RESEARCH ARTICLE

Duetting correlates with territory quality and reproductive success in a suboscine bird with low extra-pair paternity

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ABSTRACT
Duetting has been intensively studied, but we still have little consensus about its fitness consequences. Some studies suggest that duetting functions in acoustic mate guarding to prevent cuckoldry (acoustic paternity guarding hypothesis), whereas other studies argue that duetting is a cooperative behavior to defend common resources (territory defense hypothesis). We tested these 2 hypotheses by investigating the relationships among song traits, extra-pair paternity, territory quality and reproductive success in the Rufous Hornero (*Furnarius rufus*), a Neotropical, socially monogamous bird. We found a low rate of extra-pair paternity (3.33% of 120 offspring and 6.52% of 46 broods), which suggests that acoustic paternity guarding is probably not a primary function of duetting behavior in this species. Female song output was positively correlated with territory quality, measured as the availability of territory foraging patches. The number of young that survived post-fledging was positively correlated with duet duration, but not with territory features. Our results support the territory defense hypothesis, suggesting that female song in duets might be used in the defense of food resources within territories. Our study provides the first evidence that song traits correlate with both territory features and reproductive success in a duetting species.

Keywords: duet, female song, *Furnarius rufus*, joint territory defense, social monogamy

Dueto se correlaciona com qualidade territorial e sucesso reprodutivo em um suboscine com baixas taxas de paternidade extrapar

RESUMO
O canto em dueto tem sido amplamente estudado, mas não existe um consenso sobre as suas consequências em aptidão. Alguns estudos sugerem que o dueto funciona na defesa acústica de parceiro para evitar a perda de paternidade (hipótese da defesa acústica de paternidade), enquanto outros estudos argumentam que o dueto é um comportamento cooperativo para defender recursos em comum (hipótese da defesa de território). Nós testamos essas 2 hipóteses por meio da investigação da relação entre características do canto, paternidade extrapar (EPP), qualidade territorial e sucesso reprodutivo no João-de-barro (*Furnarius rufus*), uma espécie Neotropical e socialmente monogâmica. Nós encontramos uma baixa taxa de paternidade extrapar (3.33% de 120 filhotes, e 6.52% de 46 ninhadas), o que sugere que a defesa acústica de paternidade provavelmente não é a função primária do comportamento de cantar em dueto nessa espécie. O tempo despendido em canto pela fêmea foi positivamente correlacionado à qualidade do território, a qual foi medida através da disponibilidade de manchas para forrageamento no território. O número de filhotes que sobreviveram ao período de juvenis foi positivamente correlacionado com a duração do dueto, mas não com as características do território. Nossos resultados apoiam a hipótese de defesa de território, sugerindo que o canto da fêmea pode ser utilizado na defesa de recursos alimentares dentro de territórios. Nosso estudo consiste na primeira evidência de que características de canto refletem características do território e sucesso reprodutivo em uma espécie que canta em dueto.

Palavras chave: canto em fêmeas, defesa conjunta de território, dueto, *Furnarius rufus*, monogamia social

INTRODUCTION

Vocal duets are coordinated songs or calls between partners (Farabaugh 1982). Vocal duetting has fascinated biologists for the last 50 yr (Thorpe et al. 1972, Wickler 1976), and studies have been conducted on many aspects of duetting behavior, including ontogeny (Hall and Magrath 2007, Rivera-Caceres et al. 2016), proximate mechanisms for coordination (Amador et al. 2005, Logue et al. 2008, Rivera-Cáceres 2015), evolution (Logue and Hall 2014, Tobias et al. 2016) and, especially, adaptive function (reviews in Hall 2004, 2009, Dahlin and Benedict 2013). The latter has been widely investigated through the interpretation of responses to playback of solos and duets by territorial birds

(reviews in Hall 2004, 2009, Douglas and Mennill 2010, Dahlin and Benedict 2013), but the fitness consequences of duetting for males and females have seldom been explored (Hall 1999, Hall and Magrath 2007).

To understand the fitness consequences of duetting, it is necessary to know how key fitness characteristics, such as reproductive success, vary among individuals and pairs, and how these are related to duetting (Bateman 1948, Jones et al. 2002). For example, extra-pair paternity (EPP) is prevalent among socially monogamous birds (Griffith et al. 2002, Macedo et al. 2008, Biagolini-Jr et al. 2017), and it has been suggested that duetting functions as a form of mate guarding to reduce EPP (Hall 2009, Sonnenschein and Reyer 2010). However, less than 1% of duetting species have been studied in this regard (Table S1), and previous studies have suggested that EPP might be low in most duetting species, due to a set of life history and ecological traits that appear to be associated with both duetting and low EPP (Gill et al. 2005, Douglas et al. 2012, Koloff and Mennill 2013). Further information on the genetic mating systems of duetting species would allow broader and more confident inferences about general patterns.

There are several hypotheses for duet function (Hall 2004), but 2 of them make clear predictions of fitness consequences of duetting: the acoustic paternity guarding hypothesis and the territory defense hypothesis. Male-created duets (i.e. male answering female songs) might influence male and female fitness through acoustic paternity guarding (Baldassarre et al. 2016). The acoustic paternity guarding hypothesis (Hall 2009, Sonnenschein and Reyer 2010) states that males answer female songs to deter rivals attempting to engage in extra-pair copulations (EPC) with their social partners and/or to minimize the partner's propensity to pursue EPC (Gill et al. 2005, Hall 2009). However, few empirical studies have found support for this hypothesis (Baldassarre et al. 2016, Dowling and Webster 2017), suggesting that duets typically do not function to guard partners from EPC (Hall and Magrath 2000, Gill et al. 2005, Hall and Peters 2008a, van den Heuvel et al. 2014).

Alternatively, the territory defense hypothesis suggests that breeding partners coordinate their songs to defend common territories (reviews in Hall 2009, Dahlin and Benedict 2013), and a complementary hypothesis suggests that the coordination aspect of duetting can signal threat level or motivation in territorial interactions (Hall and Magrath 2007). The territory defense hypothesis is more likely to hold for species with low levels of EPP, because this would facilitate the occurrence of cooperative behaviors between partners (Hall and Peters 2008b). Several playback experimental studies provide evidence that duets can function in settling territorial disputes (Hall 2009, Dahlin and Wright 2012, Dahlin and Benedict 2013, Koloff

and Mennill 2013, Dowling and Webster 2016). If duetting signals competitive ability in acquiring and defending territories in a highly heterogeneous landscape, we could expect that individuals with high expression of duetting attributes would acquire high quality territories and have a lengthy territory tenure, which would in turn influence reproductive success (Tobias et al. 2012, Cain et al. 2015, Cain and Langmore 2016).

It is well known that male song carries information about a variety of fitness-related traits in the context of sexual selection, such as fighting ability and motivation (Ripmeester et al. 2007), aggressiveness (Searcy and Beecher 2009) and territory quality (Manica et al. 2014). Thus, variation among males in song expression mediates intrasexual competition and female mate choice in birds (Kroodsma and Byers 1991, Gil and Gahr 2002, Catchpole and Slater 2008) and has proven fitness consequences (Gil and Slater 2000, Bolund et al. 2012, Nelson and Poesel 2013). In contrast, there are a few examples that female song mediates territorial interactions (Krieg 2016, reviewed by Cain et al. 2015) or predicts reproductive success (Cain et al. 2015, Brunton et al. 2016). In fact, the links between duetting (or female song), territory quality and reproductive success have never been investigated to our knowledge, despite widely cited evidence that duet functions in territory defense (Hall 2009, Dahlin and Benedict 2013).

We tested the acoustic paternity guarding hypothesis and the territory defense hypothesis to explain song function in the Rufous Hornero (*Furnarius rufus*), by relating song traits, territory quality and EPP. The Rufous Hornero is a duetting, year-round territorial and socially monogamous Neotropical bird. Previous observational and experimental data suggest that duetting in this species is cooperative and functions in the joint defense of territorial resources and/or strengthening the partnership of social pairs (Diniz 2017, Diniz et al. 2018). Contrary to predictions of the acoustic paternity guarding hypothesis (Topp and Mennill 2008, Hall 2009), this previous study also revealed that male Rufous Horneros are not more likely to answer their partner's songs during the female fertile period, compared with the pre-breeding stage (Diniz et al. 2018).

For the Rufous Hornero, the acoustic paternity guarding hypothesis predicts that male responsiveness to female song should be negatively related to within-brood paternity loss (Gill et al. 2005). The territory defense hypothesis predicts that song traits (singing effort and responsiveness) should exhibit a positive correlation with territory quality and reproductive success (Cain and Langmore 2016), as reflected in the number of social offspring produced that survive the post-fledging stage. This is one of the few studies investigating the reproductive consequences of duetting,

thus furthering our understanding of the benefits of duets across different mating systems (Dowling and Webster 2016).

METHODS

Study Species and Field Procedures

The Rufous Hornero (family Furnariidae) is a monochromatic (Diniz et al. 2016), ground-foraging, socially monogamous and sedentary bird species (Fraga 1980, Sick 2001, Remsen and Bonan 2017), widespread in southern South America (Marreis and Sander 2006). Pairs breed only once, or sometimes twice, per year, and produce clutches of 2–4 eggs (Fraga 1980, Rodriguez and Roper 2011). Incubation lasts 14–18 days, and the nestling period 23–26 days (Fraga 1980, Remsen and Bonan 2017). Both parents provide parental care, from construction of the heavy globular mud nest (Shibuya et al. 2015) to post-fledging care of the

young (Fraga 1980, Massoni et al. 2012). Nest survival is high (80% nestlings fledged in an Argentinian population; Fraga 1980), contrasting with the low brood survival typical of other Neotropical bird species (Martin 1996), and juveniles may stay in their parents´ territories for ≥7 mo (Fraga 1980, Bobato 2012).

The Rufous Hornero sings 2 song types, one for each sex, and these are sung as solo songs or by overlapping these by either sex to form duets (Figure 1) or choruses (i.e. 3 or more individuals singing together) (Roper 2005, Diniz et al. 2018). Daytime song rate per sex is low (~10 solo songs plus duet songs per hr), most songs are duets (61%), songs are produced throughout the year, and preliminary observations suggest the absence of dawn chorus in this species (Diniz et al. 2018). Compared with females, males initiate twice as many songs, answer partner-initiated songs at higher rates and more quickly, and also have longer song duration (Diniz et al. 2018).
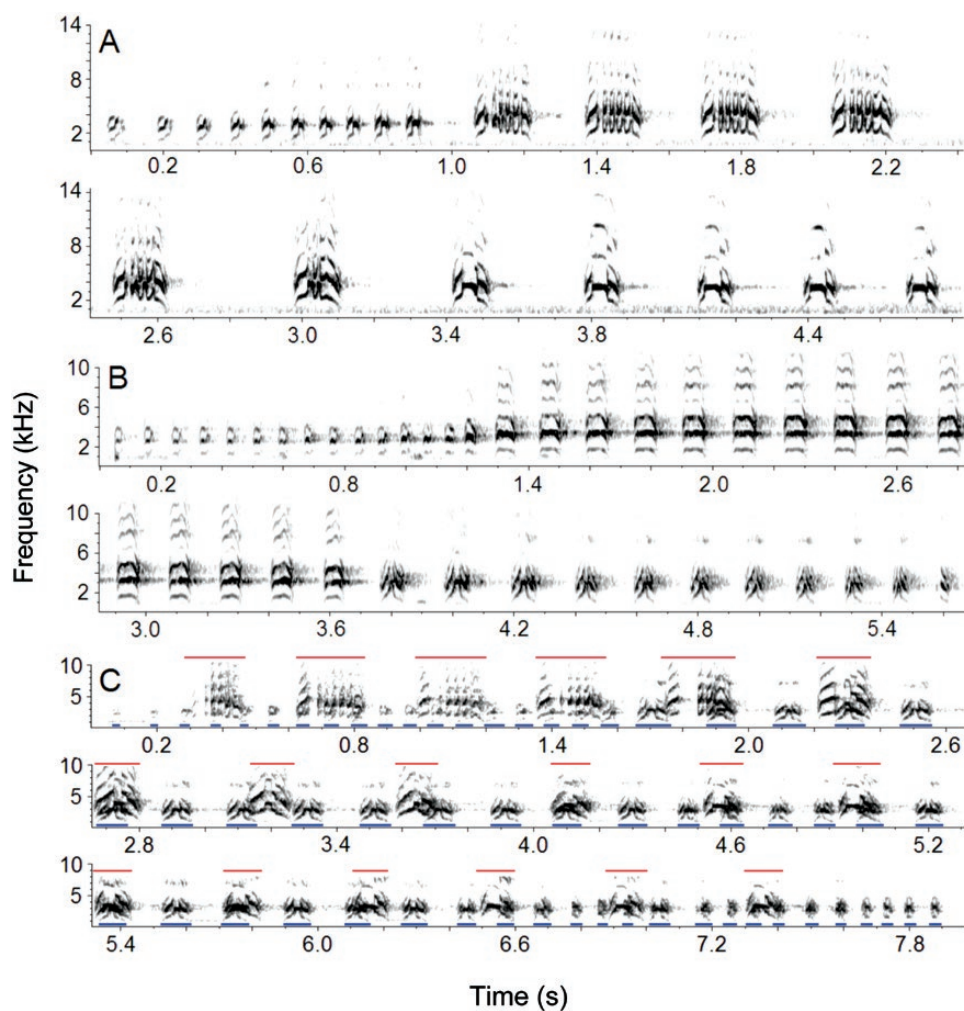

FIGURE 1. Spectrograms of solos (female in A, male in B) and duets (C) of the rufous hornero. Panel C: red and blue lines indicate female and male notes, respectively. Retrieved from Diniz et al. (2018).

We studied an urban population of the Rufous Hornero in a 175 ha section of the campus of the University of Brasilia, Brazil (15.76°S, 47.86°W) for 3 breeding seasons (September to November in 2013, 2014 and 2015) and one non-breeding season (June to August in 2015). In the field, we collected blood samples from adults and nestlings for paternity analyses during the breeding seasons (see below), and conducted focal observations on 12 groups during both non-breeding and breeding seasons in 2015 (totaling 7 mo). From these 12 groups, we recorded vocal behavior, geolocated songs and territorial interactions to estimate territory perimeter, and estimated reproductive success (number of surviving offspring during the post-fledging stage).

Banding and Blood Sampling
We captured and blood-sampled 127 adults and 126 nestlings during all 3 breeding seasons. All adults and 94 nestlings were banded. Capture methods for adults and nestlings followed Braga et al. (2014) and Shibuya et al. (2015), respectively. Blood samples (~60 μL) were obtained from brachial venipuncture for adults and nestlings, and stored in a lysis buffer (100 mM Tris HCl, pH = 8.0, 100 mM EDTA, 100 mM NaCl, 2% SDS) at 4°C. The Rufous Hornero builds heavy domed mud nests during the year, which typically are completed before the breeding season (Fraga 1980, Ferreira et al. 1992). Each year, we monitored nests at intervals of up to 15 days from the beginning of the nesting season (second half of August; Diniz 2017) to choose an optimal date (>4 days after the first egg hatched) to open nests and capture the nestlings with minimal disturbance. We conducted behavioral observations to determine if the adult birds were just building the nest, or whether they were incubating eggs or feeding nestlings (Shibuya et al. 2015). During the week prior to capturing the nestlings we confirmed the parents' identities by visiting their territories and checking their band combinations.

Song, Territory Quality and Reproductive Success
We observed 12 groups for 7 consecutive months in 2015 (from June to December) to obtain data on song, territory and reproductive success. Study groups were composed of adult pairs or pairs plus juveniles (hatched in the previous breeding season), but group size also varied across focal trials (mean ± SD = 2.83 ± 0.82, range: 2–6, n = 163 trials). All adults were banded and sexed. In brief, we observed each group at 15–day ± 0.15 (mean ± SE, n = 149) intervals for 1 hr, totaling 14 focal sessions per group (except one that lost its territory after 7 focal sessions). We focused our observations on adults, recording all the songs they produced using a digital recorder (PMD 660, Marantz, Kanagawa, Japan) coupled with unidirectional microphones (ME-66, Sennheiser, Wedemark, Germany; HT-81, Yoga, São Paulo, Brazil). Song data were also used in a previous, phenological study of the Rufous Hornero (Diniz et al. 2018).

We analyzed song data in Raven 1.5 (Bioacoustics Research Program 2014), and detailed acoustic analyses are described elsewhere (Diniz et al. 2018). We defined song as a rhythmic sequence of vocal elements (Bonnevie et al. 2018) emitted as a solo or as a contribution to a duet. In brief, we extracted the following 5 variables for each focal session and for each sex: (1) number of initiated songs (solos plus initiated duets or choruses), (2) song output (total time spent singing), (3) song answering rate (proportion of partner songs that were answered), (4) song duration in duets or choruses, and (5) latency to answer partner-initiated songs. Song duration in duets or choruses (song duration in duets, hereafter) was defined as lengths of individual contributions to duets or choruses. We averaged song duration in duets and latency to answer partner-initiated songs within focal sessions and then within groups, and averaged the other song traits within groups. We also counted the number of duets and estimated duet duration for each focal session, averaging these variables within each group.

We recorded the location of each song produced and each territorial interaction (e.g., chase, fight) involving a focal adult against strangers in each focal session. We used GPS Status 3.0.4. App for Android system (accuracy ~3 m) to demarcate points. In each focal session, we demarcated the same location only once (e.g., when the bird sang twice in the same tree). We pooled points from multiple focal sessions to obtain territory size (mean ± SD = 58.83 ± 12.90 points, n = 12 groups). Coordinated reference system was set to UTM 23S and datum WGS84. We used adehabitatHR package (Calenge 2006) from R 3.2.1 to estimate territory size (at 95% level, in ha) by Kernel utilization distribution function (smoothing parameter computed by "LSCV"; Worton 1989, Seaman and Powell 1996).

The Rufous Hornero is an insectivorous and exclusively ground-foraging species, but relies on trees (and less often on light poles) to build their nests (Fraga 1980, Remsen and Bonan 2017). They forage mainly in short grasses or litter, avoiding tall grasses (Fraga 1980), and thus may favor urban landscapes such as lawns or short-cut grasses (Fraga 1980, Leveau and Leveau 2005). We used QGIS 2.18.3 (QGIS Development Team 2016) to demarcate the contours of trees and short-grass patches at each perimeter-demarcated territory (here, we used 100% minimum convex polygon; Mohr 1947, Odum and Kuenzler 1955) in georeferenced aerial images from the study site (precision: 5 m, photos taken in 2015 by Terracap; Figure S1). The non-foraging patches consisted mostly of streets and sidewalks. We calculated the absolute area (in ha) in each territory covered by frequently managed short grass and litter, and tree canopies, as estimates of available foraging patches and nest sites, respectively.

Our focal observations on 11 groups occurred from up to 120 days before to up to 90 days after the nesting season. This allowed us to estimate reproductive success based on the number of surviving offspring during the post-fledging stage. We used social reproductive success as a relatively accurate estimate of genetic reproductive success for each study group because: (1) paternity analysis was conducted in 3 of these 11 groups and revealed no EPP, and (2) paternity analysis in our general population revealed low rates of EPP (see Results). Parents feed juveniles for ~22 days and juveniles stay in their natal territory from 4 to 9 mo after fledging (Fraga 1980, Bobato 2012). Thus, we considered that the number of surviving offspring was equivalent to the number of juveniles seen in a territory during focal observation sessions conducted after the first fledgling was recorded (mean ± SD = 3.73 ± 1.35 sessions per group, $n = 11$ groups). The single group that lost its territory was assigned a zero as the number of surviving offspring; individuals from this group were not seen in the study area after losing their territory.

Molecular Sexing and Genetic Analysis

We determined the sex of all adult birds using molecular tools ($n = 69$), by their songs ($n = 6$) (Roper 2005), or by using the partner´s known sex (52 birds). We used the molecular sexing methods of Griffiths et al. (1998) for 59 adults captured in 2013, and used the methods of Fridolfsson and Ellegren (1999) to identify the sex of an additional 10 adults captured across the 3 study years.

We determined paternity through single nucleotide polymorphisms (SNPs) markers across individuals. In comparison with microsatellite markers, SNPs have been largely used in evolutionary studies but not in parentage analyses (Kaiser et al. 2016). Although SNPs are usually not multiallelic and thus show low levels of heterozygosity, they are much more abundant in the genome than microsatellites, allowing for powerful analyses of parentage (reviewed by Kaiser et al. 2016). Studies that compare both methods reveal that SNP is equivalently successful or outperforms microsatellites in assigning paternity (Anderson and Garza 2006, Cramer et al. 2011, Weinman et al. 2015).

We used double digest restriction associated DNA sequencing (ddRAD-seq) for de novo SNP development (Peterson et al. 2012). This method provides a reduced-representation and large sample of the genome and does not require previous knowledge on genome sequence or variability (Peterson et al. 2012). The double restriction enzyme digest approach confers advantages in comparison with the previous restriction associated DNA sequencing (RAD-seq) method, mainly because the former permits a greater accuracy and repeatability in DNA fragment size-selection for library construction (Peterson et al. 2012).

SNP discovery and genotyping were conducted according to the Peterson et al. (2012) protocol with a few changes (see Supplementary Material Appendix for detailed protocol). This protocol involves 4 general steps. First, we isolated, quantified and diluted genomic DNA for 240 samples from 230 individuals. Then we digested genomic DNA samples and ligated short DNA fragments to them, which function as molecular barcodes (i.e. adapters). The third step consisted of pool reactions within each Illumina multiplexing read index (i.e. index group), which assigned a molecular barcode to each group and performed low-cycle DNA amplifications (PCRs). In the last step, a DNA fragment analysis was performed at each index group to calculate molarities and combine diluted index samples. A sample of the final solution of combined DNA from all individuals was submitted to Illumina sequencing read. The reads were checked for quality and filtered (see Supplementary Material Appendix), resulting in 183 SNP loci.

We performed parentage analysis using CERVUS 3.0.7 (Kalinowski et al. 2007) on non-duplicated data (230 individuals). We assumed that all social mothers were also genetic mothers. First, we ran an allele frequency analysis to verify loci characteristics. Characterization of SNPs loci revealed mean heterozygosity of 0.45 across all loci (Table S2). Second, we used SNP genotype information to calculate the log-likelihood (LOD) that each male was the sire of any particular offspring. Third, we ran the simulation of paternity analysis to determine the confidence level that the male with the highest LOD score had sired the offspring in question. We used the following settings to run the simulation of paternity analysis: number of simulated offspring (100,000), candidate fathers (178, estimated adult males in our population), proportion of candidate parents that were sampled (0.29), proportion of loci typed (0.98), proportion of loci mistyped (0.10), minimum typed loci (91) and confidence calculated using LOD score (relaxed level = 95%, strict level = 99%). Finally, we assigned paternity only at the strict level of confidence (99%) and at positive LOD scores.

Statistical Analyses

We analyzed our data in R 3.2.1 (R Core Team 2015). We used bootstrap procedure to estimate mean ± SE for the level of EPP, based on 1,000 bootstrap replicate estimates (Webster et al. 2004). Because some of our song variables were correlated (Table S3), we reduced the number of song variables using principal component analyses (PCA, correlation matrix, unrotated; Crawley 2013) separately for each sex. We retained the first 2 components (PC, hereafter; eigenvalues >1) from each of these 2 PCAs (Table 1). In terms of female song traits, "female singing effort" (PC1f) was positively related to the number of initiated songs and song output, and negatively related to latency to answer partner songs, whereas "female song answering and duration" (PC2f) was positively related to song duration in

TABLE 1. Principal component analysis for male and female song traits of the Rufous Hornero, showing loadings of raw variables onto principal components. Variables that were log-transformed before the analysis are indicated (log-f = female, log-m = male, log = both sexes).

	Female song		Male song	
	Singing effort (PC1f)	Song answering and duration (PC2f)	Singing effort (PC1m)	Song answering and duration (PC2m)
Loadings				
Number of initiated songs (log)	0.56	−0.15	0.58	0.18
Song output (s, log)	0.53	0.39	0.60	
Song answering rate (%, log-f)	0.31	0.57	−0.31	0.42
Latency to answer partner song (s, log-m)	−0.47	0.23	0.28	0.69
Song duration in duets (s)	−0.29	0.68	0.36	−0.56
Eigenvalue	1.38	1.23	1.55	1.10
Variance explained (%)	0.38	0.30	0.48	0.24

TABLE 2. Extra-pair paternity in our study population of the Rufous Hornero. EP = extra-pair.

Year	Percentage of broods with EP nestlings (n = broods)	Broods sampled	Percentage of EP nestlings (n = nestlings)	Nestlings sampled
2013	0% (0)	18	0% (0)	52
2014	14.29% (2)	14	6.06% (2)	33
2015	7.14% (1)	14	5.71% (2)	35
Total	6.52% (3)	46	3.33% (4)	120

duets and song answering rate. In terms of male song traits, "male singing effort" (PC1m) was positively related to the number of initiated songs and song output, whereas "male song answering and duration" (PC2m) was positively related to song answering rate and latency to answer partner song, and negatively related to song duration in duets.

We used univariate, linear models (Gaussian family for continuous data, lm function) to test whether territory size and 2 measures of territory quality, absolute area covered by (1) grasses and (2) trees, varied as a function of song traits. We included the 2 song PCs for each sex, duet rate and duet duration as predictors in these models. We used generalized linear models (glmmTMB function) (Brooks et al. 2017) to analyze the variation in reproductive success (number of surviving offspring, Conway-Maxwell Poisson family for count data with underdispersion) (Weiß 2013) as a function of song traits and territory attributes. We included the 2 song PCs for each sex, duet rate and duet duration, territory size and 2 measures of territory quality (absolute area covered by grasses and trees) in these models. We built one model for each combination of a response variable and a predictor variable for all cases described above, because our predictors were often correlated (Table S4), to prevent overfitting, to reduce the likelihood of overestimate effect sizes arising from model complexity (Harrison et al. 2018), and due to our small sample size. Model assumptions were checked and met (Table S5; Figure S2).

We compared and ranked the non-nested models (Aho et al. 2014) using the corrected Akaike's Information Criterion (ΔAIC_c < 2, Burnham and Anderson 2002).

All continuous variables were scaled before the analyses to obtain comparable beta (β) coefficients from the top model. Beta (β) coefficients were obtained from each predictor variable. We considered effective correlations between predictor and response variable when the confidence intervals (95%) of β coefficients did not cross zero in the best-ranked models (ΔAIC_c < 2). Following the same criteria, when we diagnosed the effect of a PC song in our models, we built a new model for each song or territory trait to verify which variables were better at predicting variation in territory traits or reproductive success (Table 4). We considered that variables not included in the best-ranked models (ΔAIC_c < 2) were irrelevant at predicting variation in the response variable. Results are presented with means ± SD.

RESULTS

Genetic paternity was assigned for 117 (93%) of the offspring sampled (n = 126). Extra-pair paternity was low across the study years, and only 4 (3.92% ± 1.59 SE, n = 120) nestlings from 3 (7.14% ± 3.43 SE, n = 46) broods were not assigned to the social father (Table 2). We were able to assign paternity for one of the 4 extra-pair nestlings, which was sired by a male from a contiguous territory. The remaining 3 extra-pair nestlings had low assignment probability with their social fathers (LOD score < 0, pair loci mismatches > 8) and also did not match well with any other sampled male. The remaining young for whom we could

TABLE 3. Best-ranked models (ΔAIC$_c$ < 2) resulting from linear models to analyze the interrelation among territory attributes, song traits and breeding success in the Rufous Hornero. df = degrees of freedom. w_i = weight. See all models in Table S6.

Modeling scenario	df	ΔAIC$_c$	w_i
(A) Territory size ~ song traits			
null model	2	0.00	0.40
(B) Territory quality (availability of nest sites) ~ song traits			
null model	2	0.00	0.43
(C) Territory quality (availability of foraging patches) ~ song traits			
PC female singing effort	3	0.00	0.58
(D) Number of surviving offspring ~ song traits and territory attributes			
duet duration	3	0.00	0.57

Lowest AIC$_c$ values for each modeling scenario: 38.34 (A), 38.34 (B), 36.10 (C), 30.83 (D).

not assign paternity were all young from broods where the social father had not been sampled for DNA analyses (6 young from 2 broods), probably because the social fathers were the genetic fathers as well.

Female song correlated with territory quality (Table 3). Territory quality in terms of availability of foraging patches (0.52 ± 0.27 ha, range: 0.13–0.97 ha) was correlated with female singing effort (PC1f) (β ± SE = 0.62 ± 0.25) (Figure 2), particularly female song output (β ± SE = 0.65 ± 0.24) (Table 4). Territory size (0.70 ± 0.23 ha, range: 0.37–0.99 ha, n = 12, 95% fixed-kernel) was not correlated with female, male or pair-level song traits (Table 3). Neither female song nor pair-level duet (rate and duration) were related to territory quality in terms of tree cover (a proxy for nest site availability) (0.30 ± 0.16 ha, range: 0.09–0.61 ha) (Table S6). Neither territory size nor quality varied with male song traits. Our results indicate that females that sang for longer bouts (song output) occupied territories that had larger suitable foraging areas (i.e. areas covered with short grasses).

Pair-level duets were associated with reproductive success (Table 3). The mean number of fledglings produced was 1.75 ± 0.96 (range: 0–4, n = 12). Of these, 66% (1.17 ± 0.83, range: 0–2, n = 12) survived to at least 55 days after the first fledgling in the territory had been recorded. The number of surviving offspring was correlated with duet duration (β ± SE = 0.48 ± 0.17, Figure 3), but was unrelated to female song, male song and territory features (Table S6). These results suggest that duets may be associated with reproductive success independent of territory quality in Rufous Horneros.

DISCUSSION

Extra-Pair Paternity
According to the acoustic paternity guarding hypothesis (Hall 2009, Sonnenschein and Reyer 2010), males use duets to deter rivals attracted by their mate's song, preventing them from pursuing EPCs (Gill et al. 2005, Hall 2009). Although males vary in song answering rates in the
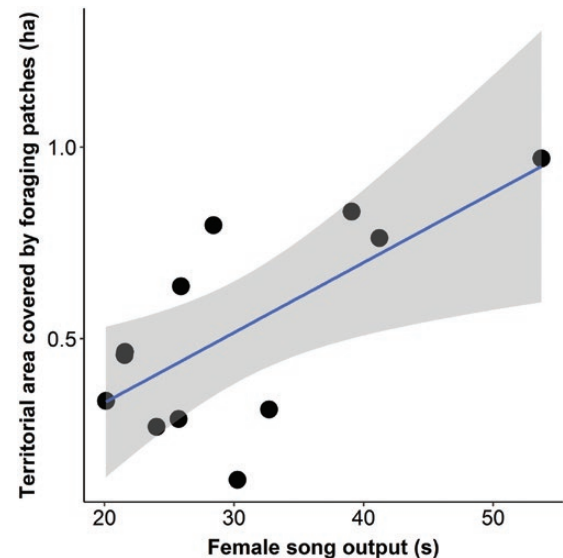
FIGURE 2. Relation between a proxy for foraging patches territory coverage and female song output (total time spent singing per hr) in the Rufous Hornero. The y-axis corresponds to absolute area and proportion of territory size covered by short-grasses and leaf litter. Mean trend (blue line) and confidence interval (shadow) are shown.

Rufous Hornero (Diniz et al. 2018), we found a low rate and variation of EPP. In addition, we found no difference in song answering rates by males during the pre-fertile and fertile periods of their partners (Diniz et al. 2018). These results suggest that the acoustic paternity guarding hypothesis has little or no influence on duetting in the Rufous Hornero. We cannot, however, discard the possibility that low EPP may be due to an efficient paternity guarding strategy (Hall and Peters 2008a). Mate guarding behaviors (including duetting) are more likely to occur in populations with intermediate EPP rates (Kokko and Morrell 2005, Dowling and Webster 2017). In the case of the Rufous Hornero, our paternity results are consistent with the more general pattern that the occurrence of duetting in birds coincides with low rates of EPP (Table S1; Gill et al. 2005, Douglas et al. 2012, Koloff and Mennill

TABLE 4. Models built to evaluate the relation of female song traits with territory area covered by foraging patches. We show coefficients for variables represented by the PC song that was related to territory area covered by foraging patches in the original model. We built one model for each predictor variable. Models followed the same structure as the original models. Coefficients with confidence intervals (95%) that did not cross zero are shown in bold. PC = principal component.

Original modelling scenario (family)	Predictor variable	β ± SE
Territory area covered by foraging patches (grasses) ~ female singing effort (PC1f) (Gaussian)	Number of initiated songs (log)	0.35 ± 0.30
	Song output (log)	**0.65 ± 0.24**
	Song answering rate	0.37 ± 0.29
	Latency to answer partner song (log)	-0.23 ± 0.31
	Song duration in duets	-0.35 ± 0.30
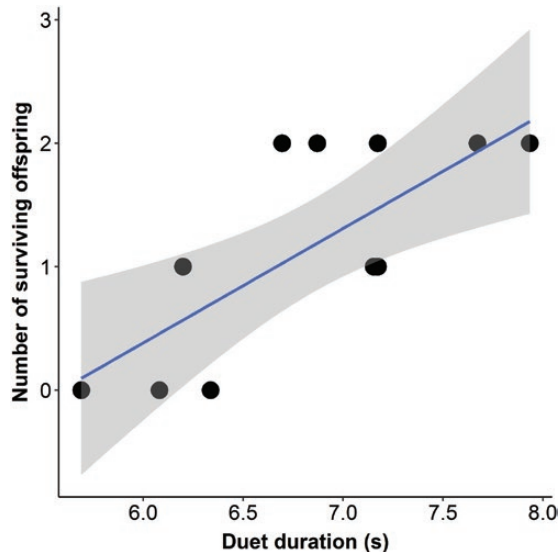
FIGURE 3. Relation between number of surviving offspring during the post-fledging stage and songs traits in the Rufous Hornero. Mean trend (blue lines) and confidence interval (shadows) are shown.

2013; but see Benedict 2008 and van den Heuvel et al. 2014) and is not associated with paternity guarding (Hall and Magrath 2000, Gill et al. 2005, Hall and Peters 2008a, van den Heuvel et al. 2014). We thus suggest that paternity guarding is more likely to apply to a few duetting species with intermediate rates of EPP.

Female Song

As predicted by the territory defense hypothesis (Tobias et al. 2012, Cain et al. 2015, Cain and Langmore 2016), we confirmed that the expression of individual attributes of duetting were positively associated with territory quality. We found that females that sang for longer bouts (i.e. song output) had territories that were richer with respect to amount of foraging substrate. Male song is commonly associated with territory quality across songbird species (Catchpole and Slater 2008). Possibly, our study provides the first evidence of a species where female and not male song is associated with territory quality, reinforcing the role of female song in territory defense (Krieg 2016).

Theoretical and empirical studies suggest females are more constrained by dependence upon ecological resources to breed than by mating opportunities (Bateman 1948, Clutton-brock 2009, Stockley and Bro-Jorgensen 2011, Tobias et al. 2012, Clutton-Brock and Huchard 2013). Thus, female aggressiveness may be important to guarantee access to ecological resources in some systems (Robinson and Kruuk 2007, Cain and Ketterson 2013). If female song signals aggressiveness or competitive ability (Tobias et al. 2011, Cain et al. 2015), either of these variables should predict reproductive success (Cain and Ketterson 2012, Cain et al. 2015, Brunton et al. 2016). Female Rufous Horneros sing at a higher rate in response to conspecific but not to heterospecific song, suggesting that female song is associated with aggressiveness in this species (Diniz 2017). These findings indicate that Rufous Horneros females with strong competitive abilities could acquire high quality territories, possibly by means of a higher song investment (i.e. song effort drives territory quality) (Rosvall 2011, Cain et al. 2015). Alternatively, females may need to sing more to defend high quality territories (i.e. territory quality drives song effort) (Cooney and Cockburn 1995, Cain et al. 2015), or high quality territories provide females with resources (time and/or energy) to invest more in singing (Strain and Mumme 1988). Future studies could address these 3 possibilities.

Male Song

It is unclear why male song was unrelated to territory quality and reproductive success. Male fitness is apparently not enhanced by extra-pair mating success (given the low rate of EPP), and males sing at higher rates and engage in more territory interactions than do females (Diniz et al. 2018). In addition, males duet with females to defend common territories (Diniz et al. 2018). Confounding factors not accounted for here include male size (Ballentine 2009), age (Poesel et al. 2006) or experience (Hyman et al. 2004), and male quality (Christie et al. 2004). These factors may possibly explain the lack of association between male song with territory features and reproductive success.

Duetting

We found that female song output correlates with territory quality in terms of territorial area covered by foraging patches. Considering that males answered most of their partner's songs in this species (Diniz et al. 2018), our results suggest that duets initiated by females predict territory quality. To our knowledge, this is the first evidence of an association between duetting behavior, or individual songs emitted in duets, and territory quality. Theory and empirical research suggest that duets function in joint territory defense (Seibt and Wickler 1977, Hall 2004, 2009; Dahlin and Benedict 2013, Koloff and Mennill 2013), and we further suggest that duets may more broadly be associated with territory quality.

Duet duration was positively associated with the number of surviving offspring produced by breeding partners (Table 3). A previous playback study of the Rufous Hornero revealed that partners tend to sing longer duets in response to conspecific (male solos and duets) song playbacks than they do in response to heterospecific song playbacks (Diniz 2017). Although this tendency was not statistically significant, when considered in light of the results of the current study, our findings confirm that in Rufous Horneros, duets function in territory defense and suggest that the performance of duets and/or aggressiveness has important fitness consequences.

Despite decades of research on duetting behavior (reviews in Hall 2004, 2009, Dahlin and Benedict 2013), this is perhaps the first documentation that duetting is associated with similar values of reproductive success for singers. In addition, our results suggest that a pair-level property of duetting (Logue and Krupp 2016), and not only individual female or male contributions, is associated with reproductive success. However, we failed to find a correlation between territory quality and fitness, suggesting that a factor other than territory features, such as the coalition quality of breeding partners competing for territories (Hall and Magrath 2007), could mediate the association between duet and reproductive success. Future studies could evaluate this possibility.

Territory Quality and Reproductive Success

We failed to find a correlation between territory quality/size and fitness. One possible explanation for this pattern is that song and/or territory may affect fitness in ways we did not consider in this study. For example, song or territory quality might affect offspring quality (Weiss et al. 2009), juvenile development (Komdeur 1992), natal dispersal success (Reid et al. 2005), length of territory tenure (Hiebert et al. 1989), or adult survival (Wilson et al. 2000). Alternatively, song expression (or aggression-mediated signal expression) might trade-off with parental care (Duckworth 2006, McGlothlin et al. 2007, Stiver and Alonzo 2009, Cain and Ketterson 2013), or high singing (or display) effort may lead to high

nest predation (Kleindorfer et al. 2016). This latter explanation seems unlikely for our system, as we found no nest predation across our study groups (Dias et al. 2010, Kleindorfer et al. 2016).

Pair members are highly coordinated in the Rufous Hornero (Massoni et al. 2012). It is possible that duet traits, such as longer duets, are produced by more coordinated pair members (Hall and Magrath 2007), and behavioral coordination can directly affect offspring fitness (Mariette and Griffith 2015). Finally, we did not use a direct measurement of food availability (e.g., ground-arthropod biomass; Maceda-Veiga et al. 2016), which may have masked a relationship between territory quality and reproductive success (Conner et al. 1986). Thus, the fitness consequences of song and territory quality remain unclear for the Rufous Hornero.

Conclusion

We found a low rate of EPP for the Rufous Hornero, a member of the species-rich Furnariidae family (~300 species, Derryberry et al. 2011). These results are among the first to determine EPP rates for a duetting species in the Suboscine clade (i.e. birds with small vocal repertoire and low plasticity in song learning and structure; Kroodsma and Konishi 1991, Liu et al. 2013, Touchton et al. 2014).

The function and benefits of duetting, female song and male song in species where both sexes sing are controversial and still not well understood (Langmore 1998, Hall 2004, 2009, Logue and Krupp 2016, Tobias et al. 2016). Our study supports the territory defense hypothesis and also demonstrates that song traits in duets are associated with both territory features and reproductive success. However, we recommend future replication of this study with a larger sample size to confirm these results. We argue that territory quality is an important pressure shaping the expression of female song and duets in socially monogamous bird species where both sexes sing, and that duetting may have similar fitness consequences for both breeding partners, contributing to the cooperative nature of this behavior.

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