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Ecology and behavior predict an evolutionary trade-off between song complexity and elaborate plumages in antwrens (Aves, Thamnophilidae)

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The environment can impose constraints on signal transmission properties such that signals should evolve in predictable directions (Sensory Drive Hypothesis). However, behavioral and ecological factors can limit investment in more than one sensory modality leading to a trade-off in use of different signals (Transfer Hypothesis). In birds, there is mixed evidence for both sensory drive and transfer hypothesis. Few studies have tested sensory drive while also evaluating the transfer hypothesis, limiting understanding of the relative roles of these processes in signal evolution. Here, we assessed both hypotheses using acoustic and visual signals in male and female antwrens (Thamnophilidae), a species-rich group that inhabits diverse environments and exhibits behaviors, such as mixed-species flocking, that could limit investment in different signal modalities. We uncovered significant effects of habitat (sensory drive) and mixed-species flocking behavior on both sensory modalities, and we revealed evolutionary trade-offs between song and plumage complexity, consistent with the transfer hypothesis. We also showed sex- and trait-specific responses in visual signals that suggest both natural and social selection play an important role in the evolution of sexual dimorphism. Altogether, these results support the idea that environmental (sensory drive) and behavioral pressures (social selection) shape signal evolution in antwrens.

KEY WORDS: Formicivorini, loudsong, plumage, sensory drive hypothesis, sexual dimorphism, transfer hypothesis.

Animal communication is subject to a complex combination of selective pressures, including sexual, social, and natural selection. Communication consists of transmitting information from signalers to receivers and can occur in different sensory modalities, including visual, auditory, olfactory, and tactile. Signals have diverse communication purposes such as courtship, territorial defense, group maintenance, and minimizing predation (Bradbury and Vehrencamp 1998). Thus, both sexual selection (Darwin 1871) and social selection (West-Eberhard 1983, 2014; Lyon and Montgomerie 2012) are thought to drive differentiation in signals between the sexes (i.e., sexual dimorphism) and diversification among species. Sexual selection occurs in sexual contexts such as mate choice and fertilization, whereas social selection on signals occurs in nonsexual contexts, such as territoriality and parental choice (Lyon and Montgomerie 2012). Moreover, signal evolution is also influenced by environmental constraints (i.e., Sensory Drive Hypothesis) and limitations on investment in multiple signal modalities (i.e., Transfer Hypothesis). The relative roles of these different selective pressures in shaping signal evolution remain an open question (Tobias et al. 2014).

Sensory drive posits that selection favors signaling traits that increase transmission efficacy in a given habitat (Endler 1992, 1993). However, the relative influence of sensory drive on signal evolution varies among signal modalities and taxonomic groups (Cummings and Endler 2018). Environmental conditions, such as vegetation density, ambient noise, and wind, can affect signal transmission (Wiley 2006, 2013). For example, sound attenuation is stronger in grasslands (open habitat) than it is in forests (closed habitat) due to a greater exposure to wind, variable temperatures, and air turbulence that affect sound propagation (i.e., Acoustic Adaptation Hypothesis; Morton 1975). Such biophysical properties place constraints on signal evolution and vary with environmental conditions. Sensory drive shapes signal evolution and diversification in several animal groups, such as insects (Rutowski et al. 2007), fishes (Endler 1980), birds (Morton 1975), and mammals (Ey et al. 2009). However, even in some of the best-studied groups, such as birds, there is mixed evidence for the role of sensory drive in signal evolution (Boncoraglio and Saino 2007; Mejías et al. 2020; Mikula et al. 2021). This mixed evidence may result from trade-offs between different selective pressures and how they play out across species.

In addition to habitat effects, other costly factors, such as energetic limits, predation, and risk of parasitism, could restrict investment in signals in more than one sensory modality (Endler 1993; Partan and Marler 1999; Partan and Marler 2005). High costs involved in producing multiple signals and mate preferences for a specific signal type could result in evolutionary trade-offs between signals of different modalities (Shutler 2011; Iwasa and Pomiankowski 1994), which is known as the Transfer (Gilliard 1956) or Trade-off hypothesis (Repentigny et al. 2000). Darwin (1871) observed that birds with elaborate plumages usually have simple songs, whereas those with simple plumages have complex songs. Nonetheless, only a few studies tested the transfer hypothesis within a comparative framework, which yielded conflicting results. Although only two studies found support for a trade-off between song complexity and plumage elaboration (Badyaev et al. 2002 and Laverde-R et al. 2017), most studies found no association (Ornelas et al. 2009; Mason et al. 2014; Gomes et al. 2017 and Matysioková et al. 2017a) or uncovered a positive association between these signal modalities (Shutler and Weatherhead 1990; Repentigny et al. 2000; Gonzalez-Voyer et al. 2013; Webb et al. 2016; Ligon et al. 2018). These conflicting results might arise from methodological differences or because this is not a universal mechanism. Additionally, such trade-offs may only occur under specific environmental constraints (i.e., sensory drive). Only a few studies have tested the transfer hypothesis considering habitat conditions as a covariate (Gonzalez-Voyer et al. 2013; Mason et al. 2014; Laverde-R et al. 2017; Gomes et al. 2017; Ligon et al. 2018), despite known environmental constraints on signals varying among habitats (Cummings and Endler 2018). Furthermore, these signal evolution hypotheses have primarily been assessed on males, and selective pressures acting on female signals remain generally unknown (Odom and Benedict 2018, Riebel et al 2019).

Antbirds (Aves, Thamnophilidae) are ideal for evaluating the relative roles of different selective pressures in shaping the evolution of male and female signals in multiple modalities. They are a Neotropical group of 235 sexually dimorphic insectivorous passerines found in humid lowland forests (Zimmer and Isler 2003). Antbirds are known for being very active vocally (Isler et al. 1998) and for having entirely innate vocalizations (Touchton et al. 2014) that have evolved partly in response to their acoustic environment (i.e., sensory drive; Seddon 2005). Their plumage coloration mostly is in shades of brown, gray, and black, and its brightness varies in response to light environments (i.e., sensory drive; Marcondes and Brumfield 2019). Within antbirds, the antwrens in the tribe Formicivorini are a group of 36 species strongly supported by recent molecular studies (Irestedt et al. 2004; Moyle et al. 2009; Bravo et al. 2012; Bravo et al. 2014). These small birds inhabit a wide diversity of habitats and exhibit contrasting patterns of acoustic and visual signals. They occur primarily in lowland forests and savannas, and different species are associated with different habitats (e.g., flooded forests, white sand forests) and microhabitats (e.g., understory, canopy), which vary significantly in light (Walther 2002) and acoustic conditions (Tobias et al 2010). Their primary vocalizations—known as loudsongs—consist of a series of notes that vary in duration, intensity, frequency, and structure (Willis 1967). Antbird loudsongs are species specific, both sexes emit them, and seem to be involved in territorial and mating defense (Zimmer and Isler 2003), particularly when produced in duets by pairs (e.g., Morton 1996; Fedy and Stutchbury 2005; Seddon and Tobias 2006; Koloff and Mennill 2011; 2013; Tobias et.al. 2011). They also produce distinctive types of calls emitted repeatedly in specific social contexts, such as avoiding predators and forming/maintaining groups (e.g., Wiley 1971; Munn and Terborgh 1979; Gradwohl and Greenberg 1980). Although antwrens show little vocal sexual dimorphism, at least to average human perceptual capacities, females of some species tend to produce higher-pitched and shorter vocalizations (Zimmer and Isler 2003). Nonetheless, variations in female vocalizations and the extent of antbird vocal sexual dimorphism remain essentially unexplored.

Antwrens are sexually dichromatic exhibiting slight variation in plumage coloration but high variation in patterning, ranging from plain colors to spots and streaks around their bodies (Zimmer and Isler 2003). Contrasting plumage patches are usually exhibited in stereotyped body motions (e.g., wing-flashing, back-ruffling) combined with vocalizations during agonistic encounters (Skutch 1996; Zimmer and Isler 2003). Another remarkable aspect of antwrens' behavior is their participation in mixed-species flocks (Wiley 1971; Jones 1977; Gradwohl and Greenberg 1980; Munn 1985). In mixed-species flocking, groups of individuals of different species meet and move together through the forest to optimize foraging and decrease the chances of predation (Powell 1979). Although some species are obligate or facultative members of mixed-species flocks, others forage in singles or small family groups (Bravo et al. 2014; Zimmer and Isler 2003). Because inter- and intraspecific communication is critical for forming and maintaining mixed-species flocks (Powell 1979), social selection on signals should be stronger in species engaging in this behavior relative to species that do not join mixed-species flocks. Altogether, this group represents an opportunity to assess the relative roles of different selective pressures in signal evolution.

Here, we integrate a genome-scale phylogeny of the tribe Formicivorini with vocal, plumage, ecological, and behavioral data within a comparative phylogenetic framework to simultaneously test the sensory drive and transfer hypotheses while assessing the influence of mixed-species flocking foraging behavior (social selection) on the diversity of acoustic and visual signals. We tested these hypotheses considering plumage and vocal traits of males and females separately, as well as the degree of sexual dimorphism. We predicted a negative association between acoustic and visual signals (transfer hypothesis) with an influence of habitat effects (i.e., sensory drive; conspicuousness or crypsis of acoustic and visual signals depending on the habitat conditions) and mixed-species flocking behavior (social selection) in the diversity of these signals (i.e., species engaging in mixed-species flocking behavior exhibiting more diversified signals than those of the species that do not engage it). This study sheds light on the mechanistic underpinnings of avian visual and acoustic signal evolution, considering multiple selective pressures while also directly examining the role of female signaling.

Methods

PHYLOGENETIC HYPOTHESIS

We subsampled a species-level phylogeny of the suborder Tyranni (Harvey et al. 2020) containing data for 54 museum specimens (Supporting Information) representing all but one (the critically endangered *Terenura sicki*) of 36 species, and 53 of 74 subspecies currently recognized in the Formicivorini (Remsen et al. 2018). This sampling captured 97% of extant species-level diversity and >70% of subspecific diversity. These data were collected using a sequence capture approach targeting ultraconserved elements (Faircloth et al. 2012) and conserved exons across the genome (Zucker et al. 2016). Our comparative analyses used a maximum likelihood tree estimated in ExaML based on a concatenated dataset with 100 bootstrap replicates (see details in Harvey et al. 2020). This tree was strongly supported with bootstrap support values lower than 70 for only nine of the 53 internal nodes. The phylogeny was time-calibrated using a node-based penalized likelihood approach with four calibration points corresponding to well-known fossils (Harvey et al. 2020).

ANALYSES OF VOCAL DATA

We collected a total of 267 audio recordings in .wav format (194 males and 73 females), corresponding to 64 and 38 taxa for males and females, respectively (Table S1). Selected recordings represent series of simple notes delivered in a stereotyped pattern (i.e., loudsongs sensu Willis 1967). Recordings were obtained from the Macaulay Library (https://www.macaulaylibrary.org), xeno-canto (https://www.xeno-canto.org), Fonoteca Neotropical Jacques Vielliard (https://www2.ib.unicamp.br/fnjv), Isler and Whitney (2002), and private audio collections. Loudsongs were analyzed using the software Raven Pro v1.5 following standardized protocols (Isler et al. 1998; Seddon 2005; Mason et al. 2014). Spectrograms, oscillograms, and power spectra were generated to measure loudsong duration, note count, note types, note rate, note diversity, minimum frequency, maximum frequency, peak frequency, loudsong bandwidth, and loudsong modulation rate (Seddon 2005; Mason et al. 2014; Matysioková et al. 2017a; Table S2). We used oscillograms to quantify time-related variables and inspected spectrograms visually to count the number of notes and note types. We used power spectra to measure frequency-based traits using a Hann window with 512 samples, a 3-dB filter bandwidth of 124 Hz, and a DFT (discrete Fourier transform) size of 512 samples (Fig. S1). We measured at least two loudsongs per recording and three males and three females per taxon, when available ($x^{-} = 3$ and 1.9 individuals/taxon for males and females, respectively). Although other types of vocalizations carrying important information in intra- and interspecific contexts, such as calls, could be relevant traits for this study (Isler et al. 2007; Tobias and Seddon 2009a), not enough well-annotated recordings were available to generate suitable sample sizes for our purposes.

To detect multicollinearity between vocal measurements, we performed a correlation analysis for each sex using the *stats* and *corrplot* version 0.84 (Wei and Simko 2017) packages in R (R Core Team 2018). Due to the high correlation between loudsong bandwidth and peak frequency, with minimum and maximum frequencies (>0.70 in males and >0.60 in females; Fig. S2), we discarded minimum and maximum frequencies, maintaining only loudsong bandwidth and peak frequency as frequency-based measurements. Although note count and note rate were highly correlated (0.74 in males and 0.76 in females; Fig. S2), we maintained both traits because note rate adds a temporal dimension to note count by representing the speed at which notes are produced. Thus, we performed downstream analyses using loudsong duration, note count, note types, note rate, note diversity, peak frequency, loudsong bandwidth, and loudsong modulation rate. All traits were log-transformed before performing analyses to ensure residuals approximate a normal distribution. Following Shultz and Burns (2017), we quantified vocal sexual dimorphism for every species as the Euclidean distance between male and female measurements across all vocal traits. Euclidean distances were calculated using the *dist* function of the *stats* package in R (R Core Team 2018).

ANALYSES OF PLUMAGE DATA

We obtained plumage coloration and pattern data from standardized photos of museum specimens allowing quantification of plumage coloration and pattern simultaneously. We photographed a total of 606 specimens (319 males; 287 females) representing 73 taxa for males and 70 for females ($x^{-} = 4.4$ and 4.1 specimens/taxon for males and females, respectively; Table S3). We gathered data from nine different topographical body regions: head (i.e., crown and nape), throat, breast, belly, back, cheek, flanks, wing coverts, and tail (Fig. S3). We grouped breast and belly as a single region—referred to as "belly"—due to the difficulty of delimiting them in museum specimens. We took photos in RAW format with a Canon T5 camera (Canon Inc.) using a standard 18% gray card (GC-3 3-in-1 Digital Gray Card; JJC Photography Equipment Co., Ltd) and a measuring tape to standardize color and size proportions across images (Stevens et al. 2007). We used the Image calibration and analysis toolbox plugins of the software ImageJ (Troscianko and Stevens 2015) to calibrate photos and measure plumage traits. We obtained standardized directive RGB reflectance values, luminance, pattern, and contrast measurements. Standardized directive RGB reflectance values corresponded to the Red, Green, and Blue color channels based on the camera color system. Images were in 16-bit, so RGB reflectance values ranged from 0 to 65,535 and were relative to the 18% gray standard card. Luminance was calculated from the sum of the RGB values and represented the intensity of luminosity (i.e., darker plumages have lower luminance values, and brighter plumages have higher luminance values) (Endler 2012). Plumage pattern analyses are based on Fast Fourier bandpass filtering and consists of filtering each image at multiple spatial frequency scales and quantifying the "energy" at each scale, measured as the standard deviation of the filtered pixels values (Troscianko and Stevens 2015; reviewed by Mason and Bowie 2020). This form of analysis is also called granularity analysis and is based on the mechanism of neurophysiological image processing in vertebrates and invertebrates (Godfrey et al. 1987; Stoddard and Stevens 2010). We performed these analyses using the green channel, which is recommended when images are not converted into the avian visual model (Spottiswoode and Stevens 2010). Pattern measurements included maximum energy (energy at the maximum frequency) and summed energy (energy summed across all spatial frequencies). High energy values are a proxy for elaborate plumage patterns, whereas low values suggest uniform patterns.

Lastly, we used a separate tool to measure contrast of topographical body regions known to commonly have spots and streaks (i.e., throat, belly, wing coverts, head, and back). Contrast was measured using the Adaptive thresholding tool in ImageJ, which automatically selects and measures the values of dark (maculation) and light (background) areas of selected regions. The calculated proportion of maculation and background luminance is a proxy for contrast. Lower proportion values represent darker maculation (i.e., lower luminance values) and brighter background (i.e., higher luminance values), corresponding to a higher contrast, whereas higher proportion values represent more similar maculation and background values (i.e., spots/streaks in less quantity or with luminance more similar to the background) indicating a lower contrast. Although our photographic methods do not consider UV spectra and the avian visual model directly, they can generate results with similar patterns as those obtained with spectrometric data (Bergeron and Fuller 2018). Furthermore, independent analyses of coloration in this group based on spectrometric data obtained from standard museum specimens showed that their proportion of UV reflectance is negligible (Seddon et al. 2010; Marcondes and Brumfield 2019).

After capturing plumage measurements for all body regions, we pooled them into dorsal (means of crown, nape, and back), ventral (means of throat, breast, belly, and flanks), and wing coverts. Tails ventral side was not included in the pooled ventral region because of the difficulties in capturing it in photographs of museum specimens. Then, we assessed pair-wise correlations for all plumage traits for each sex, as described for vocal traits. We observed a high correlation between RGB and luminance values in all body regions in both sexes (>0.8; Fig. S4). Also, maximum energy and summed energy were highly correlated for each body region in both sexes (>0.9; Fig. S4). Thus, we discarded RGB values and summed energy, maintaining luminance, maximum energy, and contrast of each body region (i.e., dorsal, ventral, and wing coverts). Although luminance was highly correlated with maximum energy in some body regions (>0.70 with male dorsal and wing regions, >0.70 with female wing; Fig. S4), we maintained both traits because they represent the intensity of luminosity and pattern, respectively, which are distinct plumage features. Finally, to obtain an index of plumage sexual dimorphism, we calculated Euclidean distances between selected plumage measurements of males and females of each taxon, as described for vocal mea-

Table 1. List of additive and interactive models tested in PGLS analyses.

	Additive models		Interactive models
1	A base model with no covariates	1.a	Base model
2	Habitat exposure as a covariate	1.b	Habitat exposure interaction
3	Foraging strata as a covariate	2.a	Base model
4	Mixed-species flocking behavior as a covariate	2.b	Foraging strata interaction
5	Habitat exposure + Foraging strata as covariates	3.a	Base model
6	Habitat exposure + Mixed-species flocking behavior as covariates	3.b	Mixed-species flocking behavior interaction
7	Foraging strata + Mixed-species flocking behavior as covariates		
8	Habitat exposure + Foraging strata + Mixed-species flocking behavior as covariates		

surements (i.e., following Shultz and Burns 2017). All traits were log-transformed before downstream analyses to ensure residuals approximate a normal distribution.

ECOLOGICAL AND BEHAVIORAL DATA

We obtained information on habitat, foraging strata, and mixed-species flocking behavior for each species from the literature (e.g., Munn 1985; Ridgely and Tudor 1994; Whitney 1994; Whitney and Pacheco 1997; Zimmer and Isler 2003; see detailed description in Bravo et al. 2014). We classified habitat exposure for each species as exposed or unexposed, according to how different habitats expose birds to direct sunlight, precipitation, and wind (e.g., birds in canopy and nonforested environments are more exposed than birds in the forest understory). Because there is no comprehensive quantitative information about habitat and microhabitat use for antwrens, this categorization represents a subjective interpretation of habitat preferences for each species based on the references above. We classified foraging strata as understory, midstory, and canopy. The classification of mixed-species flocking behavior was divided into no formation, occasional to common, and obligate mixed-species flocking formation following Bravo et al. (2014) (Table S4).

MODELS OF CHARACTER EVOLUTION FOR PLUMAGE AND VOCAL TRAITS

To assess which model of character evolution better explains the evolution of plumage and vocal traits, we used the function *fitContinuous* from the Geiger version 2.0.6.2 package in R (Harmon et al. 2008). We assessed Brownian motion (BM), which represents a stochastic process without selection, Ornstein-Uhlenbeck (OU), which represents a variation of BM with selection towards an adaptive optimum, and Pagel's lambda, which estimates the strength of phylogenetic signal using the lambda parameter value (Pagel 1999). The information for the selected mode of character evolution for each trait is summarized in Tables S5–S7. Best-fit models were based on the Akaike Information Criterion corrected for small sample sizes (AICc; Sugiura 1978; Hurvich and Tsai 1989), being the most informative model that with the lowest AICc value, and any model with a value of ΔAICc less or equal two was considered an equally informative model.

ANALYSES AND MODEL SELECTION OF PHYLOGENETIC GENERALIZED LEAST SQUARES

To assess the association between plumage and vocal traits, we conducted Phylogenetic Generalized Least Squares analyses (PGLS; Martins and Hansen 1997), a phylogenetic comparative method that allows testing the association, interaction, and additive effects between a suite of variables simultaneously under different evolutionary models. Therefore, it allowed testing sensory drive and transfer hypotheses, as well as to assess the influence of mixed-species flocking behavior on the structural diversity of acoustic and visual signals. We performed PGLS analyses in R (R Core Team 2018) using the packages Ape version 5.3 (Paradis et al. 2004), nlme version 3.1-152 (Pinheiro et al. 2013), and MuMIn version 1.42.1 (Barton 2018).

We assessed the association between plumage and vocal traits of eight different nested combinations starting with a null model in which none of the variables were covariates, and finishing with a model of additive effects of all the covariates (Table 1). We tested each combination of traits under the BM, OU, and Pagel's lambda modes of character evolution, as follows: If the same model of character evolution best explained both plumage and vocal traits, we assessed the eight combinations of PGLS analyses under this model. When different models of character evolution best explained plumage and vocal traits, we performed PGLS analyses assuming both models, summing up to a total of 16 combinations. If more than one model of character evolution explained each plumage or each vocal trait due to equally informative models (i.e., ΔAICc less or equal two), we performed PGLS analyses assuming all models, summing up to a total of 24 combinations. We arbitrarily chose plumage traits as dependent variables and vocal traits as predictors. First, we tested the association between plumage and vocal sexual dimorphism. Then, we tested the association between plumage and vocal traits for each sex separately. The best-fit models for each pair of plumage and vocal traits were chosen based on the AICc (Sugiura 1978; Hurvich and Tsai 1989). The most informative model had the lowest AICc value, and any model with a value of ΔAICc ≤ 2 was considered a competing model. Also, we calculated the Akaike weights (ω_i) to quantify their relative likelihood (Burnham and Anderson 2002). We considered no association when effect sizes of best-fit models equaled zero or when they were lower than standard errors. Positive associations were considered when the effect size had positive values higher than its standard error. Negative associations were considered when the effect size had negative values higher than its standard error.

To test for effects of ecology and behavior on associations between plumage and vocal traits, we performed a second round of PGLS analyses that included interaction effects of habitat exposure, foraging strata, and mixed-species flocking behavior (Table 1). Specifically, we assessed interactive models using those plumage and vocal trait pairs for which most informative models revealed either a negative or positive association in the first round of PGLS analyses. We performed tests under BM, OU, and Pagel’s lambda modes of character evolution, and we selected the best-fit models as described above.

PHYLOGENETIC PATH ANALYSES

To summarize the effects of habitat exposure, foraging strata, and mixed-species flocking behavior on plumage and vocal traits and assess the directionally of these effects, we conducted phylogenetic path analyses (Hardenberg and Gonzalez-Voyer 2013). This phylogenetic comparative method allows explicitly testing the relative importance of alternative models of causal evolutionary hypotheses among independent variables, while assessing direct and indirect paths of influence on a dependent variable. In other words, it offers the opportunity to test whether the association between variables implies underlying causation (Gonzalez-Voyer and Von Hardenberg 2014). Thus, phylogenetic path analyses allowed us to test the sensory drive hypothesis and possible influences of mixed-species flocking behavior on the structural diversity of acoustic and visual signals with a more accurate estimation of effect values and directionally. We performed phylogenetic path analyses using the package Phylopath version 1.0.2 (Hardenberg and Gonzalez-Voyer 2013; van der Bijl 2018) in R. Because Phylopath accepts binary categorical variables only, we reclassified foraging strata into understory/midstory and canopy, and mixed-species flocking behavior into presence and absence for mixed-species flocking behavior. Therefore, we tested 13 models considering different combinations of habitat exposure, foraging strata, and mixed-species flocking behaviors on both vocal and plumage traits (Table 2).

Table 2. List of the 13 different models tested in phylogenetic path analyses.

	Model
1	Null model (no effect of any ecological/behavioral condition on all plumage and vocal traits)
2	Habitat exposure effect on all plumage traits
3	Foraging strata effect on all plumage traits
4	Mixed-species flocking effect on all plumage traits
5	Habitat exposure + Foraging strata + Mixed-species flocking effects on all plumage traits
6	Habitat exposure effect on all vocal traits
7	Foraging strata effect on all vocal traits
8	Mixed-species flocking effect on all vocal traits
9	Habitat exposure + Foraging strata + Mixed-species flocking effects on all vocal traits
10	Habitat exposure effect on all plumage and vocal traits
11	Foraging strata effect on all plumage and vocal traits
12	Mixed-species flocking effect on all plumage and vocal traits
13	Habitat exposure + Foraging strata + Mixed-species flocking effects on all plumage and vocal traits

All models were tested under BM and OU, summing up to a total of 26 models. We conducted model selection based on the C-statistic Information Criterion corrected for small sample sizes (CICc; Cardon et al. 2011; Hardenberg and Gonzalez-Voyer 2013). The most informative model had the lowest CICc value, and any model with a value of ΔCICc ≤ 2 was considered as equally informative. Also, we used the CICc weights (ω_i) to quantify the relative likelihood of each model.

Results

ASSOCIATION BETWEEN PLUMAGE AND VOCAL SEXUAL DIMORPHISM

We found no association between plumage and vocal sexual dimorphism (Fig. 1; Table 3). The most informative models considered no ecological and behavioral covariates under BM (Fig. 1; Tables 3 and S9) and with no interaction effects of ecology and behavior (Table S12).

ASSOCIATION BETWEEN PLUMAGE AND VOCAL TRAITS IN MALES

We found inverse relationships between plumage complexity traits and frequency-based and qualitative structural vocal traits (i.e., note diversity and note type). In other words, males with

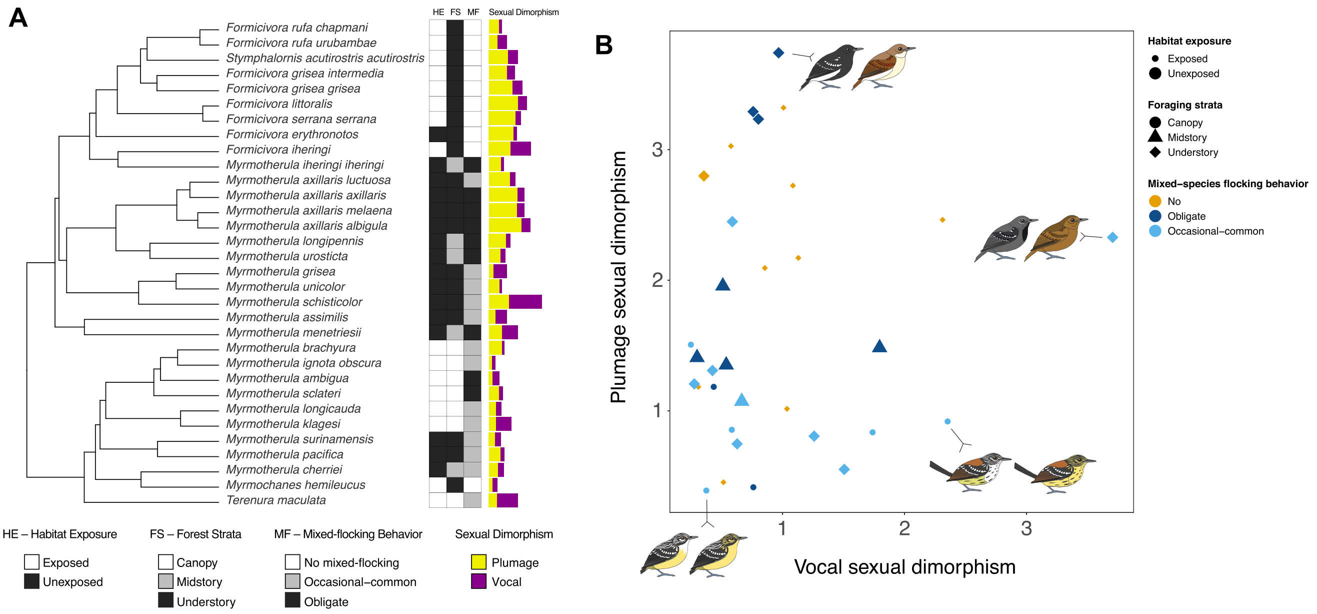

Figure 1. (A) Phylogeny of the Formicivorini with mapped ecological, behavioral, plumage, and vocal sexual dimorphism for each taxon. Habitat exposure, foraging strata, and mixed-species flocking behavior are represented in the grayscale heatmap. Plumage and vocal sexual dimorphism are represented in the bar plot. (B) Scatterplot illustrating the lack of association between plumage and vocal sexual dimorphism in antwrens. Sexual dimorphism is measured as the Euclidean distance of the average of log-transformed values for each sex per taxon. Because the standard error (0.17) is too close to the effect size value (0.16) obtained in the PGLS, there is no association between sexual dimorphism of plumage and vocal traits. Species illustrations from top to bottom: *Myrmotherula axillaris albigula*, *Myrmotherula schisticolor*, *Terenura maculata*, and *Myrmotherula ignota obscura*. Illustrations are our own.

more patterned dorsal regions and brighter dorsal and wing regions tended to have loudsongs with lower note diversity, lower number of note types, narrower bandwidth, and lower loudsong modulation rate (Figs. 2 and S5; Table 3). Also, males with more patterned dorsal regions and contrasting wing plumages tended to have longer loudsongs with more notes. (Fig. S5; Table 3). We found that mixed-flocking behavior had a prominent effect across models and traits on the variation of vocal and plumage traits. Furthermore, we found additive effects of mixed-flocking behavior and habitat to be important players in all associations between maximum dorsal energy and all vocal traits (Table 3).

Habitat and mixed-flocking behavior interaction effects strengthened the negative associations between plumage and vocal traits. We observed this result for dorsal plumage traits and frequency-based and qualitative structural vocal traits, such as dorsal maximum energy and dorsal luminance versus loudsong modulation rate, loudsong bandwidth, and note diversity (Figs. 2 and S7; Table 3). Also, positive associations between dorsal maximum energy versus loudsong duration were amplified by interactive effects of habitat and mixed-flocking behavior, and dorsal maximum energy versus peak frequency was strengthened by interactions with mixed-flocking behavior (Fig. S7; Table 3).

ASSOCIATION BETWEEN PLUMAGE AND VOCAL TRAITS IN FEMALES

For females, we found similar associations between vocal and plumage traits to those uncovered in males. We found negative associations between plumage complexity traits with frequency-based and qualitative structural vocal traits. Females with brighter, more contrasting, and more patterned plumages tended to have narrower bandwidth loudsongs with a lower note diversity, lower number of note types, as well as lower loudsong modulation rate and peak frequency (Figs. 3 and S6; Table 3). On the other hand, we observed only a few positive associations, indicating that females with more contrasting plumages, brighter wing regions, and more patterned ventral regions tended to have loudsongs with more notes produced at a higher rate (Fig. S6; Table 3). The only discordant results for this generally positive association between plumage and quantitative vocal traits were the negative associations of dorsal luminance with loudsong duration and note count. Regarding the effects of ecological and behavioral traits, they covaried in most models following no definite pattern, but they appeared not to affect those associations involving ventral contrast and wing maximum energy (Table 3).

Habitat and mixed-flocking behavior interaction effects maintained or strengthened the negative associations between plumage and vocal traits. We observed this result for dorsal and

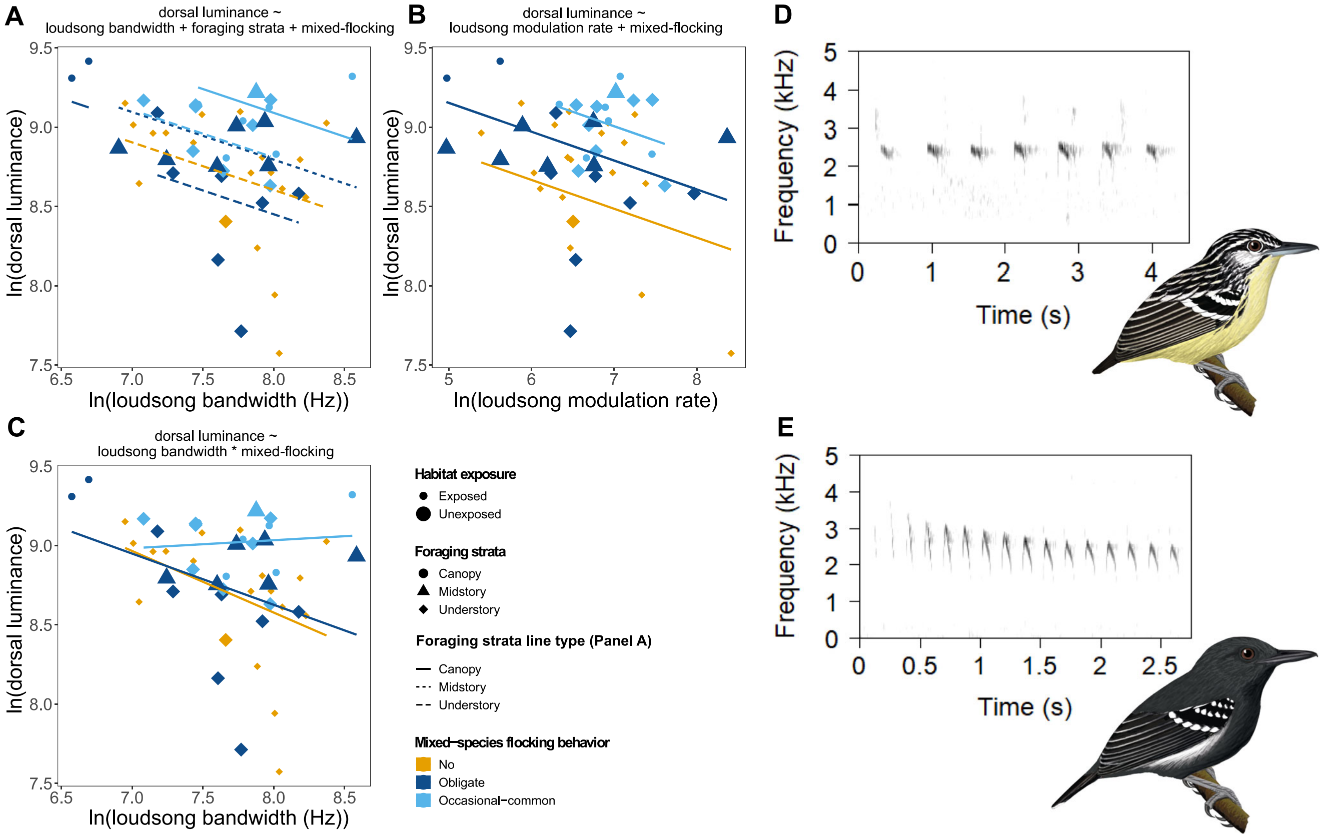

Figure 2. Subset of scatterplots illustrating the strongest trade-offs (i.e., negative associations in PGLS models) between plumage and vocal traits in male antwrens: (A) Dorsal luminance versus loudsong bandwidth with foraging strata and mixed-flocking behavior additive effects; (B) Dorsal luminance versus loudsong modulation rate with mixed-flocking behavior additive effect; and (C) Dorsal luminance versus loudsong bandwidth with mixed-flocking behavior interaction effect. Species spectrograms with their respective illustrations of males of two species with opposite trade-offs: (D) *Myrmotherula ambigua*—Elaborate plumage and a simple loudsong structure; (E) *Myrmotherula axillaris*—Simple plumage and a more complex loudsong. Species illustrations made and provided with permission by F. Ayerbe-Quiñones.

wing plumage traits and complexity vocal traits, such as dorsal and wing maximum energy, dorsal luminance, and wing contrast versus loudsong modulation rate, loudsong bandwidth, peak frequency, and note diversity (Figs. 3 and S8; Table 3). The positive association between ventral contrast and note count was amplified by interactions with habitat and mixed-flocking behavior (Fig. S8; Table 3).

PATH ANALYSES OF ECOLOGICAL AND BEHAVIORAL EFFECTS ON PLUMAGE AND VOCAL TRAITS

The most informative model considered effects of habitat exposure, foraging strata, and mixed-species flocking behavior on plumage and vocal traits under BM (CICc = 2316.97, $\omega_i = 1$; Table S15). We found both negative and positive effects of these ecological and behavioral traits depending on the type of plumage and vocal trait (Fig. 4; Table S16). Mixed-flocking behavior has a negative effect on plumage sexual dimorphism, indicating that sexes of those species that forage in mixed flocks tend to be more similar to one another than sexes of species that do not. We also found a general trend of opposite effects of ecological and behavioral traits on plumage and vocal traits. Specifically, we uncovered primarily positive effects of mixed-species flocking behavior and foraging strata and negative impacts of habitat for plumage traits of both sexes. We mainly found negative impacts of mixed-species flocking behavior and foraging strata and positive effects of habitat on vocal traits (Table S16).

Altogether, our results showed that males of species that join mixed-species flocks tended to have darker and more patterned ventral regions, brighter, more patterned, and more contrasting upper parts, and brighter and more patterned wing coverts. Likewise, females were also more likely to have darker and more patterned lower parts, more patterned and contrasting upperparts, and brighter wing coverts (Fig. 4; Table S16). Males of species that forage in mixed-species flocks tended to have loudsongs with higher peak frequencies but with fewer types of different notes than those antwrens that forage in singles, pairs, or family groups.

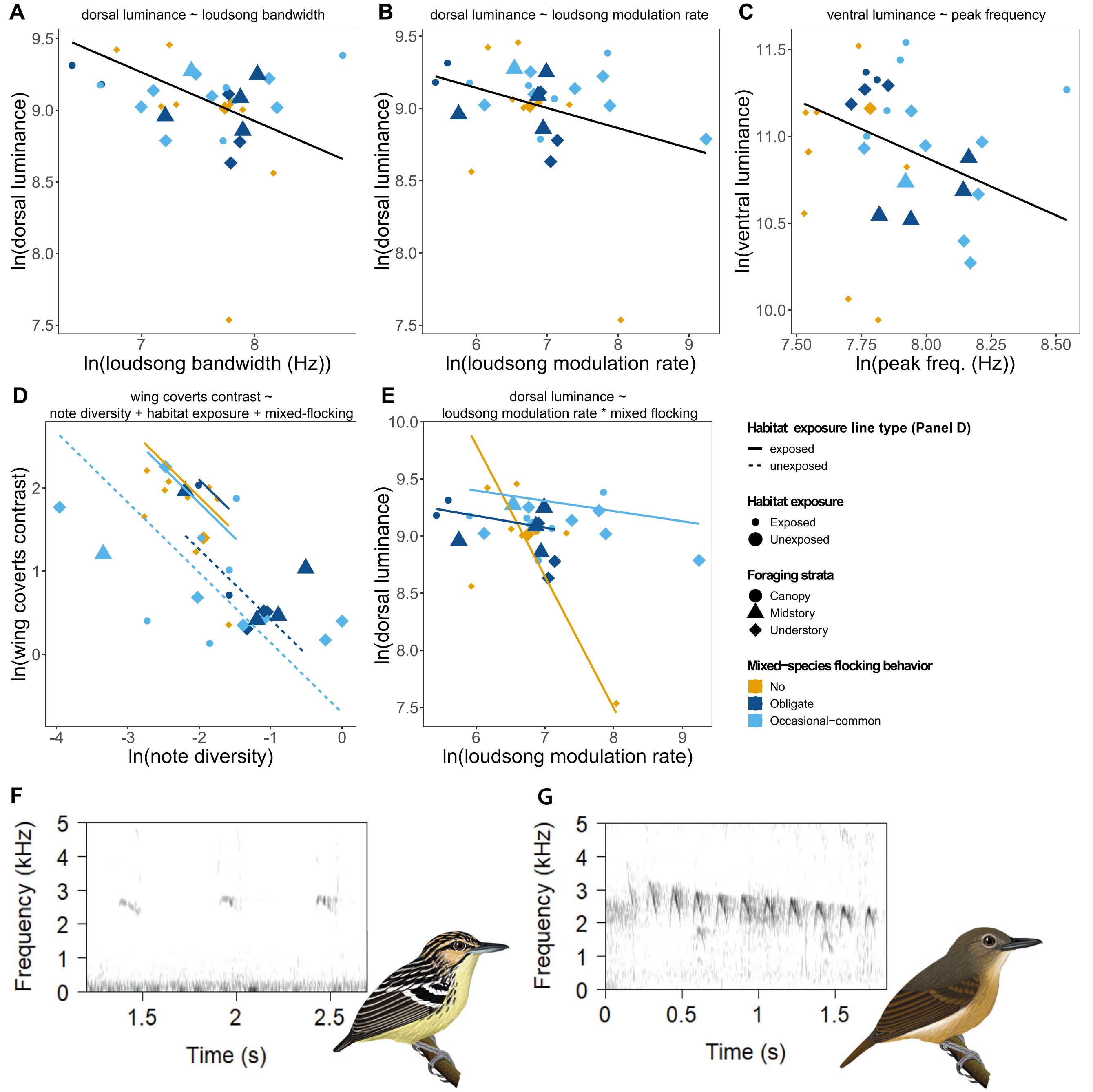

Figure 3. Subset of scatterplots illustrating the strongest trade-offs (i.e., negative associations in PGLS models) between plumage and vocal traits in females antwrens: (A) Dorsal luminance versus loudsong bandwidth; (B) Dorsal luminance versus loudsong modulation rate; (C) Ventral luminance versus peak frequency; (D) Wing coverts contrast versus note diversity with habitat exposure and mixed-flocking behavior additive effect; and (E) Dorsal luminance versus loudsong modulation rate with mixed-flocking behavior interaction effect. Species spectrograms with their respective illustrations of females of two species with opposite trade-offs: (F) *Myrmotherula ambigua*—Elaborate plumage and a simple loudsong structure; (G) *Myrmotherula axillaris*—Simple plumage and a more complex loudsong. Species illustrations made and provided with permission by F. Ayerbe-Quiñones.

Females of species in mixed-species flocks also were more likely to have fewer types of notes in their loudsongs.

Males in the lower strata — understory and midstory — tended to have darker and more patterned lower parts, more patterned and contrasting wing coverts, and loudsongs with a lower number of different note types. Females in the lower foraging strata also had darker ventral regions, but their upper parts tended to be less patterned. Their loudsongs followed the same pattern

Table 3. PGLS results for the associations between plumage and vocal sexual dimorphism, and plumage and vocal traits in males and in females.

Sex	Plumage traits (dependent)	Vocal traits (predictor)	FS	HE	MF	Evolutionary model	AICc	ΔAICc	ω_i	Effect size ± SE	*t*-value	*P*-value
Sexual dimorphism	Plumage sexual dimorphism	Vocal sexual dimorphism				BM	74.92	0.00	0.46	0.16 ± 0.17	0.94	0.35
Male	Dorsal luminance	Loudsong bandwidth	+		+	OU (α: 1)	43.29	0.00	0.34	–0.3 ± 0.11	–2.81	0.01
	Dorsal luminance	Loudsong bandwidth		+	+	OU (α: 1)	44.94	1.65	0.15	–0.26 ± 0.11	–2.40	0.02
	Dorsal luminance	Loudsong bandwidth			+	OU (α: 1)	45.13	1.83	0.14	–0.28 ± 0.11	–2.54	0.01
	Dorsal luminance	Loudsong bandwidth	+			OU (α: 1)	45.14	1.85	0.13	–0.23 ± 0.11	–2.15	0.04
	Dorsal luminance	Loudsong bandwidth	+	+	+	OU (α: 1)	45.25	1.96	0.13	–0.3 ± 0.11	–2.81	0.01
	Dorsal luminance	Loudsong modulation rate			+	PL (λ: 0.61)	40.19	0.00	0.34	–0.18 ± 0.07	–2.56	0.01
	Dorsal luminance	Loudsong modulation rate		+	+	PL (λ: 0.56)	41.82	1.63	0.15	–0.18 ± 0.07	–2.44	0.02
	Dorsal luminance	Note type	+			OU (α: 1)	46.08	0.00	0.30	–0.21 ± 0.11	–1.92	0.06
	Dorsal luminance	Note type	+		+	OU (α: 1)	47.00	0.92	0.19	–0.21 ± 0.11	–2.04	0.05
	Dorsal maximum energy	Loudsong duration		+	+	BM	48.64	0.00	0.47	0.18 ± 0.09	2.01	0.05
	Dorsal maximum energy	Loudsong duration			+	BM	48.88	0.24	0.42	0.2 ± 0.09	2.19	0.03
	Dorsal maximum energy	Loudsong modulation rate		+	+	BM	49.61	0.00	0.34	–0.13 ± 0.07	–1.76	0.08
	Dorsal maximum energy	Loudsong modulation rate			+	BM	50.12	0.51	0.27	–0.14 ± 0.08	–1.89	0.07
	Dorsal maximum energy	Loudsong modulation rate		+	+	PL (λ: 0.93)	51.14	1.53	0.16	–0.15 ± 0.08	–1.98	0.05
	Dorsal maximum energy	Note count		+	+	BM	50.24	0.00	0.47	0.14 ± 0.09	1.58	0.12
	Dorsal maximum energy	Note count			+	BM	51.78	1.54	0.22	0.13 ± 0.09	1.40	0.17
	Dorsal maximum energy	Note diversity		+	+	BM	49.34	0.00	0.45	–0.16 ± 0.09	–1.84	0.07
	Dorsal maximum energy	Note diversity			+	BM	51.08	1.74	0.19	–0.15 ± 0.09	–1.62	0.11
	Wing coverts luminance	Loudsong bandwidth	+	+	+	PL (λ: 0.76)	1.56	0.00	0.34	–0.14 ± 0.07	–1.88	0.07

(*Continued*)

Table 3. (Continued).

Sex	Plumage traits (dependent)	Vocal traits (predictor)	FS	HE	MF	Evolutionary model	AICc	ΔAICc	ω_i	Effect size ± SE	*t*-value	*P*-value
	Wing coverts luminance	Loudsong bandwidth		+	+	PL (λ: 0.81)	1.63	0.07	0.33	–0.1 ± 0.07	–1.29	0.20
	Wing coverts contrast	Loudsong duration	+	+		PL (λ: 0.73)	63.09	0.00	0.52	0.18 ± 0.11	–1.67	0.10
Female	Dorsal luminance	Loudsong duration				PL (λ: 1.09)	9.34	0.00	0.35	–0.11 ± 0	–213,777.38	<0.001
	Dorsal luminance	Loudsong duration			+	PL (λ: 1.09)	9.46	0.11	0.33	–0.11 ± 0	–151,696.88	<0.001
	Dorsal luminance	Loudsong bandwidth				PL (λ: 1.09)	7.41	0.00	0.82	–0.34 ± 0	–301,094.72	<0.001
	Dorsal luminance	Loudsong modulation rate				OU (α: 1)	27.48	0.00	0.23	–0.14 ± 0.08	–1.82	0.08
	Dorsal luminance	Loudsong modulation rate			+	BM	28.24	0.76	0.16	–0.15 ± 0.08	–1.81	0.08
	Dorsal luminance	Loudsong modulation rate			+	OU (α: 1)	29.21	1.73	0.10	–0.18 ± 0.08	–2.33	0.03
	Dorsal luminance	Note count				PL (λ: 1.09)	9.38	0.00	0.59	–0.13 ± 0	–230,623.63	<0.001
	Dorsal luminance	Note count		+		PL (λ: 1.09)	10.71	1.33	0.30	–0.13 ± 0	–150,043.90	<0.001
	Dorsal maximum energy	Loudsong bandwidth			+	BM	35.09	0.00	0.28	–0.2 ± 0.11	–1.70	0.10
	Dorsal maximum energy	Loudsong bandwidth			+	PL (λ: 1.08)	35.27	0.18	0.25	–0.16 ± 0.11	–1.49	0.15
	Dorsal maximum energy	Loudsong bandwidth		+	+	BM	36.74	1.64	0.12	–0.19 ± 0.11	–1.68	0.10
	Dorsal maximum energy	Loudsong modulation rate		+	+	OU (α: 1)	30.79	0.00	0.34	–0.29 ± 0.08	–3.49	0.002
	Dorsal maximum energy	Loudsong modulation rate			+	BM	31.10	0.32	0.29	–0.23 ± 0.09	–2.64	0.01
	Dorsal maximum energy	Loudsong modulation rate	+		+	OU (α: 1)	32.40	1.61	0.15	–0.27 ± 0.08	–3.17	0.004
	Dorsal maximum energy	Note diversity			+	BM	34.62	0.00	0.40	–0.18 ± 0.1	–1.83	0.08
	Dorsal maximum energy	Note diversity		+	+	BM	35.15	0.53	0.30	–0.21 ± 0.1	–2.08	0.05
	Dorsal maximum energy	Note diversity	+		+	BM	36.14	1.52	0.19	–0.22 ± 0.1	–2.22	0.04
	Dorsal maximum energy	Note type			+	BM	36.38	0.00	0.56	–0.23 ± 0.18	–1.29	0.21
	Dorsal contrast	Peak frequency			+	BM	–0.58	0.00	0.50	–0.34 ± 0.24	–1.43	0.16
	Dorsal contrast	Loudsong modulation rate			+	BM	–5.10	0.00	0.52	–0.13 ± 0.05	–2.57	0.02
	Dorsal contrast	Note count			+	BM	–3.52	0.00	0.35	0.11 ± 0.05	2.22	0.03

(*Continued*)

Table 3. (Continued).

Sex	Plumage traits (dependent)	Vocal traits (predictor)	FS	HE	MF	Evolutionary model	AICc	ΔAICc	ω_i	Effect size ± SE	*t*-value	*P*-value
	Dorsal contrast	Note count		+	+	BM	–2.85	0.67	0.25	0.13 ± 0.05	2.51	0.02
	Dorsal contrast	Note count	+	+		BM	–1.59	1.93	0.13	0.11 ± 0.05	2.23	0.03
	Dorsal contrast	Note count	+			BM	–1.57	1.95	0.13	0.12 ± 0.05	2.32	0.03
	Dorsal contrast	Note diversity	+	+		BM	–4.63	0.00	0.26	–0.15 ± 0.05	–2.85	0.01
	Dorsal contrast	Note diversity			+	BM	–4.61	0.02	0.25	–0.13 ± 0.05	–2.46	0.02
	Dorsal contrast	Note diversity	+			BM	–4.01	0.62	0.19	–0.16 ± 0.06	–2.83	0.01
	Dorsal contrast	Note diversity		+	+	BM	–3.70	0.93	0.16	–0.15 ± 0.05	–2.69	0.01
	Ventral luminance	Peak frequency				BM	24.76	0.00	0.42	–0.66 ± 0.33	–1.99	0.06
	Ventral luminance	Peak frequency	+			BM	25.85	1.09	0.25	–0.6 ± 0.33	–1.81	0.08
	Ventral luminance	Peak frequency		+		BM	26.17	1.41	0.21	–0.58 ± 0.34	–1.72	0.10
	Ventral maximum energy	Peak frequency				PL (λ: 1.09)	1.96	0.00	0.53	–0.45 ± 0.2	–2.21	0.03
	Ventral maximum energy	Note count	+	+	+	PL (λ: –3.55)	–33.32	0.00	1.00	0.27 ± 0.05	5.89	<0.001
	Ventral maximum energy	Note rate		+	+	PL (λ: –3.50)	–50.96	0.00	1.00	0.35 ± 0.03	12.95	<0.001
	Ventral contrast	Loudsong modulation rate				BM	10.81	0.00	0.50	–0.11 ± 0.06	–1.68	0.10
	Ventral contrast	Note count				BM	8.86	0.00	0.48	0.14 ± 0.06	2.21	0.03
	Ventral contrast	Note diversity				BM	11.13	0.00	0.44	–0.12 ± 0.07	–1.58	0.12
	Ventral contrast	Note diversity				OU (α: 1)	13.07	1.94	0.17	–0.09 ± 0.06	–1.54	0.13
	Wing coverts luminance	Note diversity		+	+	PL (λ: –0.61)	–3.70	0.00	0.61	–0.12 ± 0.05	–2.15	0.04
	Wing coverts luminance	Note diversity	+			PL (λ: –0.61)	–2.23	1.47	0.29	–0.13 ± 0.03	–4.07	<0.001
	Wing coverts luminance	Note rate		+	+	PL (λ: –3.54)	–17.68	0.00	1.00	0.12 ± 0.05	2.64	0.01
	Wing coverts maximum energy	Peak frequency				BM	51.21	0.00	0.53	–0.56 ± 0.5	–1.11	0.27
	Wing coverts contrast	Note count	+	+		PL (λ: –4.42)	38.29	0.00	0.78	0.25 ± 0.13	1.85	0.07
	Wing coverts contrast	Note diversity		+	+	PL (λ: –4.46)	28.61	0.00	0.50	–0.84 ± 0.14	–5.82	<0.001
	Wing coverts contrast	Note diversity		+		PL (λ: –4.50)	29.04	0.44	0.40	–0.74 ± 0.08	–8.91	<0.001
	Wing coverts contrast	Note rate	+	+	+	PL (λ: –4.48)	41.88	0.00	1.00	0.33 ± 0.19	1.72	<0.001

(*Continued*)

Table 3. (Continued).

Sex	Plumage traits (dependent)	Vocal traits (predictor)	FS	HE	MF	Evolutionary model	AICc	ΔAICc	ω_i	Effect size ± SE	*t*-value	*P*-value
Male	Dorsal luminance	Loudsong bandwidth			*	OU (α: 1)	48.45	0.00	0.48	–0.39 ± 0.18	–2.13	0.04
	Dorsal luminance	Loudsong bandwidth				OU (α: 1)	49.21	0.76	0.33	–0.25 ± 0.12	–2.11	0.04
	Dorsal luminance	Loudsong modulation rate		*		PL (λ: 0.61)	42.35	0.00	0.59	–0.3 ± 0.09	–3.43	0.001
	Dorsal luminance	Loudsong modulation rate				PL (λ: 0.60)	43.30	0.95	0.37	–0.17 ± 0.07	–2.42	0.02
	Dorsal luminance	Loudsong modulation rate			*	PL (λ: 0.59)	42.47	0.00	0.55	–0.33 ± 0.11	–3.00	0.004
	Dorsal luminance	Loudsong modulation rate				PL (λ: 0.60)	43.30	0.83	0.36	–0.17 ± 0.07	–2.42	0.02
	Dorsal maximum energy	Loudsong duration		*		BM	63.51	0.00	0.57	0.32 ± 0.12	2.73	0.01
	Dorsal maximum energy	Loudsong duration				BM	64.10	0.59	0.43	0.22 ± 0.11	2.01	0.05
	Dorsal maximum energy	Loudsong duration			*	BM	51.35	0.00	1.00	0.27 ± 0.1	2.60	0.01
	Dorsal maximum energy	Peak frequency			*	BM	57.28	0.00	0.98	0.76 ± 0.64	1.19	0.24
	Dorsal maximum energy	Loudsong modulation rate				BM	65.18	0.00	0.45	–0.15 ± 0.09	–1.71	0.09
	Dorsal maximum energy	Loudsong modulation rate		*		BM	65.84	0.66	0.32	–0.24 ± 0.1	–2.35	0.02
	Dorsal maximum energy	Loudsong modulation rate			*	BM	53.61	0.00	0.69	–0.23 ± 0.1	–2.23	0.03
	Dorsal maximum energy	Loudsong modulation rate			*	PL (λ: 0.93)	55.19	1.58	0.31	–0.29 ± 0.11	–2.59	0.01
	Dorsal maximum energy	Note diversity			*	BM	54.87	0.00	0.80	–0.21 ± 0.15	–1.45	0.15
Female	Dorsal luminance	Loudsong bandwidth				PL (λ: 1.09)	9.52	0.00	0.54	–0.34 ± 0	–136,866.57	<0.001
	Dorsal luminance	Loudsong bandwidth		*		PL (λ: 1.09)	9.86	0.34	0.46	–0.34 ± 0	–148,648.30	<0.001
	Dorsal luminance	Loudsong bandwidth			*	PL (λ: 1.09)	6.82	0.00	0.68	–0.34 ± 0	–141,005.34	<0.001
	Dorsal luminance	Loudsong bandwidth				PL (λ: 1.09)	8.34	1.53	0.32	–0.34 ± 0	–136,866.57	<0.001

(*Continued*)

Table 3. (Continued).

Sex	Plumage traits (dependent)	Vocal traits (predictor)	FS	HE	MF	Evolutionary model	AICc	ΔAICc	ω_i	Effect size ± SE	*t*-value	*P*-value
	Dorsal luminance	Loudsong modulation rate			*	PL (λ: –3.56)	–10.36	0.00	1.00	–1.15 ± 0.06	–18.09	<0.001
	Dorsal luminance	Note count		*		PL (λ: 1.09)	9.36	0.00	0.64	–0.13 ± 0	–139,320.89	<0.001
	Dorsal luminance	Note count				PL (λ: 1.09)	10.52	1.15	0.36	–0.13 ± 0	–130,710.72	<0.001
	Dorsal luminance	Note count				PL (λ: 1.09)	10.48	0.00	0.67	–0.13 ± 0	–130,710.72	<0.001
	Dorsal luminance	Note count			*	PL (λ: 1.09)	11.89	1.41	0.33	–0.13 ± 0	–380,585.30	<0.001
	Dorsal maximum energy	Loudsong modulation rate				BM	44.39	0.00	0.68	–0.24 ± 0.11	–2.27	0.03
	Dorsal maximum energy	Loudsong modulation rate		*		BM	45.91	1.52	0.32	–0.36 ± 0.14	–2.58	0.02
	Dorsal maximum energy	Loudsong modulation rate			*	BM	34.37	0.00	0.91	–0.49 ± 0.19	–2.57	0.02
	Ventral contrast	Note count				BM	8.86	0.00	0.49	0.14 ± 0.06	2.21	0.03
	Ventral contrast	Note count		*		OU (α: 1)	10.41	1.54	0.23	0.32 ± 0.12	2.80	0.01
	Ventral contrast	Note count				BM	8.86	0.00	0.57	0.14 ± 0.06	2.21	0.03
	Ventral contrast	Note count			*	BM	10.58	1.72	0.24	0.45 ± 0.12	3.87	0.001
	Wing coverts maximum energy	Peak frequency				BM	51.21	0.00	0.57	–0.56 ± 0.5	–1.11	0.27
	Wing coverts maximum energy	Peak frequency		*		BM	51.79	0.59	0.43	–1.36 ± 0.61	–2.22	0.03
	Wing coverts maximum energy	Peak frequency				BM	51.21	0.00	0.56	–0.56 ± 0.5	–1.11	0.27
	Wing coverts maximum energy	Peak frequency			*	BM	51.66	0.45	0.44	–2.57 ± 0.98	–2.62	0.01
	Wing coverts contrast	Note diversity		*		PL (λ: –0.61)	44.85	0.00	1.00	–0.24 ± 0.12	–1.96	0.06
	Wing coverts contrast	Note diversity			*	PL (λ: –4.58)	52.71	0.00	0.98	–1.26 ± 0.65	–1.94	0.06

Only the most informative model and those with ΔAICc < 2 for each pair-wise combination are shown. The (+) and (*) symbols, respectively, indicates the additive and interactive effects of Foraging strata (FS), Habitat exposure (HE), and Mixed-species flocking behavior (MF). α = alpha value obtained for OU model; λ = lambda value obtained for Pagel's lambda (PL) model; AICc = Akaike Information Criterion; ΔAICc = Difference between the AIC value of a model and that of the most informative model; ω_i = Akaike weight or weighted evidence in favor of a model; SE = Standard error around effect size estimates.

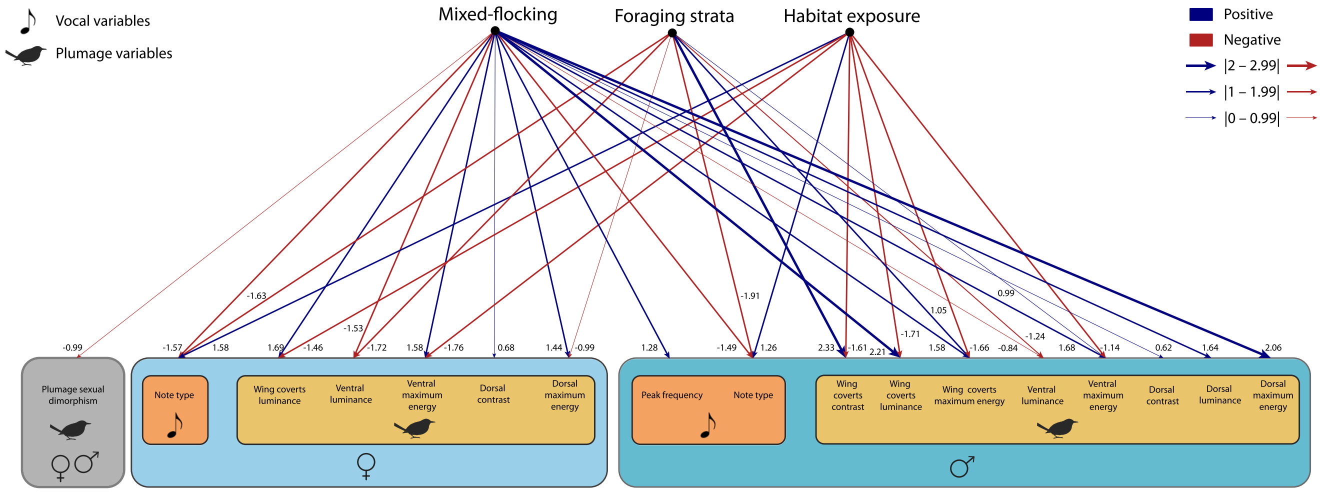

Figure 4. **Summary of the most informative path analysis model showing that mixed-flocking behavior, foraging strata, and habitat exposure have causal effects on plumage and song complexity. This summary includes variables with standard errors lower than their coefficient values only. For visualization of this model including all variables, see Figure S9.**

uncovered for males of a lower number of different note types in the understory and midstory (Fig. 4; Table S16). Finally, in unexposed habitats, males had less patterned ventral and wing regions, darker and more contrasting wing coverts, and loudsongs with a higher number of different note types. Also, females in unexposed habitats showed less patterned ventral regions, darker wing coverts, and loudsongs with a higher number of different note types (Fig. 4; Table S16).

Discussion

We present evidence supporting the transfer hypothesis of evolutionary trade-offs between song and plumage complexity in both sexes separately, but not in the context of sexual dimorphism. Consistent with our predictions, we uncovered significant effects of habitat (sensory drive) and mixed-species flocking behavior (social selection) on both sensory modalities. Specifically, male antwrens with more elaborate and brighter dorsal plumages and brighter and more highly contrasting wing patterns tended to have less complex loudsongs (Figs. 2 and S5). Similarly, females with brighter, more patterned, and more contrasting plumages also tended to produce less elaborate loudsongs (Figs. 3 and S6). Nonetheless, we also found sex-specific trade-offs between some plumage and vocal complexity traits (Figs. 2, 3, S5, and S6). Additive and interactive effects of ecology and behavior were uncovered in most of these trade-off associations in both sexes (Figs. 2, 3, S5–S8; Table 3). Moreover, phylogenetic path analyses suggested that joining mixed-species flocks and, to a lesser extent, habitat exposure and foraging strata are fundamental factors in explaining the variation of plumage and vocal traits in antwrens (Fig. 4; Table S16). Because both sexes engage differently in intra- and interspecific contexts and differ in specific plumage traits across different body regions involved in trade-offs, we suggest that plumage and vocal traits respond differently to pressures by social and natural selection. For instance, in mixed-species flocks, both processes constrain vocalizations across species within environmental optima for effective sound transmission and reception by all species in the flock. In contrast, visual displays seem to be subject to primarily divergent selection leading to distinct species-specific traits but overall decreased levels of plumage sexual dimorphism (Fig. 4; Table S16). Similarly, species restricted to closed habitats with simpler and darker plumages primarily use acoustic signals for communication, whereas species in open habitats tend to rely more on visual signals (Fig. 4; Table S16). Altogether, our integrative approach of evaluating these different hypotheses extends our understanding of the complex interplay among the selective pressures shaping the evolution of both male and female signals, as well as sexual dimorphism.

SONG COMPLEXITY AND ELABORATE PLUMAGE PATTERNS ARE SUBJECT TO EVOLUTIONARY TRADE-OFFS

Vocal traits that capture song complexity in both sexes appear to face an evolutionary trade-off with plumage complexity traits, such that species with more complex songs have less elaborate plumages and vice versa. Song complexity in antwrens is best described by the interaction of qualitative structural traits, such as note type and note diversity, with frequency-based traits—loudsong bandwidth, loudsong modulation rate, and peak frequency. Although song duration has been traditionally considered a proxy for vocal complexity (e.g., Badyaev et al. 2002; Botero et al. 2009; Gonzalez-Voyer et al. 2013; Mason et al. 2014), traits such as loudsong duration, note count, and note rate do not seem to depict vocal complexity in antwrens. As observed in other suboscines (e.g., Seddon 2005; Derryberry et al. 2012; Mason et al. 2017), taxa with longer loudsongs tend to emit just one type of note repeated several times and bounded within restricted bandwidths, whereas taxa with shorter loudsongs tend to produce fewer notes but of different types and with varying frequencies. Thus, those vocal traits that appear to best capture vocal complexity in antwrens are the same vocal traits that show trade-offs with plumage complexity in males and females.

Regarding plumage, we observed some contrast and luminance traits with sex-specific trade-off associations. This observation suggests sex-independent evolution between plumage and vocal traits and sex-specific responses to varying evolutionary pressures of different body regions (Hofmann et al. 2008; Gluckman 2014; Marcondes and Brumfield 2019), resulting in multiple associations between vocal and visual signals. For instance, we did not find any trade-off between plumage traits and peak frequency in males, whereas, in females, wing and ventral maximum energy, ventral luminance, and dorsal contrast showed a trade-off with peak frequency. In specific contexts, such as agonistic encounters or mobbing predators, antwrens commonly display stereotyped body motions (e.g., back-ruffling, wing-flashing) that expose contrasting plumage patches (e.g., white interscapular patch, contrasting flanks) in concert with vocalizations (Wiley 1971; Willis 1972; Skutch 1996; Zimmer and Isler 2003). Considering the different roles of both sexes both in intra- and interspecific contexts (e.g., male antbirds tend to be more aggressive toward conspecifics; Fedy and Stutchbury 2005), it is conceivable that different body regions are evolving distinct plumage traits in response to various pressures posed by a combination of social and natural selection. A careful inspection of these displays and the contexts in which birds produce them is critical to understand better the association of visual and vocal communication in this group.

NO SUPPORT FOR THE TRANSFER HYPOTHESIS BETWEEN PLUMAGE AND VOCAL SEXUAL DIMORPHISM

Our results showed no relationship between plumage and vocal sexual dimorphism (i.e., no support for the transfer hypothesis, at least in terms of sexual dimorphism), suggesting that the evolution of these types of sexual dimorphism is essentially decoupled. Although we found considerable differences between sexes, both on acoustic and visual signals, these differences were not strong enough to indicate a trade-off pattern. These results suggest that, possibly, the evolution of vocal and plumage sexual dimorphism is not only disconnected but that the underlying evolutionary processes of both types of sexual dimorphism could even reinforce sexual differences across signal types instead of generating an evolutionary trade-off. Although tests of the transfer hypothesis have been conducted between plumage sexual dimorphism and male song traits (e.g., Shutler and Weatherhead 1990; Repentigny et al. 2000; Ornelas et al. 2009, Webb et al. 2016), no studies have explored the relationship between vocal and plumage sexual dimorphism as accomplished here. Vocal dimorphism remains understudied mainly because our knowledge of avian female vocalizations only recently became a central focus in bioacoustics (Weir and Wheatcroft 2011; Odom et al. 2014; Mahr et al. 2016; Webb et al. 2016; Odom and Benedict 2018). Despite the lack of vocal sexual dimorphism studies, previous studies showed that the evolution of sexual dichromatism can be decoupled from sexual dimorphism of other phenotypic traits, such as body size, suggesting that sexual dimorphism evolves under different mechanisms (Figuerola and Green 2000; Owens and Hartley 1998; Badyaev and Hill 2003).

Sexual dimorphism is commonly associated with differences in reproductive investments (e.g., mating system, parental care) under sexual selection (Darwin 1871). For example, extra-pair paternity in birds is positively related to plumage brightness of males and plumage sexual dimorphism, indicating high levels of polygyny and male mating success (Møller and Birkhead 1994). Although antwrens are sexually dichromatic, plumage sexual dimorphism is not as spectacular as in other colorful avian clades (e.g., birds-of-paradise, manakins). In antwrens, the effects of sexual selection may generate nuanced sexual differences that are difficult to uncover at the scale of our analyses, and the boundary between sexual and nonsexual components of social selection is difficult to distinguish (Lyon and Montgomerie 2012; Dunn et al. 2015). It is conceivable that quantified levels of sexual dimorphism in vocal and plumage traits have a nonsexual role in visual and acoustic intraspecific recognition, as observed in other groups (e.g., Wallace 1974; Dunn et al. 2015), and that sexual dichromatism reflects distinct environmental pressures experienced by both sexes as a consequence of differential parental investment (Owens and Bennett 1997; Badyaev and Hill 2003). Consequently, in this scenario, sexual dimorphism likely resulted from a form of social selection (West-Eberhard 1983, 2014; Lyon and Montgomerie 2012) that acts on recognition during parental care of males by females, and vice versa, and by natural selection posing sex-specific pressures during parental care (Martin and Badyaev 1996; Owens and Hartley 1998). This idea is supported by assorted data on breeding biology suggesting that differential parental care is prevalent in sexually dichromatic antbird species, such as *Formicivora acutirostris* (Reinert 2008), *Myrmotherula axillaris* (Skutch 1969), *Taraba major* (Sheldon and Greeney 2008; Skutch 1969), *Microrhopias quixensis* (Greenberg and Gradwohl 1983; Skutch 1969), *Gymnocichla nudiceps* (Bradley 2008; Skutch 1969), *Hylophylax naevioides*, *Poliocrania exsul* (Rompré and Robinson 2008; Skutch 1969), *Thamnophilus caerulescens* (Oniki and Willis 1999), and *Hafferia zeledoni* (Caicedo and Londoño 2017), whereas it is absent in the sexually monochromatic *Rhopias gularis* (Perrella et al. 2017). Regarding vocal communication, there is evidence of social selection in the genus *Hypocnemis* by the use of songs and calls in both sexes to defend territory annually and maintaining pairs together (Tobias et al. 2011). However, further research is necessary to assess whether this pattern is observed in other antbirds. Thus, to directly evaluate sexual and social selection in antwrens, we need further analyses of how behavioral and reproductive traits, such as social mating system, extra-pair paternity, and fertilization success, vary at the intra- and interspecific levels in the light of sexual phenotypic differences (e.g., Owens and Hartley 1998; Figuerola and Green 2000; Dunn et al. 2001). Finally, the evolution of sexual dimorphism across multiple communication signals and how they are related to each other represents a high-priority area of study necessary to shed light on the mechanisms underlying signal evolution.

ECOLOGY AND BEHAVIOR INFLUENCE THE EVOLUTION OF BOTH PLUMAGE AND VOCAL TRAITS

Although we found evidence for ecological and behavioral traits affecting both visual and vocal signals in antwrens, mixed-species flocking behavior seems to be the most relevant factor affecting signal evolution in these birds. Species that engage in mixed-species flocks are less sexually dichromatic than those species that do not engage in such behavior (Table S16), but at the same time, we found that both sexes of species that engage in mixed-species flocks are more prone to produce more complex visual signals than those in species that do not. In contrast, those same species exhibited less complex vocal traits. Although it is challenging to assess the relative importance of both types of signals in the formation of mixed-species flocks, we know that specific types of calls and behavioral displays are used to form and maintain groups and to avoid predators (e.g., Moynihan 1962; Wiley 1971; Munn and Terborgh 1979; Gradwohl and Greenberg 1980). Usually, one family group per species (i.e., male, female, and offspring) first cues in on specific vocalizations of nuclear species emitted at greater distances—and outside their visual range—to form and maintain flocks (Greenberg 2001). Then, when species are in close interaction, presumably a combination of stereotyped visual displays and contact and alarm calls are produced to maintain intra- and interspecific communication, as well as the integrity of the flock from predators and other flocks (Munn 1986; Powell 1979; Terborgh 1990). Hence, our results are consistent with a scenario of natural and social selection bounding vocalizations of different species within environmental optima for effective sound transmission and reception by all species (Morton 1975; Seddon 2005). In contrast, visual displays appear to be under divergent social selection to signal species identity in the context of mixed-species flocks, leading to distinct species-specific traits that do not necessarily lead to intraspecific sexual divergence.

Although we did not study contact or alarm calls, we predict that contact calls would show a similar result to that of visual traits, given their importance in intraspecific communication within the flock. In contrast, alarm calls would conform to a pattern similar to that of loudsongs because they communicate potential dangers to all flock members regardless of species identity. Similarly, we predict that other signals for which we lack relevant data, such as specific aggressive displays like back ruffling or crest-raising, can be subject to similar selective pressures as loudsongs given their putative importance in intra- and interspecific contexts. Future studies addressing the evolution of calls and aggressive visual displays are warranted to confirm these predictions. Moreover, detailed studies generating quantitative information encompassing all species flock members across several flocks are necessary to attain a thorough understanding of the relative roles of visual and vocal displays in mixed-species flocks.

Regarding ecological effects, both plumage and vocal sexual dimorphism seem not to be affected by habitat exposure and foraging strata. However, as seen in other avian groups—including the Thamnophilidae (Seddon 2005; Marcondes and Brumfield 2019)—we uncovered ecological effects on specific plumage (e.g., Marchetti 1993; Endler and Thèry 1996; McNaught and Owens 2002; Gomez and Thèry 2004; Gomez and Thèry 2007; Shultz and Burns 2013) and vocal traits (e.g., Morton 1975; Wiley 1991; Badyaev and Leaf 1997; Slabbekoorn and Smith 2002; Kirschel et al. 2009; Mason and Burns 2015) for each sex. Male and female antwrens from unexposed habitats tend to have a less elaborate plumage in specific body regions (i.e., ventral and wing regions in males, the ventral region in females) and vocal signals with a greater diversity of note types than antwrens from exposed habitats. This result suggests that species in unexposed habitats (i.e., understory) tend to have less elaborate plumages and likely rely more on acoustic signals for communication, whereas species from exposed habitats (open areas, canopy) use more visual than vocal signals. Among studies testing the transfer hypothesis in birds (Mason et al. 2014; Laverde-R et al. 2017; Gomes et al. 2017), only a single study on New Word warblers suggested an effect of habitat on the trade-off between plumage and vocal traits (Laverde-R et al. 2017). Females from lower strata (i.e., darker habitat) seem to have less elaborate plumage and vocal traits than canopy (i.e., lighter habitat) species, whereas males from lower strata tended to have more elaborate plumage traits (except for ventral luminance) and simpler vocal traits than canopy species. Although results obtained for foraging strata seem to contradict what was observed for habitat exposure partially, these differences can be reconciled by the fact that our categorization of habitat exposure is likely an oversimplification of complex environments that result from the interaction of several biotic and abiotic conditions (e.g., vegetation structure, sunlight incidence, wind, and precipitation).

The patterns observed here are compatible with previous results showing that these ecological and behavioral traits are not only associated with differences in body size and shape but that they can also drive adaptive convergent evolution of various phenotypic traits across the Thamnophilidae (Bravo et al. 2014), including that of communication signals among interacting species (Tobias and Seddon 2009a). If selective pressures posed by specific habitats or microhabitats have substantial influence in the ecomorphological makeup of antwrens, it is conceivable that, via sensory drive, they influence signal communication, as shown in other thamnophilids (e.g., Seddon 2005; Derryberry et al. 2018; Marcondes and Brumfield 2019) and other avian groups (e.g., Endler and Thèry 1996; Gómez and Thèry 2004; Boncoraglio and Saino 2007; Tobias et al. 2010). On the other hand, it is possible that convergent evolution of interacting species, such as those participating in mixed-species flocks, facilitates heterospecific communication via social selection (Tobias and Seddon 2009a). Our results lack the power to tease apart the relative contribution of these two mechanisms in explaining signal similarity. Still, they are robust enough to suggest that both sensory drive (evolution of signal diversity associated with different strata and habitats) and social selection (vocal signals of species in mixed flocks constrained within phenotypic optima and decreased plumage sexual dimorphism) contribute toward the convergent pattern of some attributes of visual and vocal signals in antwrens.

Conclusions

We presented evidence for sensory drive and transfer constraints shaping the evolution of visual and vocal traits in a clade of dichromatic Neotropical birds that inhabit a wide array of habitats and microhabitats and that are known for being highly vocal and foraging in mixed-species flocks. Previous studies have documented the importance of ecological and behavioral traits in driving phenotypic evolution in antbirds (e.g., Seddon 2005; Bravo et al. 2014; Tobias and Seddon 2009a,b; Marcondes and Brumfield 2019), but our study is the first attempt to evaluate how the complexity of visual and vocal signals interacts with one another, the environment, and social behaviors.

Besides illuminating how plumage and vocal traits evolved in antwrens, this study sheds light on the transfer hypothesis while accounting for ecological and behavioral effects on both acoustic and visual signals in males and females. We suggest that further studies investigating this hypothesis should continue to incorporate high-quality quantitative information describing ecology and behavior for both sexes. Expanding this approach into broader phylogenetic scales will be critical to assess whether the observed patterns hold in other groups (Wiens and Tuschhoff 2020).

AUTHOR CONTRIBUTIONS

All authors conceived the study. RB and GAB designed the research. RB and GAB gathered the data. RB, EPD, and GAB analyzed the data. RB and GAB constructed figures. All authors contributed funding. RB wrote the manuscript with input from GAB, EPD, and LFS.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

Coloration, vocal, ecological, and behavioral data, R scripts, and the phylogenetic tree are available as Supporting Information and through the

Dryad Digital Repository database (available at https://doi.org/10.5061/dryad.zpc866t8p). Raw ultraconserved elements and exon data used to build the phylogeny were originally published by Harvey et al. (2020) and are available at NCBI BioProject PRJNA655842.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of the recordings analyzed in this study.
Table S2. Description of each vocal character used in this study.
Table S3. List of the museum specimens that were photographed and analyzed in this study.
Table S4. Ecological and behavioral data of Formicivorini
Table S5. Model fit of vocal and plumage sexual dimorphism.
Table S6. Model fit of vocal and plumage traits evolution in males.
Table S7. Model fit of vocal and plumage traits evolution in females.
Table S8. A supplementary version of Table 3 including the effect size ± standard error of the ecological and behavior covariates.
Table S9. PGLS regressions obtained from the relationship between plumage and vocal sexual dimorphism.
Table S10. PGLS regressions obtained from the relationship between plumage and vocal traits in males.
Table S11. PGLS regressions obtained from the relationship between plumage and vocal traits in females.
Table S12. PGLS regressions obtained from the relationship between plumage and vocal sexual dimorphism.
Table S13. PGLS regressions obtained from the relationship between plumage and vocal traits in males.
Table S14. PGLS regressions obtained from the relationship between plumage and vocal traits in females.
Table S15. Phylogenetic path analysis effects of Habitat exposure (HE), Foraging strata (FS), and Mixed-species flocking behavior (MF) on all plumage and vocal traits.
Table S16. Coefficient and their respective standard errors (SE) of Mixed-species flocking behavior (MF), Foraging strata (FS), and Habitat exposure (HE) effects on all plumage and vocal traits obtained in the best model of the Phylogenetic path analysis.
Figure S1. An example of an oscillogram (A) and a spectrogram (B) of a *Stymphalornis acutirostris* male individual loudsong.
Figure S2. Correlation plot of vocal traits in (A) males and (B) females.
Figure S3. In the left, an example of a photographed museum specimen.
Figure S4. Correlation plot of plumage traits in panel A.
Figure S5. Scatterplots of the additive models illustrating negative (A–F) and positive PGLS associations (G–I) between plumage and vocal traits in male antwrens: (A) Dorsal luminance versus loudsong bandwidth with foraging strata and mixed-flocking behavior additive effects; and (B) Dorsal luminance versus loudsong modulation rate with mixed-flocking behavior additive effect; (C) Dorsal luminance versus note type with foraging strata additive effect; (D) Dorsal maximum energy versus loudsong modulation rate with habitat exposure and mixed-flocking behavior additive effects; (E) Dorsal maximum energy versus note diversity with habitat exposure and mixed-flocking behavior additive effects; (F) Wing coverts luminance versus loudsong bandwidth with habitat exposure, foraging strata and mixed-flocking behavior additive effects; (G) Dorsal maximum energy versus loudsong duration with habitat exposure and mixed-flocking behavior additive effects; (H) Dorsal maximum energy versus note count with habitat exposure and mixed-flocking behavior additive effects; and (I) Wing coverts contrast versus loudsong duration with habitat exposure and foraging strata additive effects.
Figure S6. Scatterplots of the additive models illustrating negative (A–R) and positive PGLS associations (S–Y) between plumage and vocal traits in females antwrens: (A) Dorsal luminance versus loudsong duration; (B) Dorsal luminance versus loudsong bandwidth; (C) Dorsal luminance versus loudsong modulation rate; (D) Dorsal luminance versus note count; (E) Dorsal maximum energy versus loudsong bandwidth; (F) Dorsal maximum energy versus loudsong modulation rate with habitat exposure and mixed-flocking behavior additive effects; (G) Dorsal maximum energy versus note diversity with mixed-flocking behavior additive effect; (H) Dorsal maximum energy versus note type with mixed-flocking behavior additive effect; (I) Dorsal contrast versus peak frequency with mixed-flocking behavior additive effect; (J) Dorsal contrast versus loudsong modulation rate with mixed-flocking behavior additive effect; (K) Dorsal contrast versus note diversity with habitat exposure and foraging strata additive effects; (L) Ventral luminance versus peak frequency; (M) Ventral maximum energy versus peak frequency; (N) Ventral contrast versus loudsong modulation rate; (O) Ventral contrast versus note diversity; (P) Wing coverts luminance versus note diversity with habitat exposure and mixed-flocking behavior additive effects; (Q) Wing coverts maximum energy versus peak frequency; (R) Wing coverts contrast versus note diversity with habitat exposure and mixed-flocking behavior additive effects; (S) Dorsal contrast versus note count with mixed-flocking behavior additive effect; (T) Ventral maximum energy versus note count with habitat exposure, foraging strata and mixed-flocking behavior additive effects; (U) Ventral maximum energy versus note rate with habitat exposure and mixed-flocking behavior additive effects; (V) Ventral contrast versus note count; (W) Wing coverts luminance versus note rate with habitat exposure and mixed-flocking behavior additive effects; (X) Wing coverts contrast versus note count with habitat exposure and foraging strata additive effects; and (Y) Wing coverts contrast versus note rate with habitat exposure, foraging strata and mixed-flocking behavior additive effects.
Figure S7. Scatterplots of the interactive models illustrating negative (A–E) and positive PGLS associations (F–H) between plumage and vocal traits in male antwrens: (A) Dorsal luminance versus loudsong bandwidth with mixed-flocking behavior effect; (B) Dorsal luminance versus loudsong modulation rate with habitat exposure effect; (C) Dorsal luminance versus loudsong modulation rate with mixed-flocking behavior effect; (D) Dorsal maximum energy versus loudsong modulation rate with mixed-flocking behavior effect; (E) Dorsal maximum energy versus note diversity with mixed-flocking behavior effect; (F) Dorsal maximum energy versus loudsong duration with habitat exposure effect; (G) Dorsal maximum energy versus loudsong duration with mixed-flocking behavior effect; and (H) Dorsal maximum energy versus peak frequency with mixed-flocking behavior effect.
Figure S8. Scatterplots of the interactive models illustrating negative PGLS associations between plumage and vocal traits in females antwrens: (A) Dorsal luminance versus loudsong bandwidth with mixed-flocking behavior effect; (B) Dorsal luminance versus loudsong modulation rate with mixed-flocking behavior effect; (C) Dorsal luminance versus note count with habitat exposure effect; (D) Dorsal maximum energy versus loudsong modulation rate with mixed-flocking behavior effect; (E) Wing coverts contrast versus note diversity with habitat exposure effect; and (F) Wing coverts contrast versus note diversity with mixed-flocking behavior effect.
Figure S9. Most informative path analysis model showing that mixed-flocking behavior (MF), foraging strata (FS), and habitat exposure (HE) have causal effects on plumage and song complexity.