

Monochromatism, cryptic sexual dimorphism and lack of assortative mating in the Rufous Hornero, *Furnarius rufus albogularis*

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Abstract. Neotropical ovenbirds (family Furnariidae) are largely sexually monomorphic and monochromatic, which leads to the assumption that sexual selection has had little effect on the evolution of the morphological and plumage traits of the species in the family. We studied a wild population of the Rufous Hornero (*Furnarius rufus albogularis*) and used morphological measurements, molecular sexing, spectrometer analyses and visual modelling to investigate the assumption of sexual monomorphism and monochromatism in this species. We also tested for assortative mating with respect to these traits. On average, males had slightly longer wings and tails than females but there were no sexual differences in other morphological traits (mass, tarsus and bill) or in the spectral properties of plumage coloration for six body parts. Visual modelling indicated that Rufous Horneros can perceive variation in colour between individuals but colour does not vary with sex. We did not find any evidence of assortative mating for size or colour traits. In conclusion, males from the studied population differ slightly from females in external morphological measurements but not in plumage coloration. This study is among the first to demonstrate complete sexual monochromatism in birds assessed against the avian visual system.

Additional keywords: Furnariidae, neotropical birds, plumage colour, visual modelling.

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Introduction

Sexual selection is the main driver of the evolution of sexual dimorphism and dichromatism in birds (reviews by Owens and Hartley 1998; Dunn *et al.* 2001; Székely *et al.* 2007). Many species, however, show little or no differences in external morphology, including coloration, between the sexes, suggesting low levels of variation in mating success and limited opportunity for sexual selection. This may be the case in the Rufous Hornero (*Furnarius rufus*), a common Neotropical ground-foraging species of ovenbird (family Furnariidae: ovenbirds and woodcreepers) inhabiting rural and urban areas in central and southern South America (Marreis and Sander 2006). Both male and female Rufous Horneros have cryptic reddish-brown plumage coloration (Sick 2001). Rufous Horneros are socially monogamous, territorial (Burger 1979; Sick 2001) with high adult survival rates (Fraga 1980) and parental care of offspring is shared equally (Braga 2012; Massoni *et al.* 2012). It would thus appear that the conditions for sexual selection to generate sexual dimorphism in the Rufous Hornero are lacking.

The species comprising the Furnariidae are widely described as predominantly sexually monomorphic and monochromatic (Skutch 1996; Sick 2001; Remsen 2003). However, this assumption is based mostly on field observations and human

perception of colour rather than detailed objective analyses. Sexual monomorphism has been investigated in only a small number of Furnariidae species and those studies have found subtle sexual dimorphism, with males slightly larger than females (Winker *et al.* 1994; Faria *et al.* 2007; Moreno *et al.* 2007; Cardoni *et al.* 2009; Puebla-Olivares and Figueroa-Esquivel 2009).

It has been argued that cryptic sexual dichromatism in the ultraviolet (UV) range – a type of dichromatism perceived as monochromatism by human vision – is somewhat unlikely in ovenbirds (Seddon *et al.* 2010). This is because antbirds (family Thamnophilidae), and probably other tracheophone suboscines (family Furnariidae: woodcreepers, ovenbirds and allies), have a visual system sensitive only to violet within the visible spectrum (and not UV) and low levels of UV reflectance in their plumages (Seddon *et al.* 2010; Tobias *et al.* 2012). However, even among violet-sensitive bird species that are apparently monochromatic there are considerable sexual differences in colour evident to the avian eye (Eaton 2005). To date, sexual dichromatism has been objectively studied in only two furnariids, which showed contrasting patterns: sexual monochromatism in the Thorn-tailed Rayadito (*Aphrastura spinicauda*; Moreno *et al.* 2007) and

dichromatism in the Puna Miner (*Geositta punensis*; Eaton 2005).

Assortative mating is the correlation of any phenotypic trait across members of mated pairs, and can evolve through selection on mating preferences or as a consequence of ecological or physiological constraints (reviewed by Jiang *et al.* 2013). Assortative mating in birds has been investigated in mutually ornamented species (e.g. Regosin and Pruett-Jones 2001; Boland *et al.* 2004) and rarely been assessed in birds without obvious ornamental traits (Delestrade 2001), such as the Rufous Hornero. Investigation of assortative mating for colour and size in non-ornamented bird species may contribute to our understanding on the evolution of cryptic sexual dimorphism and dichromatism in birds.

Generating descriptive information about sexual dimorphism in poorly studied avian taxa, such as the Furnariidae, is crucial to substantiating comparative and behavioural research about the evolutionary causes and consequences of sexual dimorphism in birds (e.g. Owens and Hartley 1998; Dunn *et al.* 2001; Székely *et al.* 2007). We used morphometric measurements, molecular sexing, spectrophotometer analyses, and visual modelling to test for sexual dimorphism and dichromatism in a wild population of Rufous Hornero from central Brazil. In addition, we tested for assortative mating by size and plumage colour.

Methods

Field work and molecular sexing

We studied an urban and wild population of Rufous Hornero on the campus of the Universidade de Brasília, Brazil (15°45'S, 47°51'W). We captured 61 incubating birds (31 males and 30 females) in September and October 2013, using a funnel fish-trap placed over the entrance to the Rufous Hornero's domed nest as described by Braga *et al.* (2014). We captured both members of 23 breeding pairs and one parent of 15 pairs.

We banded individuals with unique combinations of unnumbered coloured plastic (Avinet, Dryden, New York, NY) or, occasionally, metal (Anilhas Capri, São Paulo, Brazil) leg-bands. On capture, we collected ~60 µL of blood using brachial venipuncture, and blood samples were transferred to filter paper for later determination of sex. We also recorded mass (using a dynamometer; Pesola AG, model Light Line 10050, Baar, Switzerland; accuracy 0.5 g) and maximum unflattened wing-chord, tarsal-length (from inter-tarsal joint to the base of the toes), tail-length (with one exception; from the uropygial gland to the tip of the longest feather), bill-length (from anterior edge of nostril to tip), and depth and width of bill at junction with skull (all with 150-mm digital callipers, Stainless Hardened, China; 0.01 mm graduations). All measurements were taken by one person (P. Diniz). We also collected 3–4 feathers from each of the following body regions: breast, throat, crown, back, rump and undertail-coverts. We wrapped feathers in aluminum foil and stored them at room temperature and dry conditions. Sex was determined for 55 individuals (27 females, 28 males) using molecular methods (Griffiths *et al.* 1998) by a commercial laboratory (Grupo São Camilo – Medicina Diagnóstica, Maringá, Paraná, Brazil); the sex of the remaining six individuals (3 females, 3 males) was based on the sex of their partners as determined by molecular methods.

Measurements of plumage coloration

We used an Ocean Optics USB4000 spectrometer and PX-2 pulsed xenon light-source (Ocean Optics, Dunedin, FL, USA) to assess the spectral characteristics of Rufous Hornero feathers. The PX-2 light-source provides illumination in the visible spectrum for birds (300–700 nm). We positioned the feathers in an overlapping pattern on a non-reflective, black velvet substrate. We placed the optical probe perpendicularly above the feathers (at an angle of 90°) and measured reflectance spectra three times – removing the probe and replacing it upon the feathers between recordings – with the spectrometer and SpectraSuite software (Ocean Optics, Dunedin, FL). We followed the SpectraSuite manual instructions to choose the configuration parameters (integration time = 40 µec, scans to average = 50, boxcar width = 30). These measurements of reflectance spectra (percentages) were obtained relative to a white standard (WS-1-SS) and a dark reference (i.e. the black velvet substrate). We used the combined average spectra for each body region of each individual to prevent pseudoreplication in the analyses described below.

We analysed sexual differences in the colour of Rufous Hornero plumage with visual modelling, which incorporates avian visual sensitivities (cone absorbance; Vorobyev and Osorio 1998; Vorobyev *et al.* 1998). All analyses were performed in the *pavo* package within R version 3.2.3 (R Development Core Team 2015), following the systematic procedure suggested by Maia *et al.* (2013). Furnariids are likely to have a violet-sensitive visual system as other suboscines (Seddon *et al.* 2010) but this has not been studied in any species in the family. We therefore applied visual modelling to consider both the average avian ultraviolet (UVS) and the average violet-sensitive (VS) visual systems. We set the models assuming homogeneous illuminance across wavelengths and absolute quantum catches, which is ideal to contrast colours through ΔS (Vorobyev and Osorio 1998; Maia *et al.* 2013).

We used the visual models to measure the intrasexual and intersexual Euclidean chromatic distances (ΔS) (Vorobyev and Osorio 1998), assuming a noise level of 0.1 (Weber fraction) for the long-wavelength sensitive photoreceptor (Vorobyev and Osorio 1998; Olsson *et al.* 2015) and relative cone proportions for the Blue Tit (*Cyanistes caeruleus*; wavelengths: UV or V = 1, short = 2, medium = 2, long = 4). ΔS is expressed in just noticeable differences (JNDs) and indicates how two spectra are perceived as different, considering the visual space of the receiver; values >1 are considered discernible by birds (Vorobyev *et al.* 1998; Endler and Mielke 2005). We made 1830 comparisons of chromatic distances for each body region within each visual system (UVS or VS): 435 intra-female comparisons, 465 intra-male comparisons and 930 intersexual comparisons (31 males and 30 females).

We also extracted three colour variables from each spectrum to investigate sexual differences in colorimetric reflectance: mean brightness (mean relative reflectance over all wavelengths), contrast (difference between maximum and minimum reflectances), and red chroma (reflectance of the red spectral range, 605–700 nm, relative to the total brightness) (Montgomery 2006; Maia *et al.* 2013). We did not use UV chroma (reflectance of the UV spectral range, 300–400 nm, relative to the total brightness) in subsequent analyses, because preliminary analyses showed low UV chroma in feathers of all body regions (<5% for all

except throat (12%) and no sexual differences in this variable (results not shown).

Statistical analysis

All analyses were carried out using R version 3.2.3 (R Development Core Team 2015). We tested for sexual dichromatism with linear mixed modelling and univariate statistics. First, we modelled variation in ΔS (log-transformed) between individuals as a function of the type of comparison (intra-female, intra-male or intersexual) interacting with body region. We included the identities of the two individuals being compared, the identity of the comparison (i.e. the combination of the two individuals being compared) and the paired status of the individuals being compared (i.e. whether or not they belonged to the same breeding pair) as random effects in the model. We tested the existence of the interaction and main effects with analysis of deviance (Wald χ^2 test). We carried out *post hoc* comparisons of least-squared means among factor levels. If the Rufous Hornero is sexually dimorphic, we would expect ΔS to be greater between sexes than within sexes and, on average, ΔS to be >1 for intersexual comparisons. Since the comparison of intrasexual and intersexual ΔS has never been conducted for this species, we also modelled the four receptor quantum catches (UV or V, short, medium and long wavelength) as a function of sex interacting with body region (similar to Eaton 2005) in a mixed model (with individual identity as a random factor). We found the same qualitative results as in the previous analyses (i.e. monochromatism; results not presented here). We also used linear mixed modelling to analyse sexual differences in each colorimetric variable (e.g. red chroma). We included sex, body region and their interaction as predictor factors, and individual identity as a random effect. Model inference followed the same protocol previously described.

We tested for sexual dimorphism with multivariate and univariate statistics. We excluded body mass of one female before all analyses because she was thought to be gravid (>60 g; Roper 2005). We used multivariate Hotelling's *T*-squared test to investigate sexual dimorphism, comparing matrices of size measurements. We identified and removed multivariate outliers (two female size data points) before the analyses using Mahalanobis distances.

We used *t*-tests with Welch approximation for degrees of freedom to compare colour and size variables between sexes. We identified and sequentially removed univariate outliers before the analyses using Grubbs' test (Grubbs 1950). To express the magnitude of morphological and plumage colour differences between the sexes, we computed the effect size (i.e. magnitude) of mean differences between sexes for each size variable using Cohen's *d* values and respective confidence intervals (see Nakagawa and Cuthill 2007). For example, Cohen's *d* values of 0.2 and 0.8 are considered small and large difference, respectively (reviewed by Nakagawa and Cuthill 2007).

We used a discriminant function analysis based on the maximum likelihood estimation method of classification to investigate the accuracy of size measurements to predict sex in the Rufous Hornero. In the discriminant analysis we did not include plumage colour variables because sexes did not differ in colour (see below) or wing-chord, because it was highly correlated with

tail-length ($r > 0.5$). Outliers (two female body size data points) were identified and removed before analyses.

Finally, to test for assortative mating in relation to size or coloration, we conducted correlation Mantel and Pearson tests of these traits between paired individuals. In the Mantel test, we used correlation of dissimilarity matrices (Euclidean distance) of multiple sexual traits, separately, for colour and size measurements (999 permutations for each one). We controlled for false discovery rates in multiple comparisons (see Benjamini and Hochberg 1995).

Results

We found no differences in plumage coloration between sexes of Rufous Hornero. Although we found high inter-individual perceived chromatic distance (mean $\Delta S \pm$ s.e.: UVS, 11.69 ± 0.14 ; VS, 5.44 ± 0.07), intersexual ΔS was not greater than intrasexual ΔS (Wald χ^2 test: UVS $\chi^2 = 0.32$, $P = 0.85$; VS $\chi^2 = 0.32$, $P = 0.85$), and this result was consistent for all body regions from which feathers were collected and analysed. We found an effect of the interaction between body region and type of comparison (i.e. intrasexual or intersexual) on ΔS (Wald χ^2 test: UVS $\chi^2 = 37.06$, $P < 0.0001$; VS $\chi^2 = 47.85$, $P < 0.0001$). This interaction was a result of a tendency of smaller intra-female ΔS compared with intersexual ΔS for undertail-coverts, but there was no difference between intersexual ΔS and intra-male ΔS for these same feathers (Fig. 1; Table S1 in supplementary material available online), as would be expected in sexual dichromatism. Moreover, we found no difference between sexes in the measurements of colourimetric reflectance (Wald χ^2 test: $\chi^2 < 0.67$, $P > 0.41$), regardless of the body region from which feathers came (Wald χ^2 test: $\chi^2 < 6.57$, $P > 0.26$), though females tended to have brighter breast feathers than males (Fig. 2; Table S2).

In contrast, male Rufous Horneros differed from females in external measurements (Hotelling's *T*-squared test = 9.24, $P < 0.0001$). Male Rufous Horneros had, on average, slightly longer ($\sim 4\%$) wings and tails than females, although sexes overlapped in measurements (Fig. 3), and males tended to have longer (1%) tarsi than females, and to be lighter (2%) than females. There were no differences between sexes in bill-depth, bill-length and bill-width (Table 1).

The discriminant function analysis had an 86% probability of correctly classifying sex, correctly allocating 22 of 26 females and 27 of 31 males (Fig. S1). The analysis generated the following discriminant function of unstandardised measurements:

$$D = (-0.28 \times \text{mass}) + (0.41 \times \text{tail-length}) \\ + (0.20 \times \text{tarsal-length}) + (2.42 \times \text{bill-depth}) \\ - (1.01 \times \text{bill-width}) - (0.91 \times \text{bill-length}) + 13.31$$

A positive *D* indicates an individual is male, and a negative *D*, female. The largest absolute loadings (i.e. contribution to the predicted sex) of standardised measurements were given by tail-length (1.14) and mass (-0.67), followed by bill-length (-0.70), bill-depth (0.54), bill-width (-0.30), and tarsal-length (0.19). Thus, for example, the longer the tail, the higher the chance of an individual being predicted as male by discriminant analysis.

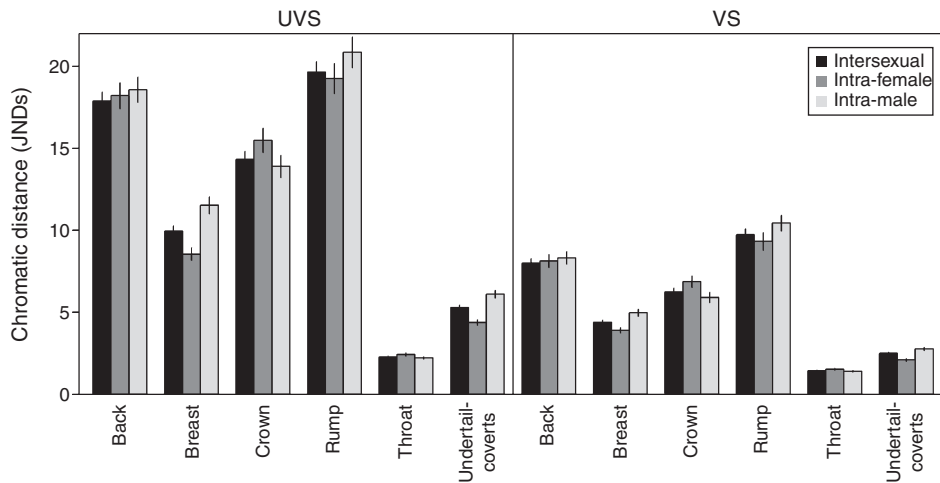


Fig. 1. Mean chromatic distances (\pm s.e.) within and between sexes of the Rufous Hornero. JNDs, just noticeable differences; UVS, ultraviolet-sensitive; VS, violet-sensitive.

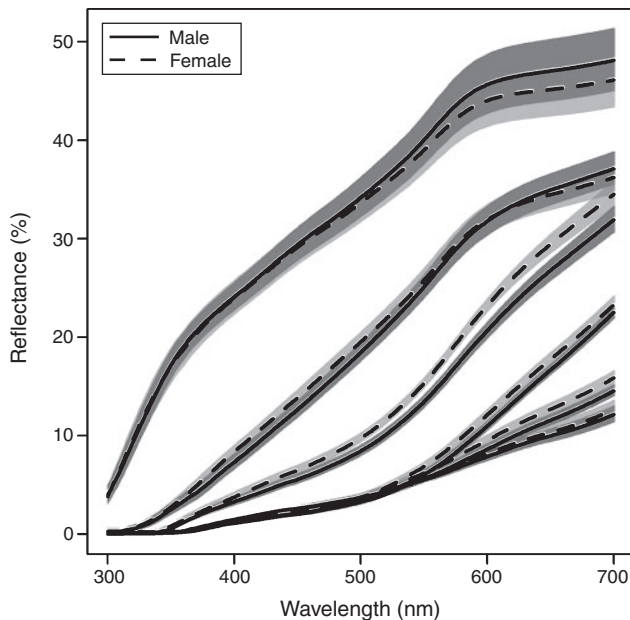


Fig. 2. Mean reflectance (\pm s.e.) of the reddish-brown feathers from six body regions of male ($n=31$, dark shade) and female ($n=30$, light shade) Rufous Horneros.

We found no correlation between paired individuals in colour (Mantel test, $P > 0.13$) or size (Mantel test, $r=0.01$, $P=0.40$, $n=23$ breeding pairs; see Tables S3 and S4).

Discussion

Our results show that our population of Rufous Hornero males from central Brazil have slightly longer tails and wings (~4%) and tend to have longer tarsi than females, and that females tend to be marginally heavier than males. Despite the slight differences in size between sexes and the overlap in size between sexes, the discriminant analysis correctly classified most of the studied birds (86%). We found no differences in

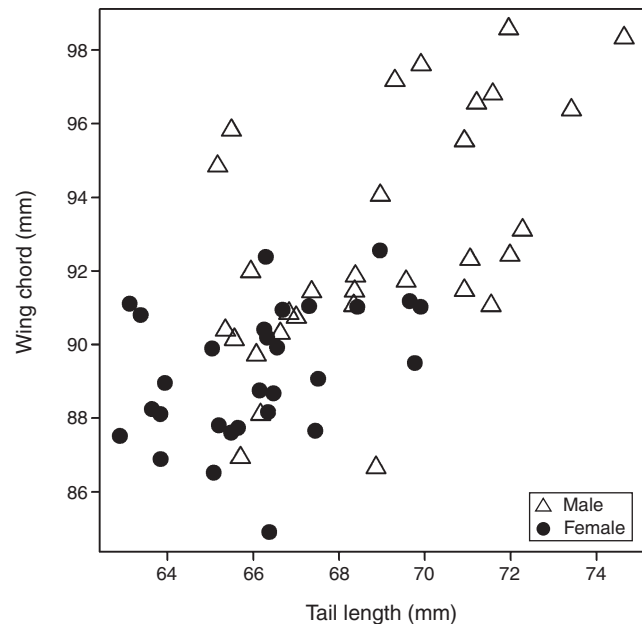


Fig. 3. Covariation between lengths of wing and tail of male ($n=31$) and female ($n=29$) Rufous Horneros.

sex for other measurements of size, a pattern of sexual dimorphism also described for the Henna-capped Foliage-gleaner (*Hylocryptus rectirostris*; Faria *et al.* 2007) and similar to the pattern found in other ovenbirds, where males are slightly larger than females (Moreno *et al.* 2007; Cardoni *et al.* 2009; Puebla-Olivares and Figueroa-Esquivel 2009). Montalti *et al.* (2004) found no differences between sexes in length of wing or tail in the Rufous Hornero, but the mean values for both traits for males that they presented were outside the range of their measurements, indicating some error in their analysis. Because of the subtle nature of sexual dimorphism in ovenbirds, we suggest that future studies of horneros (*Furnarius* spp.) use highly precise measurements (e.g. reducing measuring bias)

Table 1. Sexual differences in external morphology of adult Rufous Horneros

Cohen's d expresses the effect size (\pm 95% confidence interval (CI)) of mean differences in morphological attributes between the sexes (Nakagawa and Cuthill 2007). The t -test: all birds is testing means for all males vs all females; the paired t -test is testing means for males vs females of a mated pair; the degrees of freedom (d.f.) for all birds is computed assuming the Welch approximation. Values of P in bold indicate significant results ($P < 0.05$) after controlling for false discovery rates (Benjamini and Hochberg 1995)

Measurement	Mean \pm s.e.		Cohen's d (CI)	t -test: all birds		Paired t -test ($n = 23$ breeding pairs, d.f. = 22)	
	Males ($n = 31$)	Females ($n = 30$)		t (d.f.)	P	t	P
Bill-depth (mm)	5.69 \pm 0.04	5.64 \pm 0.04	0.23 (−0.29, 0.75)	0.90 (57.73)	0.37	1.45	0.16
Bill-length (mm)	15.64 \pm 0.11	15.70 \pm 0.17 ^A	−0.08 (−0.60, 0.45)	−0.30 (48.62)	0.77	−1.26	0.22
Bill-width (mm)	5.78 \pm 0.04	5.84 \pm 0.07	−0.24 (−0.76, 0.28)	−0.92 (46.64)	0.36	−0.73	0.47
Mass (g)	52.34 \pm 0.40	53.57 \pm 0.44 ^A	−0.53 (−1.07, 0.0008)	−2.07 (57.10)	0.043	−1.16	0.26
Tail-length (mm)	68.92 \pm 0.48	66.12 \pm 0.37 ^B	1.18 (0.60, 1.75)	4.60 (55.16)	<0.0001	3.78	0.001
Tarsal-length (mm)	32.92 \pm 0.18	32.45 \pm 0.15	0.51 (−0.02, 1.04)	2.01 (58.13)	0.049	1.50	0.15
Wing-length (mm)	92.75 \pm 0.58	89.36 \pm 0.34	1.28 (0.70, 1.85)	5.02 (48.27)	<0.0001	6.23	<0.0001

^A $N = 29$, with single outlier removed.

^B $N = 29$, with data missing for one female.

and include measurements of additional morphological traits to increase the accuracy of sex-determination by morphology.

Sexual size-dimorphism in birds may have arisen from differences between sexes in mating competition, display agility and resource division, or female fecundity (Székely *et al.* 2007). Sexual dimorphism in the flight feathers of our studied Rufous Hornero population may have resulted from differences between sexes in territorial competition (Owens and Hartley 1998), in which the reproductive value of a territory is typically higher for males than for females. Alternatively, Rufous Horneros may not be able to recognise sexes based on this small difference in size between sexes, which in turn may have evolved as a by-product of fertility selection for smaller females (Székely *et al.* 2007). Other hypotheses could include sex-specific feather abrasion (Merilä and Hemborg 2000), for example as a result of the long incubation bouts of female Rufous Horneros at night (Fraga 1980), or age-specific differences in length of feathers (Francis and Wood 1989) coupled with sex-specific adult mortality. We found no assortative mating for size, suggesting that mutual mate-choice is unlikely to drive the evolution of these traits. Future studies could address these functional explanations for the evolution of sexual dimorphism in this Rufous Hornero population and test if these birds can distinguish sexes by size.

Our results suggest the Rufous Hornero is sexually monochromatic. We found high chromatic distances (ΔS) between individuals. However, ΔS was not greater between sexes than within sexes. Since ΔS measures how birds can discriminate colours, in relation to the avian visual colour space (Endler and Mielke 2005), these results suggest that Rufous Horneros can use colour to discriminate between individuals but not between sexes. In addition, we found no differences in plumage reflectance between the sexes of the Rufous Hornero, except a tendency of females to have brighter breast feathers. Finally, we did not find any evidence of assortative mating based on plumage colour. These results suggest that, for this species, sexual selection is unlikely to have been important in the evolution of plumage colour, and that natural selection may have influenced the evolution of this trait in a similar way for both sexes.

Previous studies have suggested that selection for female crypsis may drive the evolution of sexual dichromatism (Burns 1998), with nest predation being among the mechanisms favouring female crypsis (Martin and Badyaev 1996; Götmark *et al.* 1997). However, rates of nest predation appear to be low in the Rufous Hornero (25%, Massoni *et al.* 2012), and another study suggests weaker selection on plumage crypsis in species with concealed nests (i.e. hanging baskets or domed nests, such as the Rufous Hornero) compared with open-nesting birds (Drury and Burroughs 2015). The Rufous Hornero forages on the ground and both sexes have very similar foraging and parental care behaviours (Fraga 1980), suggesting males and females are under similar predation risk. Thus, we suggest that adult predation rather than nest predation may be favouring the evolution of crypsis in both sexes of the Rufous Hornero.

Our study is among the first to demonstrate complete sexual monochromatism in birds in relation to the avian visual system (see also Eaton 2005; Burns and Shultz 2012; Doutrelant *et al.* 2013). Sexual monochromatism is likely to evolve in birds that exhibit negligible UV-reflection (Seddon *et al.* 2010), and such seems to be the case for furnariids. On the other hand, cryptic sexual dichromatism could be more likely in UV-reflecting taxa, like tanagers and cardinals (Burns and Shultz 2012).

It has been suggested that individual recognition of conspecifics may be rare among species of ovenbirds because of their apparent monomorphism and monochromatism (Skutch 1996). However, our study suggests that individual identity may be assessed by plumage colour, with such recognition possibly selected in socially monogamous species with high pair-fidelity and permanent territoriality (Fraga 1980), like the Rufous Hornero. Rufous Horneros also appear to be able to recognise conspecific individuals acoustically, and their song duets are characterised by sex-specific elements (Roper 2005). In summary, male Rufous Horneros in the studied population are slightly larger than females but the sexes do not differ in plumage coloration. Cryptic sexual dimorphism and sexual monochromatism are probably widespread in ovenbirds (furnariids), and more studies on sexual differences in colour and size in other species of Furnariidae are desirable to shed light on this hypothesis.

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