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Article

Duetting behavior in a Neotropical ovenbird: sexual and seasonal variation and adaptive signaling functions

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Duetting is a collective behavior and might have multiple functions, including joint territory defense and mate guarding. An important step toward understanding the adaptive function of bird song is to determine if and how singing behavior varies seasonally. However, seasonal patterns for duetting species are different from the pattern described for species in which only the male sings, because song function may vary according to sex, singing role (initiator vs responder) and level of duet organization (individual vs pair). We investigated whether patterns of seasonal variation in duetting depends on these factors, which would suggest different interpretations of song function. We studied social pairs of a Neotropical bird species (rufous hornero *Furnarius rufus*) for seven consecutive months, recording vocal and territorial behaviors. Overall, partners coordinated 61% of their songs into duets and many song traits (song initiation rate, song output and duet rate) peaked in territorial contexts. Males engaged in territorial interactions with strangers more often, initiated more songs, and answered proportionately more of their partners' songs than females. Male song initiation rate peaked during the pre- and post-breeding stages, whereas females initiated more songs during the non-breeding season. Both sexes answered partner songs faster and at higher rates during the pre-breeding and female fertile stages. Partners duetted at a higher rate during the pre- and post-breeding stages. Finally, song initiation rates and duet rate, but not song answering rates, correlated with frequency of territorial interactions with strangers. Although our findings indicate that song function may vary with sex, singing role and level of duet organization, our results suggest that in general duet functions to defend common territories and as a mutual mate guarding strategy in the rufous hornero.

Keywords: bird song, female song, duet, territoriality, joint territory defense, *Furnarius rufus*



Introduction

Understanding the adaptive function of bird song relies on knowing the phenology and context in which the bird sings (Catchpole and Slater 2008). This is well documented for males in north-temperate bird species, whose song rate usually peaks during the spring before pairing (Catchpole 1973, Amrhein et al. 2002) and is associated with territoriality (Nowicki et al. 2016), suggesting that songs function to attract females and repel rivals (i.e. the dual function of bird song; Catchpole and Slater 2008). However, the singing and breeding phenology of tropical birds differ substantially from north-temperate birds: females sing year-round and join male songs to create duets in many tropical species (Slater and Mann 2004, Odom et al. 2014, Tobias et al. 2016). For a more global understanding of variation in the phenology of singing effort, we must study species that exhibit female song (Langmore 1998, Cain and Langmore 2015) and coordinated song, such as duetting (Hall 2006, 2009, Topp and Mennill 2008, Bradley and Mennill 2009a, Dowling and Webster 2013, Odom et al. 2016).

Duetting occurs mainly when mated pairs coordinate vocal behaviors (Farabaugh 1982). The function of duetting is often difficult to discern (Hall 2004), because duetting is a collective behavior composed of two ‘levels of organization’: the individual level and the pair level (Logue and Krupp 2016). The individual level includes behaviors such as song initiation (solo songs plus initiated duets or answered songs) and song answering (proportion of partner’s songs answered), whereas the pair level includes behaviors such as duet rate and duration (Logue and Krupp 2016). Either or both levels may influence individual fitness independently or as a whole. For example, duet rate may vary due to changes in song initiation, song answering, or both behaviors, in one or both sexes, but only duet rate may affect fitness for these individuals (Logue and Krupp 2016). Song initiation can be considered as a solo if not answered by the partner, and thus

may be under similar selection as the usual solo songs (Hall 2009, Logue and Krupp 2016). Therefore, it is important to consider the possibility that each ‘duetting’ behavior (song initiation, song answering and pair-level duetting) may have different functions (Logue and Krupp 2016, Odom et al. 2017). However, most studies investigate seasonal variation in duetting behavior only at the pair-level (e.g. duet and solo song rates) (Bradley and Mennill 2009a, Benedict 2010, Tobias et al. 2011, Koloff and Mennill 2012, Dowling and Webster 2013, but see Hall 2006, Odom et al. 2016).

Duetting can reflect conflict or cooperation between partners and may be used in within- or extra-group communication (Hall 2004, 2009). At the pair level, duetting may function to defend common resources (Bradley and Mennill 2009b, Koloff and Mennill 2013) or as a mutual mate guarding display (van den Heuvel et al. 2014a) (Table 1). At individual and inter-group levels, song answering might have evolved as a mate guarding strategy, whether to prevent the partner from attracting extra-pair mates or to repel same-sex rivals (Grafe and Bitz 2004, Rogers et al. 2006) – thus song answering and song initiation could have different functions for each sex in this scenario (Odom et al. 2017). Finally, duetting may have a role in communication between partners, such as stimulating and coordinating breeding activities in environments that have little seasonality (Dilger 1953, Hall 2009).

Mate guarding and territorial defense hypotheses predict higher signal expression during aggressive interactions with conspecifics (Hall 2004). A few species exhibit peaks in duet rate in the pre-breeding stage, which decrease as the breeding season progresses (Sonnenschein and Reyer 1983, Hall 2009, Dowling and Webster 2013, Odom et al. 2016), generally resulting from a decreasing female song rate (Hall 2006, Topp and Mennill 2008). However, studies rarely assess if these peaks match the time of highest occurrence of aggressive interactions with strangers (Dowling and Webster 2013). Without recording seasonal variation in aggressive

Table 1. Predicted seasonal variation in solos and duets according to six popular functional hypotheses. Song mode: song initiation or solo (I), song answering (A), pair-level duetting (D). Sex: male (M), both (B).

Hypotheses	Description	Song mode	Sex	Expected peak in signal expression	Territorial aggressive context?
Coordination of parental care ^{1,2}	Parents use song exchange to coordinate nest visits	IA	B	Nesting stage ²	No
Ensuring reproductive synchrony ³	Song stimulates and synchronizes reproductive activities	IA	B	Pre-breeding stage ¹³	No
Territorial defense ^{4,5,6}	Song is used to defend resources in a territory	IAD	B	When there are more territorial intrusions ^{4,6,12}	Yes
Mate guarding (partnership) ^{6,7,8}	Song is used to guard social partner	IAD	B	Pre-breeding and female fertile stages ^{6,7,13}	Yes
Mate guarding (paternity) ^{6,9,10}	Male song prevents female partner engaging in extra-pair copulation	IA	M	Female fertile stage ^{6,7,13}	Yes
Male attraction of extra-pair mates ^{7,10}	Initiated and solo songs are intended to attract extra-pair mates	I	M	When most females are fertile in the population ^{10,11}	No

References: 1 – Langmore (1998), 2 – Halkin (1997), 3 – Dilger (1953), 4 – Catchpole and Slater (2008), 5 – Seibt and Wickler (1977), 6 – Hall (2004), 7 – Moller (1991), 8 – Stokes and Williams (1968), 9 – Sonnenschein and Reyer (1983), 10 – Mace (1987), 11 – Chiver et al. (2015), 12 – Levin (1996), 13 – Hall (2009).

interactions, it is difficult to distinguish if seasonal peaks in singing effort are due to communication within the social pair (e.g. to ensure reproductive synchrony) or between social pairs (e.g. territory defense).

In this study, we investigated seasonal variations in territory interactions and singing behavior in the rufous hornero *Furnarius rufus*, a socially monogamous, Neotropical, suboscine bird species, in which males and females sing solo songs and also combine their songs into duets. The rufous hornero maintains territories year-round but breeds seasonally (Fraga 1980, Massoni et al. 2012), and apparently, both sexes sing year-round (Diniz unpubl.), allowing us the opportunity to study the selective pressures shaping the evolution of song in this species (Odom et al. 2016, 2017). If a signal is used exclusively in the breeding season, evolutionary theory suggests it is likely to be shaped by sexual selection (Price et al. 2008, Illes and Yunes-Jimenez 2009, Odom et al. 2016). However, if a species sings year-round, this may represent social selection (i.e. the evolution of traits driven by social interactions not necessarily related to mating success) (reviewed by Tobias et al. 2012, Odom et al. 2016).

We tested the general hypothesis that song function varies with sex, singing role and level of duet organization, which might be evident through seasonal variation. We studied social pairs of horneros and recorded vocal behavior and territorial, aggressive interactions with strangers across seven months. At the individual level, we measured the number and duration of territorial interactions, singing effort (rates of song initiation, song output and phrase duration in coordinated songs) and song attentiveness to partner songs (i.e. song answering rate and latency to answer). At the pair level, we recorded duet rate and duration. Our study innovates by treating three signals (song initiation, song answering and pair-level duetting) as fairly independent behaviors (Logue and Krupp 2016, but see Odom et al. 2016, 2017) and draws together hypotheses established in previous studies for both solo song and duet (Table 1). If these three signals evolved under the same selective forces, we expect them to show similar patterns of variation across breeding and non-breeding stages.

Material and methods

Study species

The rufous hornero is a sexually monochromatic and socially monogamous bird species from South America (Sick 2001, Diniz et al. 2016, Remsen and Bonan 2016). This species lives in open habitats, mainly urban parks and agricultural land, from central Brazil to central Argentina (Remsen and Bonan 2016). Social pairs maintain territories year-round, build a domed nest and normally produce a single brood (3–4 eggs) per year (Fraga 1980, Massoni et al. 2012). Both parents contribute similarly to parental care (Massoni et al. 2012) and nesting success is high (Fraga 1980). Little is known about the vocal behavior of the rufous hornero: male and female

overlap sex-specific phrases in duets, which are initiated by both males (Laje and Mindlin 2003, Amador et al. 2005, Roper 2005) and females (this study). In addition, parents and juveniles can all sing together simultaneously in choruses (i.e. three or more individuals coordinating songs; Diniz unpubl.), which likely have similar function to pair-level duets (Bradley and Mennill 2009b). Vocal repertoire is determined by variations of two song types for each sex, and duet phrases are similar to solo songs in structure, but differ in tempo (Diniz unpubl.): females respond to note acceleration of males by switching their note production rate to a different locking state, suggesting rhythmic coordination (Laje and Mindlin 2003).

Study area and field methods

We studied 12 social groups from an urban and banded population of the rufous hornero on the campus of the Universidade de Brasilia, central Brazil (15°45'S, 47°51'W). The study area has a seasonal climate, which includes a dry season (from May to September) and a wet season (from October to April). The rufous hornero breeds seasonally across its distribution, between late August and December (Supplementary material Appendix 1 Fig. A1; Fraga 1980, Massoni et al. 2012).

Groups varied in size from two to six individuals (mean \pm SD = 2.83 \pm 0.82, n = 163 trials), depending on whether the pair was accompanied by retained offspring. At the beginning of the study two groups were composed of adults only (social pair) and 10 groups had both adults and juveniles. All studied juveniles hatched in the previous breeding season and stayed within their natal territories, as found in an Argentinian population of the rufous hornero (Fraga 1980). Although juveniles may help the parents to build a new nest during the year, they disperse before the nesting season and never incubate or feed nestlings (Fraga 1980, Massoni et al. 2012, Diniz unpubl.). Group size varied across the study period for all the studied groups, except one group that lost its territory (see below). Group size varies seasonally due to juvenile dispersal and recruitment of new offspring.

We monitored 11 social groups for seven months (June–December 2015), which covered non-breeding and breeding seasons. One additional group was monitored only until September, which was when this group lost its territory to an unbanded pair. We observed each of these groups for one hour at 15-d \pm 0.15 (mean \pm SE, n = 149) intervals, for a total of 14 focal sessions per group (except the one group that lost its territory and was observed for 7 focal sessions). We chose a 15-d interval between focal sessions so that we could divide our study period in the five phenological stages described below. Before starting the trials, we determined the order of observation using random permutation in R (R Core Team). We maintained this order during the study period to preserve equality of sampling intervals within groups. All focal sessions occurred from zero until five hours after sunrise (preliminary observations reveal that there is no dawn chorus in the species; sunrise time retrieved from <www.timeanddate.com>).

Observations were generally carried out by two observers (range = 1–4) and always focused on the mated pairs. Observers had previous experience with the rufous hornero and its associated behaviors and normally each observer focused on a different adult bird. During each 1 h-focal session, we followed the pair and recorded their vocalizations using a Marantz PMD 660 recorder (settings: WAVE format, sampling rate = 48 kHz, resolution = 24-bits) combined with a Sennheiser ME66 (frequency response = 0.04–20 kHz) or Yoga HT-81 microphone (frequency response = 0.1–16 kHz). We also recorded behaviors, including aggressive interactions (chasing, approach followed by vocalization, song overlapping, displacement and/or fights) involving adult focal individual(s) against strangers (normally neighbors), and estimated the duration of these interactions whenever possible. Juveniles were often near their parents and we are confident we did not confuse unbanded juveniles with strangers. We could not measure sex-specific duration of these interactions when both sexes participated and thus considered the same duration for both sexes in this case. All these focal birds forage near pedestrians in the study area and we are confident our presence had little effect on the focal birds' behaviors.

Finally, we recorded the occurrence of the following breeding behaviors in the same 1-h focal sessions: nest building, incubation, brooding, feeding nestlings or fledglings (Massoni et al. 2012). Incubation and brooding phases were defined when at least one adult visited its nest, without bringing any nest building material (e.g. mud) or food, and spent five or more minutes inside the nest chamber (Massoni et al. 2012). When a parent was observed bringing food to the nest, we considered it to be at the nestling phase. We used these behavioral data to estimate the breeding stages.

Breeding phenology

The study periods were broken down into five stages: non-breeding, pre-breeding, fertile, nesting and post-breeding (similar to Hall 2006, Topp and Mennill 2008). We considered the non-breeding stage from 31–120 d before the first sign of incubation; pre-breeding from 16–30 d before the first sign of incubation; and fertile stage from 1–15 d before the first sign of incubation. The nesting stage comprised both incubation and nestling stages. The post-breeding stage comprised 1–90 d after fledging, when juveniles stayed in their natal territories (Fraga 1980). Seven study groups bred once and two groups bred twice during the study period. One group renested after its nest was depredated, and another group renested after the young from the first brood fledged. Because this latter group had juveniles from the current breeding season while the adults were incubating a new clutch, we classified the group as being both in the 'nesting stage' and in the 'post-breeding stage'. Accordingly, we classified the group as both 'fertile stage' and 'nesting stage' in the prior focal session (~15 d before). We did not consider a category for nest building, since rufous horneros build their nests throughout the year and building rhythms seem to vary daily as a function of precipitation regimes (Fraga 1980).

Acoustic analyses

Acoustic analyses were performed in Raven Pro 1.5 (Bioacoustics Research Program 2014). Because rufous hornero partners overlap sex-specific phrases in duets (Amador et al. 2005), we could identify male and female contributions (Fig. 1). We used the waveform and the spectrogram (Hann window, window size = 256, overlap in time = 50%) to demarcate the start and end of each phrase and song of each adult whenever possible. Then, we counted the number of initiated and answered songs in each 1 h recording, obtained the duration of phrases and songs, and the latency to answer the partners' songs in coordinated songs.

We classified initiated songs as solos plus initiated duets or chorus (Hall and Peters 2008a), where solo songs were those not coordinated with the social partner. Song answering was computed when the focal individual answered partner-initiated duets or chorus (reviewed by Logue and Krupp 2016). Importantly, since we focused on the adults, we ignored the phrase contributions and the solos of juveniles (Dowling and Webster 2013). We adopted this approach because rufous horneros have a very low song output (< 2% of the time singing, see Results), juveniles initiated a minority of group songs (< 5%), rarely answered a parent song before the other parent had sung, and emitted, on average, shorter songs than adults. We argue that by overlooking the juvenile songs we increased our statistical power to explain seasonal variation of singing behavior.

Rufous hornero males, and occasionally females, can emit long solo song bouts (Diniz unpubl.) composed of subunits of monosyllabic and accelerated trills (Fig. 1A and B). We considered such a solo song bout a single initiated song, if the intervals between their consecutive subunits were no longer than 30 s (an interval value rarely reached by consecutive subunits) – otherwise we classified these subunits, separated by more than 30 s intervals, as separately initiated solo songs. We considered as two independent solos those cases where partners overlapped their long monosyllabic song bouts if there was a very low degree of overlap (< 5%) and no clear coordinating structure (Hall 2004, Diniz unpubl.). When an individual joined a partner's lengthy solo song bout (> 1 min), we computed this as both a solo song bout and a duet, using as a marker the beginning of the partner's last accelerated trill before the individual joined the vocalization. Low amplitude solo songs lasting less than 2 s and short songs emitted during chases across territories in aggressive territory interactions were not counted. Individuals' songs overlapping by only one or two partner notes were classified as solos.

Since rufous horneros may emit long solo song bouts, song rate does not fully represent song output in this species. We measured song output as the total time each adult spent singing in each 1 h focal session. We could not measure phrase or song duration from 15% of the vocalizations recorded (n = 208 of 1395) due to poor quality of some recordings. Thus, we estimated the missing phrase durations using the mean duration of the other phrases during the same 1 h recording. We then used the real measured duration plus

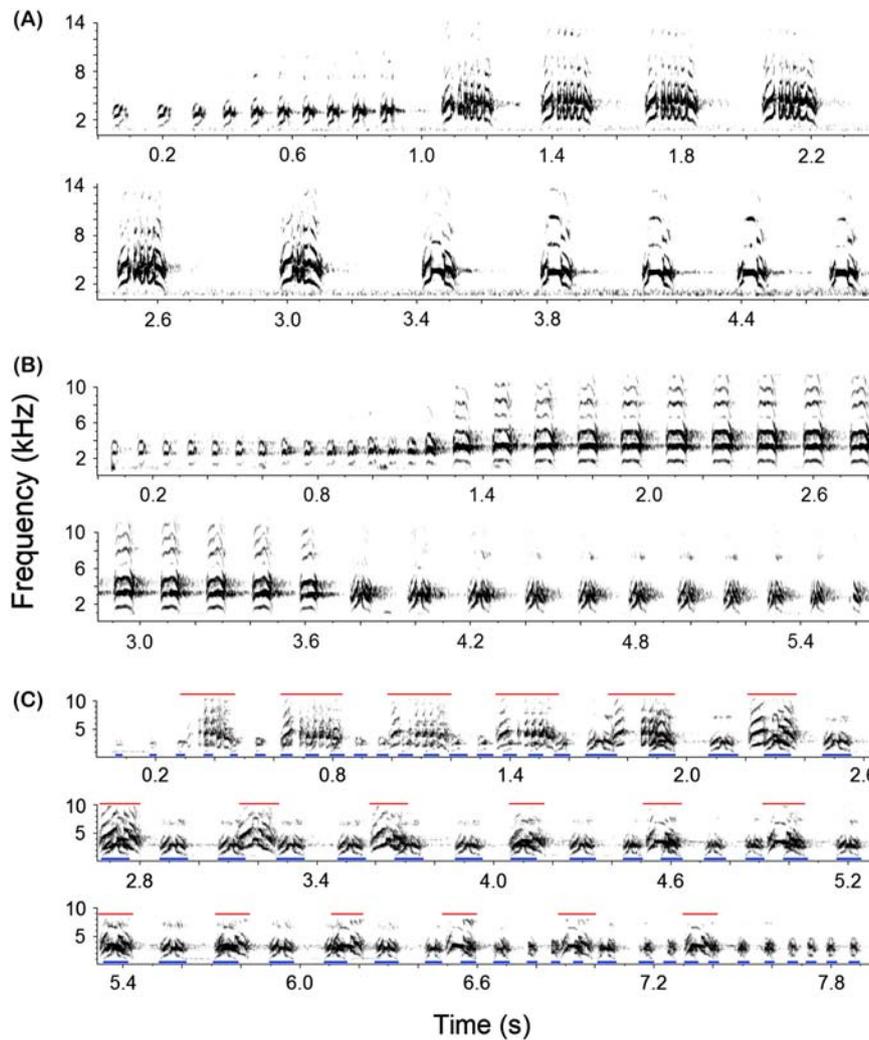


Figure 1. Examples of female solo (A), male solo (B) and male–female duet (C) in the rufous hornero. (C) Lines above and below notes indicate female and male notes, respectively.

the estimated duration values to obtain the song output for each recording. We believe this is a conservative approach for a species with low song output such as the rufous hornero (see above).

Statistical analyses

Statistical analyses were performed in R. We analysed separately each of the following seven individual-level response variables: 1) number and 2) duration of territorial aggressive interactions with strangers, 3) song initiation and 4) answering rates, 5) song output, 6) latency to answer partner's song, and 7) phrase duration in duets. We also analyzed two response variables at the pair-level: 8) duet rate (number of duets h^{-1}) and 9) duet duration. Song initiation rate means the number of initiated songs in a 1 h focal session. Song answering rate was considered as the proportion of partner's initiated songs that were answered by the focal bird (reviewed by Logue and Krupp 2016). Structure of the global models

for all response variables are described in the Supplementary material Appendix 1 Table A1.

We analyzed our dataset with linear (LMM) or generalized mixed modelling (GLMM) depending on the scale of our response variable (according to Zuur et al. 2009) (Supplementary material Appendix 1 Table A1). We chose this statistical approach to deal with varying error distributions, presence of random factors and unbalanced design (Zuur et al. 2009). We modelled the response variables 1), 3) and 8) assuming a Poisson distribution of errors, and the variable 4) according to the Binomial family for proportional data. The remaining response variables were analyzed according to the Gaussian family. We log-transformed variables 5) and 6) to achieve a normal distribution of errors.

We included breeding phenology as a fixed effect in all models. We included sex to model individual-level song behaviors. We also included the identity of the social pair (random factor), group composition (adults or adults plus juveniles) and decimal hour at the beginning of each focal

trial (covariates) in all models. Additionally, we added aggressive contexts as fixed effects to model all song variables (Supplementary material Appendix 1 Table A1). Territorial, aggressive context during the 1 h focal sessions was a factor composed of three levels: aggressive, non-aggressive and unknown role. Aggressive context occurred when the focal bird engaged in one or more agonistic interactions with strangers whereas non-aggressive context consisted of the lack of such agonistic interactions. Unknown role meant the focal bird engaged in aggressive interaction, but we did not know if the bird interacted with strangers or other group member(s). We kept this 'unknown role' level to avoid decreasing sample size and statistical power.

We added song type (i.e. duet or chorus) as a fixed effect to model latency to answer partner's songs and phrase duration in duets. We included the identity of the focal session nested within the identity of the social pair as a random nested effect to model the variables 2), 6), 7) and 9). Finally, we added the interaction sex \times breeding phenology in all models, and the interaction sex \times aggressive context to model song variables (Supplementary material Appendix 1 Table A1).

We tested the 'attraction of extra-pair mates hypothesis' for male song initiation rate and male song output. We created two new global models (one for each response variable), exclusively for males, to perform these analyses. To these models we added all the variables included in the global models for both sexes, except the variable 'sex'. We also added the proportion of studied females that were fertile in each 15-d study period (e.g. 1–15 August) as an estimate of the number of fertile females in the studied population.

We used the function 'dredge' from the 'MuMIn' (Baron 2015) package to select the best-fit models based on the AICc criteria ($\Delta AICc < 2$; Burnham and Anderson 2002). For continuous predictors, we obtained β estimates for the retained variables from the top model in which the variable occurred. For categorical predictors, we used the commands 'glht' (multcomp package, Hothorn et al. 2008) and 'lsmeans' (lsmeans package, Lenth 2015) to obtain post-hoc comparisons among factor levels, using the top model in which the variable occurred. We controlled for false discovery rate in post-hoc comparisons according to Benjamini and Hochberg (1995). Model selection steps for each response variable are described in the Supplementary material Appendix 1.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.tq3m0>> (Diniz et al. 2018).

Results

Territorial interactions

For both sexes, the number and duration of aggressive interactions with strangers did not vary across breeding and non-breeding stages (GLMM and LMM, model selection

and post hoc results: Supplementary material Appendix 1 Table A2; A3; A4). On average, males engaged in aggressive interactions 1.5 times more than did females ($\beta=0.43 \pm 0.13$; mean \pm SE; male= 0.89 ± 0.08 ; female= 0.58 ± 0.07), although the sexes did not differ in the time spent in each territorial interaction (mean \pm SE; male= 32.89 ± 6.49 s; female= 41.09 ± 9.75 s; Supplementary material Appendix 1 Fig. A2).

Individual-level duetting behaviors

We recorded, on average, 10 adult songs h^{-1} ($n=1611$ adult songs, 12 social groups), including solos and duet phrases. For 184 recorded songs (10% of total songs recorded, $n=1795$), we could not determine the singer origin. We determined the singing role (i.e. initiator or responder) in 88% of the recorded and identified songs ($n=1611$). Overall, most songs (61%) were duets. Results from song output are described in the Supplementary material Appendix 1.

Song initiation

According to the best-ranked model (weight [wi]: 0.47), song initiation rate was associated with breeding phenology and territorial, aggressive context, but sexes differed in how their song behavior varied relative to breeding phenology (GLMM, model selection and post hoc results: Table 2, Supplementary material Appendix 1 Table A7, A8; Fig. 2A). Female song initiation rate peaked during non-breeding (mean \pm SE= 1.94 ± 0.22 songs h^{-1}) and post-breeding stages (mean \pm SE= 2.51 ± 0.25 songs h^{-1}), and gradually decreased from the non-breeding season through the breeding season. In contrast, male song initiation rate peaked in the post-breeding stage (mean \pm SE= 5.10 ± 0.54 songs h^{-1}) and, less noticeably, in the pre-breeding stage (mean \pm SE= 4.42 ± 0.68 songs h^{-1}). Females tended to initiate fewer songs in the nesting stage (mean \pm SE= 0.75 ± 0.15 songs h^{-1}), and males sang at their lowest rate in the non-breeding stage (mean \pm SE= 2.84 ± 0.36 songs h^{-1}).

Males and females initiated more songs in contexts that included at least one territorial aggressive interaction (mean \pm SE: female= 2.02 ± 0.21 songs h^{-1} , male= 4.53 ± 0.34 songs h^{-1}) compared to those without any territorial interaction involving the focal individual ($\beta \pm$ SE= 0.25 ± 0.08 ; mean \pm SE: female= 1.56 ± 0.16 songs h^{-1} , male= 2.02 ± 0.16 songs h^{-1}). The third best-ranked model ($\Delta AICc=1.77$) indicates this result is exclusively for males, which suggests that females initiated fewer songs than males in response to territorial, aggressive contexts. Although sexes differed in their singing initiation behavior relative to breeding phenology, males initiated, on average, twice the number of songs that females initiated, irrespective of breeding stage and the occurrence of territorial, aggressive interactions with strangers (pooled data, $\beta \pm$ SE= 0.90 ± 0.10 ; mean \pm SE: male= 3.74 ± 0.24 songs h^{-1} ; female= 1.76 ± 0.13 songs h^{-1}).

In the subset model that included only male song data, we found a negative correlation between male song initiation rate and the estimated proportion of females that were fertile

Table 2. Modelling comparison of song variables as a function of breeding phenology and territorial aggressive interaction.

	df	AICc	Δ AICc	wi
Song initiation rate (GLMM, poisson family)				
aggression + phenology + sex + time + phenology \times sex	14	1303.4	0.00	0.47
aggression + phenology + sex + group + time + phenology \times sex	15	1304.9	1.50	0.22
aggression + phenology + sex + time + aggression \times sex + phenology \times sex	16	1305.2	1.77	0.20
Song answering rate (GLMM, binomial family)				
phenology + sex + group + time	9	603.0	0.00	0.52
Song latency (LMM, log)				
phenology + time + sex + song type	11	1328.3	0.00	0.44
phenology + time + sex	10	1329.2	0.91	0.28
Phrase duration in duets (LMM)				
phenology + sex	9	3862.2	0.00	0.313
phenology + sex + song type	10	3863.5	1.27	0.17
phenology + sex + time	10	3863.9	1.71	0.13
Duet rate (GLMM, poisson family)				
aggression + phenology + time + group	11	640.7	0.00	0.513
Duet duration (LMM)				
phenology + time	9	1746.1	0.00	0.26
phenology + song type + time	10	1747.0	0.90	0.16

Models about individual-level singing behavior also include sex as a fixed effect. All models contained the identity of the social group as a nested random term. We show results from top models (Δ AICc < 2) derived from modelling comparison among all combinations of predicted variables included in the global model (command 'dredge' in 'multcomp' package). Aggression=aggressive context; phenology=breeding phenology; time=decimal hour; group=group composition; df=degrees of freedom; wi=weight.

in the population ($\beta \pm SE = -0.16 \pm 0.07$). The parameter, estimated proportion of fertile females, occurred in the two top-ranked models for male song initiation rate (Δ AICc < 2, cumulated wi=0.70); the results for the other variables of interest (breeding phenology and territorial, aggressive context) remained qualitatively unchanged.

Song answering

According to the best-ranked model (wi=0.52), male and female song answering rates differed but were similarly associated with breeding phenology (GLMM, model selection and post hoc results: Table 2, Supplementary material Appendix 1 Table A9, A10; Fig. 2B). On average, males answered 73% (± 2.97 SE) of partner songs, whereas females answered 61% (± 2.59 SE) of male-initiated songs ($\beta \pm SE = 0.56 \pm 0.16$). For both sexes, song answering rate clearly peaked during pre-breeding (mean \pm SE; male=0.97 \pm 0.03, female=0.77 \pm 0.08) and female fertile stages (mean \pm SE; male=0.97 \pm 0.03, female=0.78 \pm 0.08). Song answering rate did not differ between non-breeding, nesting and post-breeding stages (sexes pooled, mean \pm SE: non-breeding=0.62 \pm 0.03; nesting=0.65 \pm 0.05; post-breeding=0.62 \pm 0.03). Finally, song-answering rates did not correlate with territorial interaction for either males or females.

According to the best-ranked models (Δ AICc < 2), song latency to answer partner's initiated songs varied with sex, breeding phenology and song type (i.e. duet or chorus), but did not vary with the occurrence of territorial, aggressive encounters (LMM, model selection and post hoc results: Table 2, Supplementary material Appendix 1 Table A11, A12; Fig. 2C). Males answered partner's initiated songs faster than females, irrespective of breeding phenology or song

type ($\beta = 0.56 \pm 0.11$; mean \pm SE; male=0.84 \pm 0.08 s; female=1.46 \pm 0.10 s). Both sexes answered partner initiated songs more quickly during the female fertile and nesting stages (and, less clearly, in the pre-breeding stage), compared with the post-breeding stage. Both sexes tended to have lower latency in answering their partner's song in duets compared with chorus (sexes pooled, $\beta \pm SE = 0.27 \pm 0.15$; mean \pm SE: duets=1.13 \pm 0.07 s; chorus=1.85 \pm 0.24 s).

Phrase duration

According with the best-ranked model (wi=0.22), the duration of phrases emitted in duets varied with sex and breeding phenology (LMM, model selection and post hoc results: Table 2, Supplementary material Appendix 1 Table A14; Fig. 2D). Males emitted longer phrases than females, irrespective of breeding phenology ($\beta = 0.95 \pm 0.10$; mean \pm SE; male=6.37 \pm 0.08 s; female=5.41 \pm 0.07 s). For both sexes, the duration of phrases peaked in the pre-breeding and female fertile stages (mean \pm SE; pre-breeding=6.43 \pm 0.16 s; fertile=6.63 \pm 0.15 s), and tended to be longer in the nesting stage compared to the non-breeding stage (sexes pooled, $\beta = 0.54 \pm 0.21$; mean \pm SE; nesting=6.03 \pm 0.15 s; non-breeding=5.50 \pm 0.10 s).

Pair-level duetting behaviors

Duet rate

According to the best-ranked model (wi=0.51), duet rate varied with breeding phenology and territorial, aggressive context (GLMM, model selection and post hoc results: Table 2, Supplementary material Appendix 1 A15, A16;

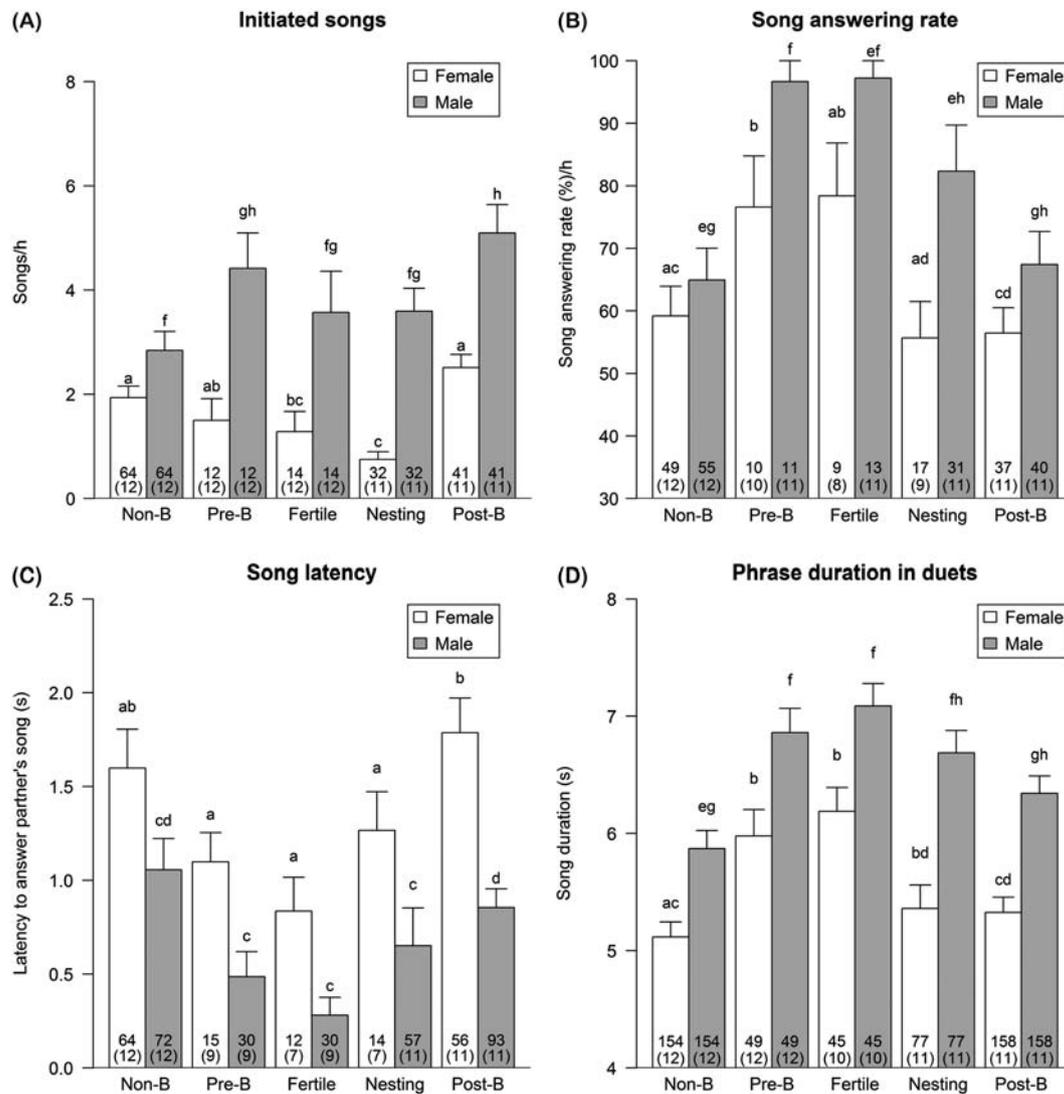


Figure 2. Seasonal variation in duetting behavior at the individual level (means \pm SE) in the rufous hornero. Seasonal stages: Non-B = non-breeding (31–120 d before incubation started); Pre-B = pre-breeding (16–30 d before incubation started); Fertile (1–15 d before incubation started); Nesting (incubation and nestling periods); Post-B = post-breeding (1–90 d after fledging). Different letters indicate post-hoc differences in the response variable between factor levels. Numbers without parentheses indicate total focal sessions. Numbers of social pairs are shown within parentheses.

Fig. 3A). Duets peaked in the pre- (mean \pm SE = 4.67 ± 0.79 duets h^{-1}) and post-breeding stages (mean \pm SE = 4.20 ± 0.31 duets h^{-1}), and were less frequent in the nesting stage (mean \pm SE = 2.69 ± 0.31 duets h^{-1}). The peaking of duetting during the pre-breeding stage was mainly a result of high song initiation by males and high answering rates by both sexes. In contrast, the duetting peak during the post-breeding stage was mainly a result of high song initiation by both sexes despite the moderate song answering rates at this stage.

Partners duetted at the highest rate when one pair member engaged in one or more territorial, aggressive interactions with strangers ($\beta \pm$ SE = 0.21 ± 0.10 ; mean \pm SE: non-aggressive context = 2.45 ± 0.28 duets h^{-1} , aggressive

context = 3.74 ± 0.20 duets h^{-1}). However, the second best-ranked model (Δ AICc = 0.37) does not indicate this relationship.

Duet duration

According to the best-ranked models (Δ AICc < 2), duet duration varied with breeding phenology, but not with the occurrence of territorial, aggressive interactions with strangers. The duration of duets was higher in the breeding season relative to the non-breeding season (LMM, model selection and post hoc results: Table 2, Supplementary material Appendix 1 Table A17, A18; Fig. 3B; see Supplementary material Appendix 1 for detailed results of model selection).

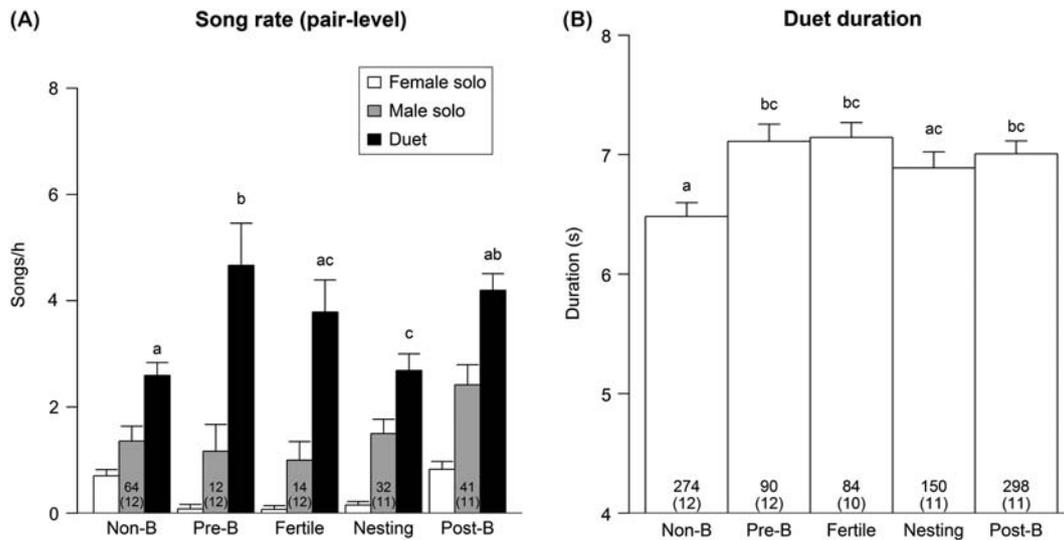


Figure 3. Seasonal variation in duetting behavior at the pair level (means \pm SE) in the rufous hornero. Phenological stages: Non-B = non-breeding (31–120 d before incubation started); Pre-B = pre-breeding (16–30 d before incubation started); Fertile (1–15 d before incubation started); Nesting (incubation and nestling periods); Post-B = post-breeding (1–90 d after fledgling). Different letters indicate differences in the response variable between factor levels. Numbers without parentheses indicate total focal sessions. Numbers of social pairs are shown within parentheses.

Discussion

Seasonal patterns of song vary with sex, singing role and level of duet organization

In general, our results suggest that year-round territorial defense is one of the possible functions of both rufous hornero male and female songs (Hall 2004, 2009), but this idea needs further experimental investigation (Dowling and Webster 2016). Both males and females engaged in territorial, aggressive interactions with strangers, sang solo songs, and initiated and answered songs in duets during both the non-breeding and breeding stages. Partners coordinated the majority of their songs (61%) into duets, and three song traits (song initiation rate, song output and duet rate) peaked when there was a territorial interaction involving the focal individual or pair.

Although rufous hornero males and females sang year-round, suggesting a role of social selection on song evolution in this species (Tobias et al. 2012, Odom et al. 2016), we found sex-differences in singing behavior that also suggest that sexual selection plays a role in the evolution of song in this and other duetting species (Mennill et al. 2005, Odom et al. 2016). We found sex differences in aggressive and singing behavior, regardless of seasonality. Males engaged more in territorial interactions with strangers, and sang at higher rates and for longer periods than females. In addition, males initiated more songs, answered their partner's songs more quickly to create duets, and did so at higher rates, compared with females. Male bias in singing effort is common among other duetting species (Mennill et al. 2005, Rogers 2005, Valderrama et al. 2008,

Tobias et al. 2011, Koloff and Mennill 2012, Odom et al. 2016).

Seasonal variation in the rufous hornero's duetting behavior also varied between levels of organization (individual-level vs pair-level) and singing roles (initiation vs answering) within the individual-level (Topp and Mennill 2008). We found sex-specific seasonal variation in song initiation but not in answering behavior, suggesting that the function of duetting components may differ between the sexes. Indeed, the few studies that focus on this issue have shown component-specific seasonal variation in duetting behavior (Topp and Mennill 2008, Odom et al. 2016, 2017). For example, in rufous-and-white wrens *Thryothorus rufalbus*, female song answering and output decrease as the breeding season progresses, whereas males continue to sing solo songs at high rates through the breeding season (Topp and Mennill 2008). In the venezuelan troupial *Icterus icterus*, male song initiation is higher during the breeding season, whereas female song is consistent year-round and duets occur more often during the non-breeding season (Odom et al. 2016). Evidence therefore suggests that song function varies with sex, singing role and level of duetting organization (Logue and Krupp 2016).

Individual-level duetting behaviors

Song initiation

Song initiation rate was highest during territorial interactions for both sexes, regardless of phenological stage. However, our results only partially support the territory defense hypothesis for the function of male and female song initiation behaviors. First, females initiated songs more often in the non-breeding season, and second, both sexes initiated songs more frequently

in the post-breeding stage. The number of territorial interactions with strangers however did not vary across seasons. Our data also partially support the ‘mate guarding’ and ‘ensure reproductive synchrony’ hypotheses for the function of male song initiation behavior (Table 1).

Singing effort in birds usually peaks in the pre-breeding and egg-laying stages (Amrhein et al. 2002, 2004, Dowling and Webster 2013), occasionally in the nesting season (Cain and Langmore 2015, Chiver et al. 2015), but seldom in the post-breeding stage. Increased competition for nest sites, territories and social mates during the post-breeding stage could explain the unexpected peak in song initiation rates during this phase. The rufous hornero starts to build a new nest for the following breeding season just after its current seasonal nesting season has ended (Fraga 1980). Also, some of the juveniles might disperse during the post-breeding stage (Diniz unpubl.). Alternatively, high song initiation rate may encourage juvenile singing in the post-breeding stage in order to join parents in territory defense (Farabaugh et al. 1992) or stimulate vocal learning in juveniles.

Male song initiation did not peak during their partner’s fertile stage and it was not positively associated with the estimated phenological variation in the number of fertile females in the studied population. These results indicate that rufous hornero males do not initiate songs to assure paternity or attract extra-pair mates (Forstmeier and Balsby 2002). Finally, the peak in male song initiation during the pre-breeding season provides evidence supporting the ‘ensure reproductive synchrony’ hypothesis, indicating that male song initiation could also function to stimulate or respond to their partner’s reproductive activity (e.g. increased nest building) (Leboucher et al. 1998, Bentley et al. 2000).

Song answering

Both sexes answered their partner’s initiated songs with shorter latency and at significantly higher rates (100%, males; ~80%, females) during the pre-breeding and female fertile stages. Our results are concordant with studies of the rufous-and-white wren, where males answered their partner-initiated songs at the highest rate during the fertile stage, although females showed very low responsiveness during this period (Topp and Mennill 2008). In contrast, other studies have found that males and females do not increase their duet responsiveness during the female fertile stage (Hall and Magrath 2000, Gill et al. 2005, Hall 2006, Hall and Peters 2008b).

Song attentiveness behaviors (i.e. song answering rate and latency) may have a similar function for male and female rufous horneros, since they showed similar patterns of variation across non-breeding and breeding stages. Our results provide support for the hypothesis that song attentiveness functions to ensure reproductive synchrony (Table 1), and in mutual partnership guarding, despite the fact that we did not find a link between song answering and territorial interactions, required for full support of this last hypothesis (Rogers et al. 2006). We also did not find a higher rate of

territorial interactions during the pre-breeding and female fertile stages, providing no support for the territory defense hypothesis. Thus, song answering in itself should not be enough to promote territory defense in the rufous hornero.

Contrary to predictions of the ‘paternity guarding’ hypothesis, male song answering rate and latency were not higher in the female fertile stage compared with the pre-breeding stage (Hall 2009). Similarly, the proportion of answered songs did not differ between pre-fertile and fertile stages in the buff-breasted wren (Gill et al. 2005). Thus, acoustic paternity assurance is probably not driving these song components in the rufous hornero. However, this idea needs to be further evaluated by relating within-brood paternity loss and male song answering behaviors (van den Heuvel et al. 2014b).

Pair-level duetting behaviors

Duet rate peaked in the pre- and post-breeding stages and was associated with territorial aggressive context, providing partial support for the ‘territory defense hypothesis’ (Table 1). Seasonal patterns in duet rate vary among species, but usually peaks in the pre-breeding stage (rufous-and-white wrens, Topp and Mennill 2008, red-backed fairy-wrens, Dowling and Webster 2013; rufous hornero), and other breeding stages (barred antshrike, Koloff and Mennill 2012; California towhee, Benedict 2010). Our study confirms that duetting can also peak in the non-breeding season (Venezuelan troupial, Odom et al. 2016), such as the post-breeding stage (rufous hornero).

Considering that song answering rates were not associated with territorial interactions, our results also partially support the mutual mate-guarding hypothesis, and suggest that the pair-level component of duetting should be more important for defending a territory or the pair bond than an individual-level duetting property (i.e. song answering). This means that duetting is important for territory, mate guarding or both, regardless of which sex initiates a duet, and that unilateral acoustic mate-guarding through song answering (Rogers et al. 2006) does not seem to occur in the rufous hornero. However, we cannot rule out the possibility that duet rate is a by-product of male song initiation rate, since these behaviors vary in parallel with season (Fig. 2A, Fig. 3A). Finally, the higher duet duration during the breeding season indicates that duet duration should mediate territorial or mate disputes during the breeding season, or facilitate within-pair communication in this period.

Conclusions

Our data suggest that seasonal variation in duetting behavior is dependent upon a complex interaction between sex, singing role (song initiation vs song answering) and levels of duetting organization (individual vs pair-level). Males seem to use song initiation to defend the territory, their mate or both and to stimulate female reproductive activity. In contrast, females seem to use song initiation to defend territorial resources, especially in the non-breeding season. Our study

does not support the idea that song answering is associated with territory defense, but instead that it may function in mutual partnership guarding and stimulation of reproduction (e.g. hormonal profiles). Finally, seasonal variation in duetting at the pair-level partially supported the territory defense and mutual mate guarding hypotheses.

Our study sustains the concept that singing roles and levels of duetting organization may vary across time in different ways and thus may have unique adaptive functions. In addition, we suggest that the pair-level component of duetting contains information arising from the combination of individual-level components (song initiation or answering). Consequently, we suggest that a better understanding of bird song evolution may be attained through studies of duetting behavior at both the individual and pair levels.

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Supplementary material (Appendix JAV-01637 at <www.avianbiology.org/appendix/jav-01637>). Appendix 1.