Females don't always sing in response to male song, but when they do, they sing to males with higher pitched songs

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Abstract

The long-held view that bird song is exclusively a male trait has been challenged recently by a number of studies and reviews highlighting the prevalence of female song. In spite of that, there remains a lack of knowledge on the function of female song, with most evidence thus far focusing on females performing duets with males in courtship displays, for joint territory defence, or for mate guarding purposes. Here we show in a tracheophone suboscine passerine *Formicarius moniliger*, a sexually monomorphic species in which both sexes sing, that females may participate in both intrasexual and intersexual territory defence. Females sing more in response to females than to males yet demonstrate an unexpected pattern of singing back to playback of males singing higher frequency song than themselves. Unlike males, who respond indiscriminately to playback of any song performed by either sex, females appear to discern not only the sex, but also the size of the presumed intruder, perceiving a strong negative relationship between body mass and frequency. Our findings suggest females will only engage in territory defence with males when they expect those males to be weaker than they are. While our results are consistent with expectations of a shared ancestral function of song in territory defence, they also suggest females may suffer greater costs in engaging in territorial disputes and thus limit their vocal contribution according to the perceived threat.

Keywords: Animal communication, female song, intersexual interactions, sex roles, intrasexual territoriality, Neotropical birds.

Introduction

Sexual dimorphism is manifested in animals in a variety of ways. Male elephant seals can be 10 times the size of females (Mccann et al., 1989), and sport highly modified proboscises; male deer grow antlers; male peacocks develop iridescent plumage and a long train with eyespots (Yorzinski et al., 2013); all this in aid of attracting females and fighting off rival males (Lande, 1980). Such dimorphism represents conventional sex roles of males competing for mates and females investing in parental care (Kokko and Jennions, 2008).

Yet many species are sexually monomorphic. No differences in body size; no differences in colour or pattern. Genetic correlations in body size between the sexes may constrain sexual dimorphism (Merilä et al., 1998). Also, strong stabilizing selection acting on the sexes (Price and Grant, 1985), largely driven by them occupying similar niches, might explain their lack of dimorphism (Székely et al., 2007). Many such animals use acoustic communication for mate attraction and territory defence. Insects, frogs and birds create a cacophony of sounds in natural habitats as a result (Kirschel et al., 2009a), but except in some cases of sex-role reversal (Goymann et al., 2004), song has typically been considered a sexually divergent behaviour performed by males (Odom et al., 2014).

There are, however, some animals in which both sexes sing. For instance in tropical birds, many females sing as well as males (Slater and Mann, 2004). Females in these instances may at times sing loosely in association with the male or at others sing a tightly-coordinated duet (Slater and Mann, 2004), the latter a phenomenon which has received much attention in the literature (Langmore, 1998, Slater and Mann, 2004, Hall, 2004). Duetting has been attributed to territory defence, whereby the female sings to defend the territory jointly with her mate from a rival of

either sex (Fedy and Stutchbury, 2005, Hall, 2004), or she may sing to defend the territory specifically from same sex rivals (Langmore, 1998, Cain and Langmore, 2015). Alternatively, duets could function in mate guarding, whereby either the male or the female ensures their partner is not singing solo in an attempt to attract extra-pair mating opportunities (Levin, 1996a, Levin, 1996b, Seddon and Tobias, 2006, Tobias and Seddon, 2009).

The prevalence of female song in the tropics has been attributed to sex role convergence in locations where birds are resident and defend territories year-round (Slater and Mann, 2004), but this view has been challenged by studies suggesting female song is ancestral in songbirds (Odom et al., 2014, Riebel et al., 2019). So while songs may represent ornaments attractive to the opposite sex, their primary function in females is thought to be in intrasexual competition in species defending territories year-round from same-sex rivals (Tobias et al., 2011, Tobias et al., 2012b). A further study across all birds identified year-round territoriality as the trait most closely associated with duetting (Tobias et al., 2016). Such year-round territoriality is particularly evident in insectivorous birds (Hau et al., 2000, Slater and Mann, 2004, Tobias et al., 2011), with much previous work on duetting birds focusing on insectivorous wrens and antbirds (Fedy and Stutchbury, 2005, Levin, 1985, Seddon and Tobias, 2006). Female song is also common in many Australian passerines, including in the insectivorous fairy-wrens, whistlers, shrike-thrushes, and bell birds, which like the wrens and antbirds, have extended longevity when compared to most temperate passerines, and defend territories year-round. In these taxa, the sexes are either sexually dimorphic or dichromatic (e.g., antbirds, (Kirschel et al., 2019, Tobias and Seddon, 2009), fairy-wrens and whistlers (Hall and Peters, 2008, van Dongen and Mulder, 2008), sing distinctly different songs (e.g., wrens (Mennill and Vehrencamp,

2008), or both (again antbirds (Tobias and Seddon, 2009), and fairy-wrens (Hall and Peters, 2008), suggesting songs may still serve different functions among the sexes. Might there be situations in species where the sexes are monomorphic and sing indistinguishable songs, and what might such cases reveal regarding sex roles? Perhaps sexually monomorphic vocalisations could play a role in intersexual competition (Tobias et al., 2012a). Here we examine such a case. We studied a population of sexually monomorphic Mexican antthrush – a.k.a. Mayan antthrush (Krabbe and Schulenberg 2019) - (*Formicarius moniliger*), for which previous studies have shown both sexes sing (Blumstein et al., 2011, Kirschel et al., 2009b). Despite evidence showing that individuals can reliably be recognized from the subtle spectral and temporal idiosyncrasies in their songs, efforts thus far have not been able to distinguish male from female song (Kirschel et al., 2011b).

Mexican antthrush is a tracheophone suboscine passerine (Tobias et al., 2012a), a group whose simple stereotypic songs have allowed investigators to identify songs to species (Trifa et al., 2008), and to track movements of individuals in space and time using an acoustic sensor network (Collier et al., 2010). Previous work on Mexican antthrush has shown how songs can reliably be assigned to individuals (Kirschel et al., 2009b), and using such song classifications, resulting territory maps have demonstrated little territory overlap between same sex rivals suggesting strong intrasexual territoriality (Kirschel et al., 2011b).

We investigated how male and female Mexican antthrush perceive song produced by possible territory intruders of the same or opposite sex using playback experiments. We hypothesized that a vocal response to same sex playback represented territory defence, though could also represent mate guarding. Conversely, a vocal response to opposite sex playback could represent intersexual territory defence or

joint territory defence, if the mate also responded vocally, but potentially promiscuous intentions if not. Our overall aim was to determine when each sex used songs in response to possible intruders, thus informing us of the function of female song, which remains understudied across birds (Odom and Benedict, 2018, Riebel et al., 2019). Moreover, because of much evidence of a negative correlation between body size and song frequency in birds (Ryan and Brenowitz, 1985a, Wallschlager, 1980), we also tested whether such a relationship exists within antthrushes. If there is such a relationship, might individuals perceive differences in body size? If larger birds sang lower frequency song, responses might differ based on the size of the presumed intruder. We tested this hypothesis by comparing responses to differences in frequency between responder's song and playback stimulus, as well as differences in body mass between responder and presumed intruder.

Materials and methods

Fieldwork

Fieldwork took place at the Estación Chajul in the Montes Azules Biosphere Reserve, in south-eastern Chiapas, Mexico (16˚6′44′′N; 90˚56′27′′W), during 8-17 June 2007, 7-18 December 2008, 7-28 May 2009, and 11-31 May 2012. Montes Azules, also known as Selva Lacandona, represents the largest expanse of pure tropical rainforest in North America (ParksWatch, 2003). The study was focused within a 50-ha study plot at an elevation range of 150-165 m, on the northern side of the Lacantún River (Kirschel et al., 2011b).

We captured birds using target netting techniques and marked captured birds with a unique combination of color rings to aid visual confirmation of their identity. We deployed individual mist nets (Avinet or Ecotone, 30- or 36-mm mesh, 12 x 2.5

147 m) along 1 - 2 m-wide trails, with the bottom of each net set at ground level. We
148 target netted antthrushes using conspecific playback. Captured birds were also
149 weighed and measured and 50-100µL of blood was obtained via venepuncture of the
150 brachial vein for genetic sex identification. Individuals caught in 2012 also had a
151 radio-frequency identification (RFID) tag fitted on their backs with a harness as part
152 of a parallel study, and methods used are described therein (Kirschel et al.
153 unpublished ms). We recorded ringed birds singing along trails in the study area as
154 previously described and in accordance with methods used previously (Kirschel et al.,
155 2011b, Kirschel et al., 2009c). Specifically, we used a Marantz PMD 670 / 661
156 recorder with Sennheiser microphones ME-67/K6, MKH20 microphone with a
157 Telinga parabolic reflector, or MKH8050 housed in a Rycote windshield, as well as
158 an acoustic sensor network (see (Collier et al., 2010, Kirschel et al., 2011b).
159
160 *Playback experiments*
161 Fifty playback stimuli were prepared using Raven Pro 1.4 (Cornell Lab of
162 Ornithology) using songs recorded during previous field seasons (Kirschel et al.,
163 2011a), and additional recordings obtained during the 2012 field effort. The songs
164 used belonged to 24 ringed individuals and had been recorded while color-ring
165 combinations were confirmed, or were classified unambiguously as belonging to
166 specific individuals (Kirschel et al., 2011b, Kirschel et al., 2009c). Sex of individuals
167 whose songs were used in experiments had been previously identified genetically
168 (Blumstein et al., 2011, Kirschel et al., 2009b), or had been predicted based on
169 behaviour typical of one of the sexes during the 2012 field season and subsequently
170 confirmed genetically (see below). Each stimulus was prepared with songs that were
171 high-pass filtered at 400 Hz to remove background noise, maximum amplitude

normalized at 20,000 units (Raven's unit of amplitude measurement), and arranged temporally with two songs of an individual within a one-minute stimulus with the remainder silence and then looped continuously for the duration of the experiment. Playback apparatus consisted of an Apple iPod mp3 player and a TivoliAudio PAL loudspeaker, with output volume set at the same level for all experiments. Playbacks were performed at different times of day and stimuli were randomly selected. Experiments varied in length and depended on an approach by focal individuals. Antthrushes are inconspicuous, terrestrial birds (Cody, 2000), which may approach gradually and silently on the ground, possibly from far within their territory. In such cases it could take them 10 - 20 minutes to approach to within a distance of the loudspeaker where a recording of suitable quality might be obtained. Recordings were thus obtained opportunistically when birds started vocalizing in response to the playback and only those experiments where recordings were obtained are included in analyses. Our aim was to document who sang and what sex they were, in response to which individual playback and the sex, song characters, and body mass of the individual whose song was used in the experiment. A parallel systematic study performed in 2012 focused on approaches to specific stimuli (Kirschel et al. unpublished ms). In field seasons prior to 2012, on some occasions we may not have ringed both individuals of a focal pair. In such cases we still use the data of the experiment from the one identified individual but do not consider any partner's response in analyses.

Genetic sex identification

DNA was extracted from blood or feather samples collected from 21 individuals in the field in 2012 using a QIAGEN DNEasy Blood and Tissue Kit (QIAGEN,

197 Valencia, CA) following manufacturer's protocols. Highly conserved primers (2550F
198 and 2718R, (Fridolfsson and Ellegren, 1999)) were used in polymerase chain reaction
199 (PCR) to amplify the differently sized introns of Z- and W- linked chromohelicase-
200 DNA binding protein 1 (CHD1) genes. PCR products were separated in a 1 or 2%
201 agorose gel run in TAE buffer, revealing one or two bands for males and females
202 respectively.
203
204 *Song feature extraction*
205 Eighty-three recordings from fieldwork in 2012 were imported into RAVEN Pro 1.4
206 (Cornell Lab of Ornithology, Ithaca, NY, USA) where song sequences were cut into
207 separate WAV files, which were then processed in a feature extraction program in
208 MATLAB 7 (MathWorks 2005). The procedure is described in detail in (Kirschel et
209 al., 2009c). Here, we follow the approach used in (Kirschel et al., 2011b), extracting
210 19 temporal and spectral features of song (See supplement).
211
212 *Canonical discriminant analysis*
213 The majority of songs used for this study had been identified to individual in previous
214 studies (Kirschel et al., 2011b, Kirschel et al., 2009c) or by sight or with radio
215 telemetry in 2012. However, there remained 39 recordings of antthrush songs for
216 which we did not know the singer. We followed (Kirschel et al., 2011b) in using
217 linear canonical discriminant analysis (CDA) to identify those songs to individuals.
218 The CDA was performed in STATA 11.2 (StataCorp 2009) on songs cut from
219 recordings obtained in May 2012 using the 19 variables extracted from the songs.
220 Following (Kirschel et al., 2011b), we used 1189 songs from recordings where the

221 singer could be unambiguously confirmed by sight or radio telemetry as training data
222 and predicted the singer of 619 songs on the remaining 39 recordings (see ESM for
223 details of post CDA classification filtering). The resultant songs classified to
224 individual were then pooled with the 2011 songs from 168 recordings previously
225 classified (Kirschel et al., 2011b, Kirschel et al., 2009c), and statistical analyses were
226 performed on a total of 3022 songs attributed to 24 individuals. Moreover, we tested
227 whether with the combined dataset of 50 individuals we could distinguish between
228 male and female song in a CDA with leave-one-out-classification using the mean
229 values of the 19 song features from the 230 recordings included in the study.

230

231 *Statistical analyses*

232 We first tested whether one of the sexes sings more than the other in response to
233 playback of either sex using a chi-squared test. We restricted this analysis to 158
234 experiments (78 male and 80 female song playbacks) in territories where both
235 members of the pair were ringed. To test for what determines when each sex sings, we
236 used a Bayesian Generalized Linear Mixed Model (GLMM) in 'blme' in R, fitted
237 with the binomial distribution and logit link function using the function bglmer. We
238 determined the effect on the binary response variable "female song response" or
239 "male song response" of the difference in peak frequency between the mean peak
240 frequency of the responder's song (from all recordings of the individual obtained that
241 year) and the peak frequency of the playback stimulus. Also included as fixed factors
242 in the model were the binary predictor of sex of the individual whose song was used
243 in the playback experiment, and its interaction with difference in peak frequency.
244 Subject of experiment and playback stimulus used were included as crossed random
245 effects. We then tested whether each sex responded to different frequencies of male or

246 female playback using Bayesian GLMM fitted with a Gaussian distribution. Because
247 the function blmer does not provide P values by default, these were computed using
248 the packages 'sjstats' and 'parameters' in R.
249 To determine whether there was a relationship between body mass and song
250 frequency we first calculated the mean peak frequency from all recordings of each
251 individual for each field trip. For this analysis, we calculated the mean peak frequency
252 only from recordings where the bird's ring combination was identified, or where the
253 bird was identified using radio telemetry (Kirschel et al. unpublished ms). We then
254 ran a GLMM in lme4 in R, fitted with a Gaussian distribution, with mean peak
255 frequency as the dependent variable and body mass (g) and sex as fixed effects and
256 individual included as a random effect, to account for individuals recorded (and body
257 mass measured) over several years. We then tested if the relative size influenced
258 responses based on sex of the presumed intruder. Specifically, we ran Bayesian
259 GLMMs to test whether the interaction between difference in body mass (centred and
260 standardized, (Schielzeth, 2010) between subject and playback singer and the latter's
261 sex affected male or female response levels, with individual subject and individual
262 whose song playback was used as crossed random effects.
263
264 **Results**
265 *Genetic sex identification*
266 Of the 21 birds we obtained samples from in 2012, 13 were male and 8 were female.
267 This information was combined with the data from previous genetic analyses
268 (Kirschel et al., 2011b), from which 12 sexed males and 11 females, were included as
269 playback stimuli singers (13 male, 11 female) and/or test subjects (21 male, 17
270 female) in experiments.

Canonical discriminant analysis

Based on the CDA trained using songs of 20 individuals, 619 songs from 39 recordings were classified. Of these, 88.7% were assigned to the predicted individual, consistent with classification rates found previously for similar numbers of individuals in a season (Kirschel et al., 2011b). By contrast, the CDA could only classify 75.1% of male song and 55.9% of female song to the correct sex (See ESM for detailed results of the CDA).

Playback experiments

Males responded with song significantly more than females did to both male (94.9% vs 16.7% of experiments; $\chi^2 = 21.08$, $P < 0.0001$) and female playback (89.9% vs 26.6% of experiments; $\chi^2 = 24.59$, $P < 0.0001$). Males showed no difference in song response levels based on sex of playback, and difference in peak frequency between the subject and playback stimulus singer or their interactions (Table 1, Fig. 1). By contrast, females sang more in response to female playback than male playback, but not in relation to differences in peak frequency between subject and playback stimulus singer (Table 1). There was, however, a significant negative interaction between sex of playback and difference in peak frequency, indicating that females increasingly respond to male song the lower their song is in frequency compared to the playback stimulus (Fig. 1). Further, while there was no difference in the peak frequency of female playback that males and females responded, females responded to significantly higher frequency male playback than males did (Table S2).

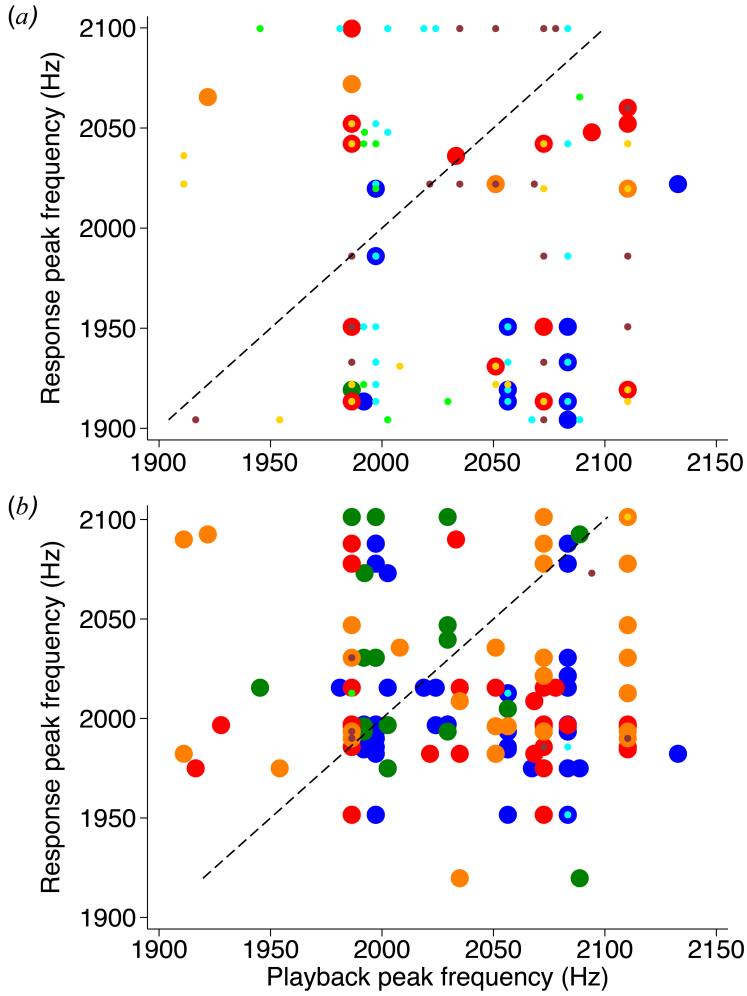

Figure 1

Females (a) sing back in response to higher frequency male song than their own, and to males that are smaller than they are, but do not discriminate between frequencies or body mass in response to female song. Males (b) sing back in response to the vast majority of playback experiments (large circles) and do not discriminate between sexes or according to body size. Blue and green circles – vocal response to song playback of smaller and larger males respectively. Red and orange circles – vocal response to song playback of smaller and larger females respectively. Cyan and lime green dots – no vocal response to song playback of smaller and larger males respectively. Maroon and gold dots - no vocal response to song playback of smaller and larger females respectively. Dotted line represents y = x.

306 **Table 1:** Bayesian generalized linear mixed models with binomial distribution of the
307 effect of sex of singer on playback experiment, difference in peak frequency of songs
308 on the playback and responder's song, and the interaction of those effects, on vocal
309 responses of females (a) and males (b).

a) Female responses	**Estimate**	**SE**	**Z**	**P**
Intercept	-0.81	0.43	-1.89	0.058
Sex	-2.17	0.81	-2.67	**0.0076**
Peak frequency difference (standardized)	0.34	0.33	1.01	0.314
Sex/peak frequency difference interaction	-0.02	0.008	-3.12	**0.0018**
b) Male responses				
Intercept	3.95	1.45	2.73	**0.0063**
Sex	1.51	1.12	1.35	0.177
Peak frequency difference (standardized)	-0.004	0.008	-0.49	0.622
Sex-peak frequency difference interaction	0.02	0.015	1.49	0.137

310

311

312 While there was no difference in peak frequency according to sex (GLMM: t = 0.719,
313 P = 0.48) there was a significant negative relationship between body mass and peak
314 frequency (t = -3.29, P = 0.002), meaning larger individuals sang lower frequency
315 songs (Fig. 2). Yet, neither females nor males responded significantly differently to
316 song of each sex in relation to the body mass of the singer (Table S3). However, in
317 females specifically, there was a pattern of greater response to male song the lower
318 his body mass was in relation to the female's, but it was not significant.

319

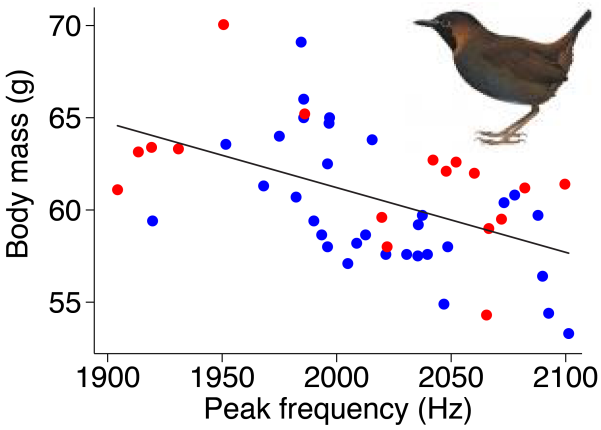

Figure 2

There is a significant negative relationship between body mass and peak frequency, with larger individuals singing lower frequency song, though no differences between males (blue dots) and females (red dots). *Formicarius moniliger* illustration courtesy of Del Hoyo et al. (2019).

Discussion

Female birds are widely recognized as being more discriminating than males in response to playback stimuli (Searcy and Brenowitz, 1988, Seddon and Tobias, 2010). But males are also more typically involved in territory defence and the cost of responses to abnormal species-specific song or to heterospecific song would be lower than in females (Searcy and Brenowitz, 1988). In this study, antthrush females responded to playback less often than males did, supporting the view that males devote more effort to territory defence than females do. Indeed, males appeared to respond indiscriminately to song, whether performed by males or females and irrespective of the body size of the presumed intruder. Such responses suggest either heightened aggression towards intruders of both sex in males, promiscuous intentions when a female trespasses into his territory, or an inability to distinguish song to sex. By contrast, females responded significantly more often to female song than to male

song, suggesting they do discriminate between the songs of each sex, in spite of the extent of overlap in song characteristics (Fig. 2), and our failure to reliably classify songs to sex in a discriminant analysis. Their responses suggest they do identify song to sex, consistent with the hypothesis that signals that may appear sexually monomorphic to human observers are still likely to contain information on sex-specific differences (Price, 2015). Females singing in response to female song is consistent with both the function of intrasexual territory defence and mate guarding (Langmore, 1998, Levin, 1996b, Tobias and Seddon, 2009, Cain and Langmore, 2015). Yet, on occasion, females responded to male song. They responded significantly more to male song the lower the frequency of their song compared to the male song. In other words, they respond to those males they perceived as singing higher pitched songs than they did.

Frequency has been shown to be negatively correlated with body size in birds, both among species (Wallschlager 1980, (Ryan and Brenowitz, 1985b), and within species (Hall et al., 2013). Here, we tested whether there was a relationship between frequency and body mass in individuals of Mexican antthrush. We found that larger, heavier antthrushes do indeed sing lower frequency songs than lighter antthrushes, while song frequency does not differ between the sexes. What this relationship suggests is that females responding to males singing at higher frequencies are responding to smaller males. Our test of that specific relationship found a pattern in that direction, but it was not significant. Of course, there is variation in song frequency that is not explained entirely by body mass (Fitch, 1999), and the birds responded to what they heard and not what they saw. Other aspects of the playback stimulus might provide further information to the receiver regarding the size of the singer and the threat (or opportunity) represented. Indeed, the one female whose song

365 was higher in frequency than the playback in Fig. 1 was actually heavier than the
366 male whose song she responded to, and that male on average sang at higher
367 frequencies than that female, just not on the selected playback stimulus.
368 Not only did females respond to higher frequency male song then theirs, they
369 also sang back in response to higher frequency male song than males did, providing
370 further support that females responded to the smallest males. Might females be
371 attracted to males that are smaller than them? Or are they simply attracted to higher
372 frequency song? We suggest an alternative explanation. These paired females are not
373 responding to male song for mutual attraction purposes. Instead, we believe that
374 females will participate in intersexual territory defence by singing back only when
375 they perceive the intruding male to be smaller, and thus weaker, than they are.
376 Sexually monomorphic songs are expected to fulfil a similar function between the
377 sexes (Riebel et al., 2019), and thus could be used for both intrasexual and intersexual
378 territory defence. But in a species where the female sings a fraction of what the male
379 does, it seems she chooses carefully when she will use her song for the purpose of
380 intersexual territory defence.
381 We did not test whether female song was influenced by the male mate's
382 response and thus formed a coordinated territorial response to intruders (e.g., (Hall
383 and Peters, 2008)– males responded to almost every experiment rendering such a test
384 unworkable. In any case, such behaviour is more typical of duetting birds that
385 coordinate their songs into duets, which antthrushes do not do. Neither do female
386 antthrushes sing in tandem with the male or jam his song as a mate guarding strategy
387 (Tobias and Seddon, 2009). Instead, females sometimes sing solo (see also (Kirschel
388 et al., 2011b). We also caution that our results are based on a large number of
389 recordings of individuals identified based on song classifiers, and that we excluded

songs on recordings that we were unable to classify to specific individuals. What this means is that there were individuals singing on a number of the recordings that we could not classify as belonging to a known ringed individual. It does not mean that those were not female or male partners of individuals we did identify singing on recordings. Just that our CDA failed to identify them. Nevertheless, any situations where we were unable to identify the individual singer reduced our sample size and overall statistical power. We have no reason to assume any missing data would not be representative of the patterns reported here. We also caveat that nonvocal responses may play an important part in both territorial defence and mate guarding, so it would be important to associate nonvocal responses such as approaches to playback stimuli as well as vocal responses.

Female song has typically been thought of as a component of coordinated duets in tropical birds (Fedy and Stutchbury, 2005). We have shown here that female antthrushes sing independently of males and that their songs cannot reliably be distinguished from male song. Rather than female song representing evidence for convergence in sex roles, a notion that has been challenged by recent studies (Riebel et al., 2019), our study on suboscine passerines is consistent with the premise that female song is ancestral in songbirds (Odom et al., 2014), with females singing to defend territories much in the way that males do. Nevertheless, with costs of responding to the wrong stimulus potentially greater in females (Searcy and Brenowitz, 1988), we find that females respond far less than males do and pick and choose when they will respond with song to intruders, especially when they are males.

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