whether competition relates solely to mates and mating opportunities (Clutton-Brock, 2007). This proves difficult to determine, particularly when the territorial or aggressive function of mutual ornaments are only considered in the breeding season (e.g. Cooney & Cockburn, 1995; Jones & Hunter, 1999; Velando *et al.*, 2001; Kraaijeveld *et al.*, 2004; Viera *et al.*, 2008).

Our results provide several lines of evidence suggesting that male and female *Hypocnemis* antbirds use song to defend territories, even in the nonbreeding season. But are nonbreeding territories nonsexual resources? We agree with Stutchbury & Morton (2001) that, via year-round territoriality, 'tropical females are defending food resources for themselves, and less importantly for their young, on a permanent basis'. At a stretch, nonbreeding territories may be perceived as purely sexual resources on the grounds that they ensure access to favourable breeding habitat. However, it is generally accepted that the value of maintaining territories through the nonbreeding season lies at least partly in providing access to nonsexual resources such as a safe haven from predators and a familiar food supply (Tobias, 1997b; Wiley & Goldizen, 2003; Amrhein & Erne, 2006). The importance of nonbreeding territories as resources with some nonsexual component is vividly demonstrated by widespread solo territories in both males and females during the nonbreeding season (e.g. George, 1987; Kelsey, 1989; Tobias, 1997b; Sogge *et al.*, 2007; Townsend *et al.*, 2010). In *Hypocnemis*, strong competition with heterospecifics provides further corroboration. Given that heterospecific individuals have no direct relevance to mate attraction or mate defence, we assume that interspecific contests have a minor sexual motive, particularly in the nonbreeding season.

Overall, our results offer evidence that armaments mediate a range of competitive interactions, some of which target nonsexual resources. They therefore add to an increasing body of empirical (e.g. Bleiweiss, 1985; Ord *et al.*, 2001; Tibbetts & Dale, 2004; Senar, 2006; Stanko-

wich & Caro, 2009; Tibbetts & Safran, 2009) and theoretical research (e.g. Tanaka, 1996; Moore *et al.*, 1997; Wolf *et al.*, 1999), suggesting that social competition for nonsexual resources contributes to selection on exaggerated traits (weapons, dominance signals, badges of status, etc.). We conclude that processes leading to ornamentation – mutual or otherwise – are only partly captured by sexual selection and can best be understood in the context of social selection (West-Eberhard, 1979, 1983).

## Acknowledgments

This research was funded jointly by the Royal Society and the British Ecological Society. We thank Instituto Nacional de Recursos Naturales (INRENA) and Asociación para la Conservación de la Cuenca Amazónica (ACCA) for granting permission to carry out research at CICRA. Nigel Pitman and Thomas Valqui kindly offered logistical support in Peru. We are grateful to Jorjany Botero, Julissa Cabrera, Dominic Cram, Jayden van Horick and Claire Salisbury for assistance with data collection.

## References

- Al-khairulla, H., Warburton, D. & Knell, R.J. 2003. Do the eyestalks of female diopsid flies have a function in intrasexual aggressive encounters? *J. Insect Behav.* **16**: 679–686.
- Amrhein, V. & Erne, N. 2006. Dawn singing reflects past territorial challenges in the winter wren. *Anim. Behav.* **71**: 1075–1080.
- Amrhein, V., Kunc, H.P. & Naguib, M. 2004. Non-territorial nightingales prospect territories during the dawn chorus. *Proc. R. Soc. B: Biol. Sci.* **271**: S167–S169.
- Amundsen, T. (2000) Female ornaments: genetically correlated or sexually selected? In: *Signalling and Signal Design in Animal Communication*, (Y. Espmark, T. Amundsen & G. Rosenqvist, eds), pp. 133–54. Tapir Academic Press, Trondheim.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Bard, S.C., Hau, M., Wikelski, M. & Wingfield, J.C. 2002. Vocal distinctiveness and response to conspecific playback in the Spotted Antbird, a neotropical suboscine. *Condor* **104**: 387–394.
- Behr, O., von Helversen, O., Heckel, G., Nagy, M., Voigt, C.C. & Mayer, F. 2006. Territorial songs indicate male quality in the sac-winged bat *Saccopteryx bilineata* (Chiroptera, Emballonuridae). *Behav. Ecol.* **17**: 810–817.
- Beletsky, L.D. 1983. Aggressive and pair-bond maintenance songs of female red-winged blackbirds. *Z. Tierpsychol.* **62**: 47–54.
- Benson, K.E. & Basolo, A.L. 2006. Male-male competition and the sword in male swordtails *Xiphophorus helleri*. *Anim. Behav.* **71**: 129–134.
- Berglund, A. & Rosenqvist, G. 2008. An intimidating ornament in a female pipefish. *Behav. Ecol.* **20**: 54–59.
- Berglund, A., Bisazza, A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* **58**: 385–399.
- Bleiweiss, R. 1985. Iridescent polychromatism in a female hummingbird: is it related to feeding strategies? *Auk* **102**: 701–713.

- Borgia, G. & Coleman, S.W. 2000. Co-option of male courtship signals from aggressive display in bowerbirds. *Proc. R. Soc. B: Biol. Sci.* **267**: 1735–1740.
- Bradbury, J.W. & Vehrencamp, S.L. 1998. *Principles of Animal Communication*. Sinauer Associates, Sunderland, MA.
- Bretagnolle, V., Genevois, F. & Mougeot, F. 1998. Intra and intersexual function in the call of a non-passerine bird. *Behaviour* **135**: 1161–1184.
- Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* **127**: 415–445.
- Byers, B.E. 1995. Song types, repertoires and song variability in a population of chestnut-sided warblers. *Condor* **97**: 390–401.
- Catchpole, C.K. & Slater, P.J.B. 2008. *Bird song: Biological Themes and Variations*. Cambridge University Press, Cambridge, UK.
- Clutton-Brock, T.H. 2007. Sexual selection in males and females. *Science* **318**: 1882–1885.
- Clutton-Brock, T.H. 2009. Sexual selection in females. *Anim. Behav.* **77**: 3–11.
- Clutton-Brock, T.H. 2010. We do not need a Sexual Selection 2.0 - nor a theory of Genial Selection. *Anim. Behav.* **79**: 7–10.
- Clutton-Brock, T.H., Hodge, S.J., Spong, G., Russell, A.F., Jordan, N.R., Bennett, N.C. et al. 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature* **444**: 1065–1068.
- Cockburn, A., Dalziell, A.H., Blackmore, C.J., Double, M.C., Kokko, H., Osmond, H.L. et al. 2009. Superb fairy-wren males aggregate into hidden leks to solicit extragroup fertilizations before dawn. *Behav. Ecol.* **20**: 501–510.
- Cody, M.L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor* **71**: 222–239.
- Collins, S. (2004) Vocal fighting and flirting: the functions of birdsong. In: *Nature's Music: The Science of Birdsong*, (P. Marler & H. Slabbekoorn, eds), pp. 39–78. Elsevier Academic Press, San Diego, CA.
- Cooney, R. & Cockburn, A. 1995. Territorial defence is the major function of female song in the superb fairy-wren, *Malurus cyaneus*. *Anim. Behav.* **49**: 1635–1647.
- Dalziell, A.H. & Cockburn, A. 2008. Dawn song in superb fairy-wrens: a bird that seeks extrapair copulations during the dawn chorus. *Anim. Behav.* **75**: 489–500.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. J. Murray, London.
- Doutrelant, C., Blondel, J., Perret, P. & Lambrechts, M.M. 2000. Blue tit song repertoire size, male quality and interspecific competition. *J. Avian Biol.* **31**: 360–366.
- ESRI 1999. *ArcView 3.3*. Environmental Systems Research Institute, Inc., Redlands, CA.
- Fedy, B.C. & Stutchbury, B.J.M. 2005. Territory defence in tropical birds: are females as aggressive as males? *Behav. Ecol. Sociobiol.* **58**: 414–422.
- Fleischer, R.C., Tarr, C., Morton, E.S., Derrickson, K.D. & Sangmeister, A. 1997. Mating system of the Dusky Antbird (*Cercomacra tyrannina*), a tropical passerine, as assessed by DNA fingerprinting. *Condor* **99**: 512–514.
- Footo, J.R., Fitzsimmons, L.P., Mennill, D.J. & Ratcliffe, L.M. 2008. Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis. *Behav. Ecol.* **19**: 1192–1199.
- Friedman, N.R., Hofmann, C.M., Kondo, B. & Omland, K.E. 2009. Correlated evolution of migration and sexual dichromatism in the New World orioles (*Icterus*). *Evolution* **63**: 3269–3274.
- Geberzahn, N., Goymann, W. & ten Cate, C. 2010. Threat signaling in female song—evidence from playbacks in a sex-role reversed bird species. *Behav. Ecol.* **21**: 1147–1155.
- Geberzahn, N., Goymann, W., Muck, C. & ten Cate, C. 2009. Females alter their song when challenged in a sex-role reversed bird species. *Behav. Ecol. Sociobiol.* **64**: 193–204.
- George, T.L. 1987. Behavior of territorial male and female Townsend's solitaires (*Myadestes townsendi*) in winter. *Am. Midl. Nat.* **118**: 121–127.
- Gill, S.A. & Stutchbury, B.J.M. 2006. Long-term mate and territory fidelity in neotropical buff-breasted wrens (*Thryothorus leucotis*). *Behav. Ecol. Sociobiol.* **61**: 245–253.
- Gill, S.A., Alfson, E.D. & Hau, M. 2007. Context matters: female aggression and testosterone in a year-round territorial neotropical songbird (*Thryothorus leucotis*). *Proc. R. Soc. Lond B: Biol. Sci.* **274**: 2187–2194.
- Greenberg, R. & Gradwohl, J. 1983. Sex roles in the dot-winged ant wren (*Microrhopias quixensis*), a tropical passerine. *Auk* **100**: 920–925.
- Greenberg, R. & Gradwohl, J. 1986. Stable territories and constant densities in tropical forest insectivorous birds. *Oecologia* **69**: 618–625.
- Greenberg, R. & Gradwohl, J. 1997. Territoriality, adult survival, and dispersal in the checker-throated antwren in Panama. *J. Avian Biol.* **28**: 103–110.
- Grether, G.F. 1996. Intrasexual competition alone favors a sexually dimorphic ornament in the rubyspot damselfly *Hetaerina americana*. *Evolution* **50**: 1949–1957.
- Grether, G.F., Losin, N., Anderson, C.N. & Okamoto, K. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biol. Rev.* **84**: 617–635.
- Griggio, M. & Hoi, H. 2008. Dual utility of a melanin-based ornament in bearded tits. *Ethology* **114**: 1094–1100.
- Griggio, M., Zanollo, V. & Hoi, H. 2010. Female ornamentation, parental quality, and competitive ability in the rock sparrow. *J. Ethol.* **28**: 455–462.
- Gröning, J. & Hochkirch, A. 2008. Reproductive interference between animal species. *Q. Rev. Biol.* **83**: 257–282.
- Hall, M.L. 2000. The function of duetting in magpie-larks: conflict, cooperation, or commitment? *Anim. Behav.* **60**: 667–677.
- Hall, M.L. & Magrath, R.D. 2007. Temporal coordination signals coalition quality. *Curr. Biol.* **17**: R406–R407.
- Hankison, S.J. & Morris, M.R. 2003. Avoiding a compromise between sexual selection and species recognition: female swordtail fish assess multiple species-specific cues. *Behav. Ecol.* **14**: 282–287.
- Harper, D.G.C. 1985. Pairing strategies and mate choice in female robins *Erithacus rubecula*. *Anim. Behav.* **33**: 862–875.
- Hasselquist, D. & Bensch, S. 2008. Daily energy expenditure of singing great reed warblers *Acrocephalus arundinaceus*. *J. Avian Biol.* **39**: 384–388.
- Hau, M., Stoddard, S.T. & Soma, K.K. 2004. Territorial aggression and hormones during the non-breeding season in a tropical bird. *Horm. Behav.* **45**: 40–49.
- Hoeschele, M., Moscicki, M.K., Otter, K.A., van Oort, H., Fort, K.T., Farrell, T.M. et al. 2010. Dominance signalled in an acoustic ornament. *Anim. Behav.* **79**: 657–664.
- Hooper, P.L. & Miller, G.F. 2008. Mutual mate choice can drive costly signaling even under perfect monogamy. *Adaptive Behav.* **16**: 53–70.

- Huxley, J. 1914. The courtship-habits of the Great Crested Grebe (*Podiceps cristatus*): with an addition to the theory of sexual selection. *Proc. Zool. Soc. London* **35**: 491–562.
- Illes, A.E. & Yunes-Jimenez, L. 2009. A female songbird out-sings male conspecifics during simulated territorial intrusions. *Proc. R. Soc. B: Biol. Sci.* **276**: 981–986.
- Isler, M.L., Isler, P.R. & Whitney, B.M. 2007. Species limits in antbirds (Thamnophilidae): the *Hypocnemis cantator* complex. *Auk* **124**: 11–28.
- Johnson, K. 1988. Sexual selection in pinyon jays II. Male choice and female-female competition. *Anim. Behav.* **36**: 1048–1053.
- Jones, I.L. & Hunter, F.M. 1993. Mutual sexual selection in a monogamous seabird. *Nature* **362**: 238–239.
- Jones, I.L. & Hunter, F.M. 1999. Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament. *Anim. Behav.* **57**: 521–528.
- Kelsey, M.G. 1989. A comparison of the song and territorial behaviour of a long-distance migrant, the Marsh Warbler *Acrocephalus palustris*, in summer and winter. *Ibis* **131**: 403–414.
- Klatt, P.H. & Ritchison, G. 1994. The effect of mate removal on the vocal behavior and movements of male and female Eastern Screech-Owls. *Condor* **96**: 485–493.
- Kodric-Brown, A. & Brown, J.H. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Am. Nat.* **124**: 309–323.
- Kokko, H. & Johnstone, R.A. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philos. Trans. R. Soc. Lond B-Biol. Sci.* **357**: 319–330.
- Kraaijeveld, K., Gregurke, J., Hall, C., Komdeur, J. & Mulder, R.A. 2004. Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behav. Ecol.* **15**: 380–389.
- Kraaijeveld, K., Kraaijeveld-Smit, F.J.L. & Komdeur, J. 2007. The evolution of mutual ornamentation. *Anim. Behav.* **74**: 657–677.
- Krebs, J.R., Avery, M. & Cowie, R.J. 1981. Effect of removal of mate on the singing behaviour of great tits. *Anim. Behav.* **29**: 635–637.
- Kunc, H.P., Amrhein, V. & Naguib, M. 2005. Seasonal variation in dawn song characteristics in the common nightingale. *Anim. Behav.* **70**: 1267–1271.
- Langmore, N.E. 1998. Functions of duet and solo songs of female birds. *Trends Ecol. Evol.* **13**: 136–140.
- Langmore, N.E. 2000. *Why Female Birds Sing*. Tapir Academic Press, Trondheim.
- Langmore, N.E., Davies, N.B., Hatchwell, B.J. & Hartley, I.R. 1996. Female song attracts males in the alpine accentor *Prunella collaris*. *Proc. R. Soc. B: Biol. Sci.* **263**: 141–146.
- LeBas, N.R. 2006. Female finery is not for males. *Trends Ecol. Evol.* **21**: 170–173.
- Leitão, A. & Riebel, K. 2003. Are good ornaments bad armaments? Male chaffinch perception of songs with varying flourish length. *Anim. Behav.* **66**: 161–167.
- Levin, R.N. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: I. Removal experiments. *Anim. Behav.* **52**: 1093–1106.
- Liu, W.-C. & Kroodsma, D.E. 2007. Dawn and daytime singing behavior of chipping sparrows (*Spizella passerina*). *Auk* **124**: 44–52.
- Liu, W.-C. & Nottebohm, F. 2005. Variable rate of singing and variable song duration are associated with high immediate early gene expression in two anterior forebrain song nuclei. *Proc. Natl Acad. Sci. USA* **102**: 10724–10729.
- Logue, D.M. & Forstmeier, W. 2008. Constrained performance in a communication network: Implications for the function of song-type matching and the evolution of multiple ornaments. *Am. Nat.* **172**: 34–41.
- Mace, R. 1987. The dawn chorus in the great tit *Parus major* is directly related to female fertility. *Nature* **330**: 745–746.
- McElroy, D.B. & Ritchison, G. 1996. Effect of mate removal on singing behavior and movement patterns of female northern cardinals. *Wilson Bull.* **108**: 550–555.
- McGhee, K.E., Fuller, R.C. & Travis, J. 2007. Male competition and female choice interact to determine mating success in the bluefin killifish. *Behav. Ecol.* **18**: 822–830.
- Mennill, D.J. & Vehrencamp, S.L. 2008. Context-dependent functions of avian duets revealed by microphone-array recordings and multispeaker playback. *Curr. Biol.* **18**: 1314–1319.
- Merilä, J. & Sorjonen, J. 1994. Seasonal and diurnal patterns of singing and song-flight activity in bluethroats (*Luscinia svecica*). *Auk* **111**: 556–562.
- Møller, A.P. 1993. Sexual selection in the barn swallow *Hirundo rustica* III. Female tail ornaments. *Evolution* **47**: 417–431.
- Moore, A.J. 1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual selection and intersexual selection. *Evolution* **44**: 315–331.
- Moore, A.J. & Moore, P.J. 1999. Balancing sexual selection through opposing mate choice and male competition. *Proc. R. Soc. B: Biol. Sci.* **266**: 711–716.
- Moore, A.J., Brodie, E.D. & Wolf, J.B. 1997. Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution* **51**: 1352–1362.
- Moore, I.T., Wingfield, J.C. & Brenowitz, E.A. 2004. Plasticity of the avian song control system in response to localized environmental cues in an equatorial songbird. *J. Neurosci.* **24**: 10182–10185.
- Morton, E.S. (1996) A comparison of vocal behavior among tropical and temperate passerine birds. In: *Ecology and Evolution of Acoustic Communication in Birds*, (D.E. Kroodsma & E.H. Miller, eds), pp. 258–268. Cornell University Press, Ithaca, New York.
- Morton, E.S., Stutchbury, B.J.M. & Derrickson, K.C. 2000. Territory switching behavior in a sedentary tropical passerine, the Dusky Antbird *Cercomacra tyrannina*. *Behav. Ecol.* **11**: 648–653.
- Murphy, T.G., Hernández-Muciño, D., Osorio-Beristain, M., Montgomerie, R. & Omland, K.E. 2009. Carotenoid-based status signaling by females in the tropical streak-backed oriole. *Behav. Ecol.* **20**: 1000–1006.
- Ord, T.J., Blumstein, D.T. & Evans, C.S. 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. *Proc. R. Soc. B: Biol. Sci.* **268**: 737–744.
- Payne, R.B. & Groschupf, K.D. 1984. Sexual selection and interspecific competition: A field experiment on territorial behavior of nonparental finches (*Vidua* spp.). *Auk* **101**: 140–145.
- Penteriani, V. 2002. Variation in the function of Eagle Owl vocal behaviour: territorial defence and intra-pair communication? *Ethol. Ecol. Evol.* **14**: 275–281.
- Price, J.J., Yunes-Jiménez, L., Osorio-Beristain, M., Omland, K.E. & Murphy, T.G. 2008. Sex-role reversal in song? Females

- sing more frequently than males in the Streak-backed Oriole. *Condor* **110**: 387–392.
- Price, J.J., Lanyon, S.M. & Omland, K.E. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. *Proc. R. Soc. B: Biol. Sci.* **276**: 1971–1980.
- Pryke, S.R. 2007. Fiery red heads: female dominance among head color morphs in the Gouldian finch. *Behav. Ecol.* **18**: 621–627.
- Regosin, J.V. & Pruett-Jones, S. 2001. Sexual selection and tail-length dimorphism in scissor-tailed flycatchers. *Auk* **118**: 167e–175e.
- Riebel, K., Hall, M.L. & Langmore, N.E. 2005. Female songbirds still struggling to be heard. *Trends Ecol. Evol.* **20**: 419–420.
- Rubenstein, D.R. & Lovette, I.J. 2009. Reproductive skew and selection on female ornamentation. *Nature* **462**: 786–789.
- Russell, E.M., Yom-Tov, Y. & Geffen, E. 2004. Extended parental care and delayed dispersal: Northern, tropical, and southern passerines compared. *Behav. Ecol.* **15**: 831–838.
- Searcy, W.A. & Nowicki, S. 2000. *Male-Male Competition and Female Choice in the Evolution of Vocal Signaling*. Tapir Academic Press, Trondheim.
- Seddon, N. 2005. Ecological adaptation and species recognition drive vocal evolution in Neotropical suboscine birds. *Evolution* **59**: 200–215.
- Seddon, N. & Tobias, J.A. 2003. Communal singing in the cooperatively breeding subdesert mesite *Monias benschi*: evidence of numerical assessment? *J. Avian Biol.* **34**: 72–80.
- Seddon, N. & Tobias, J.A. 2006. Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). *Behav. Ecol.* **17**: 73–83.
- Seddon, N. & Tobias, J.A. 2007. Song divergence at the edge of Amazonia: an empirical test of the peripatric speciation model. *Biol. J. Linn. Soc.* **90**: 173–188.
- Seddon, N. & Tobias, J.A. 2010. Character displacement from the female perspective: species and mate recognition despite convergent signals in suboscine birds. *Proc. R. Soc. B: Biol. Sci.* **277**: 2475–2483.
- Seddon, N., Merrill, R.M. & Tobias, J.A. 2008. Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. *Am. Nat.* **171**: 620–631.
- Seddon, N., Tobias, J.A., Eaton, M. & Ödeen, A. 2010. Human vision can provide a valid proxy for avian perception of sexual dichromatism. *Auk* **127**: 283–292.
- Senar, J.C. (2006) Bird coloration as an intrasexual signal of aggression and dominance. In: *Bird Coloration, vol. 2: Function and Evolution*, (G.E. Hill & K.J. McGraw, eds), pp. 125–193. Harvard University Press, Cambridge, MA.
- Slater, P.J.B. & Mann, N.I. 2004. Why do the females of many bird species sing in the tropics? *J. Avian Biol.* **35**: 289–294.
- Sogge, M.K., Koronkiewicz, T.J., Van Riper, C. & Durst, S.L. 2007. Willow flycatcher nonbreeding territory defense behavior in Costa Rica. *Condor* **109**: 475–480.
- Sonnenschein, E. & Reyer, H.-U. 1983. Mate-guarding and other functions of antiphonal duets in the slate-coloured boubou (*Laniarius funebris*). *Z. Tierpsychol.* **63**: 112–140.
- Southwood, T.R.E. 1966. *Ecological Methods*. Methuen, London.
- Spector, D.A. 1992. Wood-warbler song systems. A review of paruline singing behaviors. *Curr. Ornithol.* **9**: 199–238.
- Staicer, C.A. 1989. Characteristics, use, and significance of two singing behaviors in Grace's warbler (*Dendroica graciae*). *Auk* **106**: 49–63.
- Staicer, C. 1996. Honest advertisement of pairing status: evidence from a tropical resident wood-warbler. *Anim. Behav.* **51**: 375–390.
- Staicer, C.A., Ingalls, V. & Sherry, T.W. 2006. Singing behavior varies with breeding status of American redstarts (*Setophaga ruticilla*). *Wilson J. Ornithol.* **118**: 439–610.
- Stankowich, T. & Caro, T. 2009. The evolution of weaponry in female bovids. *Proc. R. Soc. B* **276**: 4329–4334.
- Stutchbury, B.J.M. & Morton, E.S. 2001. *Behavioral Ecology of Tropical Birds*. Academic Press, London, UK.
- Stutchbury, B.J.M., Woolfenden, B.E., Fedy, B.C. & Morton, E.S. 2005. Nonbreeding territorial behaviour of two congeneric antbirds, *Myrmeciza exsul* and *M. longipes*. *Ornithol. Neotrop.* **16**: 397–404.
- Stutchbury, B.J.M., Morton, E.S. & Woolfenden, B. 2007. Comparison of the mating systems and breeding behavior of a resident and a migratory tropical flycatcher. *J. Field Orn.* **78**: 40–49.
- Tanaka, Y. 1996. Social selection and the evolution of animal signals. *Evolution* **50**: 512–523.
- Tibbetts, E.A. & Dale, J. 2004. A socially enforced signal of quality in a paper wasp. *Nature* **432**: 218–222.
- Tibbetts, E.A. & Safran, R.J. 2009. Co-evolution of plumage characteristics and winter sociality in New and Old World sparrows. *J. Evol. Biol.* **22**: 2376–2386.
- Tobias, J. 1997a. Asymmetric territorial contests in the European robin: the role of settlement costs. *Anim. Behav.* **54**: 9–21.
- Tobias, J.A. 1997b. Food availability as a determinant of pairing behaviour in the European robin. *J. Anim. Ecol.* **66**: 629–639.
- Tobias, J.A. 2009. *Antbirds of Peru and Bolivia*. The Field Museum, Chicago (Available at: [http://fm2.fieldmuseum.org/plantguides/guide\\_pdfs/256\\_Antbirds\\_v1.pdf](http://fm2.fieldmuseum.org/plantguides/guide_pdfs/256_Antbirds_v1.pdf)).
- Tobias, J.A. & Seddon, N. 2000. Territoriality as a paternity guard in the European robin *Erithacus rubecula*. *Anim. Behav.* **60**: 165–173.
- Tobias, J.A. & Seddon, N. 2009a. Sexual selection and ecological generalism are correlated in antbirds. *J. Evol. Biol.* **22**: 623–636.
- Tobias, J.A. & Seddon, N. 2009b. Signal design and perception in *Hypocnemis* antbirds: evidence for convergent evolution via social selection. *Evolution* **63**: 3168–3189.
- Tobias, J.A. & Seddon, N. 2009c. Signal jamming mediates sexual conflict in a duetting bird. *Curr. Biol.* **19**: 577–582.
- Tobias, J.A., Bates, J.M., Hackett, S.J. & Seddon, N. 2008. Comment on “The latitudinal gradient in recent speciation and extinction rates of birds and mammals”. *Science* **319**: 901c.
- Tobias, J.A., Aben, J., Brumfield, R.T., Derryberry, E., Halfwerk, W., Slabbekoom, H. et al. 2010. Song divergence by sensory drive in Amazonian birds. *Evolution* **64**: 2820–2839.
- Townsend, J.M., Rimmer, C.C. & McFarland, K.P. 2010. Winter territoriality and spatial behavior of Bicknell's thrush (*Catharus bicknelli*) at two ecologically distinct sites in the Dominican Republic. *Auk* **127**: 514–522.
- Trail, P. 1990. Why should lek breeders be monomorphic? *Evolution* **44**: 1837–1852.
- Trivers, R.L. 1972. *Parental Investment and Sexual Selection*. Aldine, Chicago.
- Vasconcelos, R.O., Simões, J.M., Almada, V.C., Fonseca, P.J. & Amorim, C.P. 2010. Vocal behavior during territorial intrusions in the Lusitanian toadfish: boatwhistles also function as territorial ‘keep-out’ signals. *Ethology* **116**: 155–165.
- Veit, A.C. & Jones, I.L. 2003. Function of tail streamers of red-tailed tropicbirds (*Phaethon rubricauda*) as inferred from patterns of variation. *Auk* **120**: 1033–1043.

- Velando, A., Lessells, C.M. & Márquez, J.C. 2001. The function of male and female ornaments in the Inca Tern: evidence for links between ornament expression and both adult condition and reproductive performance. *J. Avian Biol.* **32**: 311–318.
- Viera, V.M., Nolan, P.M., Côté, S.D., Jouventin, P. & Groscolas, R. 2008. Is territory defence related to plumage ornaments in the king penguin *Aptenodytes patagonicus*? *Ethology* **114**: 146–153.
- Vondrasek, J.R. 2006. Social factors affect the singing rates of female northern cardinals *Cardinalis cardinalis*. *J. Avian Biol.* **37**: 52–57.
- Watson, N.L. & Simmons, L.W. 2010. Mate choice in the dung beetle *Onthophagus sagittarius*: are female horns ornaments? *Behav. Ecol.* **21**: 424–430.
- West-Eberhard, M.J. 1979. Sexual selection, social competition, and evolution. *Proc. Am. Phil. Soc.* **123**: 222–234.
- West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**: 155–183.
- Wiley, C.J. & Goldizen, A.W. 2003. Testosterone is correlated with courtship but not aggression in the tropical Buff-banded Rail, *Gallirallus philippensis*. *Horm. Behav.* **43**: 554–560.
- Willis, E. 1967. The behavior of bicolored antbirds. *Univ. Calif. Publ. Zool.* **79**: 1–132.
- Wolf, J.B., Brodie, E.D. & Moore, A.J. 1999. Interacting phenotypes and the evolutionary process: II Selection resulting from social interactions. *Am. Nat.* **153**: 254–266.
- Zimmer, K.J. & Isler, M.L. (2003) Family Thamnophilidae (typical antbirds). In: *Handbook of Birds of the World, vol. 8, Vol. 8* (J. del Hoyo, A. Elliott & D. Christie, eds), pp. 448–681. Lynx Edicions, Barcelona.

## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Seasonal patterns of natural singing by (a) female and (b) male antbirds (*Hypocnemis peruviana*) at CICRA in 2006–2008.

**Figure S2** Seasonal patterns of natural singing by (a) female and (b) male antbirds (*Hypocnemis subflava*) at CICRA in 2006–2008.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be reorganized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Received 2 January 2011; revised 22 May 2011; accepted 24 May 2011