

## 1 **Defending as a unit: sex- and context-specific territorial defence in a duetting bird**

2 Lucia Mentesana<sup>1†</sup>, Maria Moiron<sup>1,2†</sup>, Ernesto Guedes<sup>3</sup>, Enzo Cavalli<sup>3</sup>, Bettina Tassinio<sup>3</sup>,

3 Nicolas M. Adreani<sup>1,4\*†</sup>

4

5 <sup>1</sup> Max Planck Institute for Ornithology, Seewiesen, Germany.

6 <sup>2</sup> Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175 Campus CNRS, Montpellier,  
7 France.

8 <sup>3</sup> Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

9 <sup>4</sup> Konrad Lorenz Research Center, University of Vienna, Grünau im Almtal, 4643, Austria

10 \* Author for correspondence: [nicolas.adreani@univie.ac.at](mailto:nicolas.adreani@univie.ac.at)

11 † Contributed equally to the manuscript

12

### 13 **Abstract**

14 Behaviours such as territorial defence represent functionally integrated traits that underlie  
15 multiple behavioural variables such as physical and acoustic responses. Characterizing the  
16 multivariate structure of such traits is fundamental to understand their evolution. In bird species  
17 that form stable pair bonds and are territorial year-round, both sexes are expected to defend  
18 their territory; however, the role that each sex plays in defending their shared territory remains  
19 largely unknown. Evidence for the sex-roles during territorial defence is mixed and sex- and  
20 context-specific characterizations of territorial defence embracing the multivariate nature of the  
21 trait are currently lacking. Here we investigated sex- and context-specific variation in a  
22 hypothesised latent variable called “territorial defence” and tested whether duets were part of  
23 territorial defence in a wild population of rufous hornero (*Furnarius rufus*). To do so, we  
24 combined a simulated territorial intrusion approach during nest building and provisioning  
25 contexts with a structural equation modelling approach. Our results showed that, in males and  
26 females, the six measured behavioural variables were linked by a single latent trait, territorial  
27 defence, in both contexts. Flights over the decoy and duet songs were equally good proxies of  
28 territorial defence. Although males were defending more the territory than females, pair  
29 members showed a positive correlation in their behaviour. The structural equation modelling  
30 framework enabled us to capture a complex correlation pattern among behavioural variables,  
31 expanding upon a classic body of research on territorial defence. Thus, the combination of  
32 classical behavioural approaches with sophisticated statistical analyses brings new exciting  
33 possibilities to the field of behavioural ecology.

34 **Keywords:** territorial aggression, duets, behavioural character, phenotypic integration, female  
35 aggression, structural equation analysis

36 **Significance statement**

37 Territorial defence is a key behaviour in territorial species as it plays a major role in an  
38 individual's reproductive success and survival. Additionally, territorial defence has been  
39 proposed as one possible evolutionary driver of duetting behaviour, one of the most fascinating  
40 vocal behaviours in birds. As behaviours are evolutionary characters, they must be studied in a  
41 multivariate framework. In this study we focused on characterizing territorial defence during a  
42 simulated territorial intrusion in an integrative manner using a classical territorial intrusion  
43 framework. We did so in male and female rufous horneros (*Aves: Furnaridae*) across two  
44 breeding contexts, while simultaneously testing theoretical predictions about the role of  
45 duetting behaviour as key part of territorial defence. Overall, our study provides for the first  
46 time a sex- and context-comparison of the multivariate, latent variable "territorial defence" in  
47 duetting birds, while highlighting the potential of combining field behavioural approaches with  
48 structural equation modelling.

49

## 50 Introduction

51 Behaviours, such as territorial defence, are typically studied by simultaneously measuring  
52 different observable variables (e.g. “number of attacks”, “latency of response”, “proximity”  
53 measures, and/or “vocal responses”; Wingfield 1994; Bollen 2002). Extensive empirical  
54 research over the last decades has focused on analyzing male and, to a lesser extent, female  
55 territorial defence behaviour using different approaches. Evidence generally shows that  
56 multiple components of an animal's defence response in a territory intrusion are intercorrelated  
57 (e.g. Huntingford 1976; Sprenger et al. 2012). When these multiple behaviours are functionally  
58 related, they might be considered expressions of a single evolutionary character (Araya-Ajoy  
59 and Dingemanse 2013). Their study should therefore not be addressed by means of bivariate  
60 correlations but integrate the multivariate nature of the behaviour by quantifying unobserved,  
61 biologically-relevant latent variables (Houle et al. 2011; Carter and Feeney 2012; Araya-Ajoy  
62 and Dingemanse 2013). One way to characterize “territorial defence” as an evolutionary  
63 character while also quantifying which of the observed behavioural variables should be  
64 considered expressions of it, is to apply a Structural Equation Modelling approach (SEM; e.g.  
65 Card and Little 2007). This statistical framework allows to explore complex correlation patterns  
66 among multiple behavioural variables, and to test *a priori* defined hypotheses of how multiple  
67 observed behavioural variables are linked by the unmeasured latent variable (Araya-Ajoy and  
68 Dingemanse 2013).

69 Territorial defence behaviour has been widely studied in diverse organisms from insects  
70 to several groups of vertebrates (reviewed in Smith and Blumstein 2008), likely because of its  
71 impact on fitness (Stamps and Krishnan 1997; Smith and Blumstein 2008). During territory  
72 defence, aggressive interactions can be beneficial for both males and females because an  
73 intrusion of a conspecific into the breeding territory might, for example, lead to loss of limited  
74 resources (Stamps and Krishnan 1997; Garcia and Arroyo 2002). Nevertheless, the sex-specific  
75 contribution to territory defence differs among species according to variation in mating systems  
76 and parental care (Emlen and Oring 1977; Clutton-Brock and Vincent 1991; Owens and  
77 Thompson 1994). In birds, among those species that form stable pair bonds and are territorial  
78 year round, it is expected that males and females equally contribute to territory defence  
79 (Greenberg and Gradwohl 1983). In line with this prediction, in dot-winged antwrens  
80 (*Microrhopia quixensis*) and in the purple-crowned and red-backed fairy-wrens (*Malurus*  
81 *coronatus*, *Malurus melanocephalus*) both sexes contribute to the same extent to defend their  
82 territory (Greenberg and Gradwohl 1983; Hall and Peters 2008; Dowling and Webster 2016).  
83 However, these findings were not observed in other antbird species (*Phaenostictus mcleannani*,

84 Willis 1972; *Cercomacra tyrannina*; Morton and Derrickson 1996; *Hylophylax naevioides*;  
85 Bard et al. 2002; *Myrmeciza longipes*; Fedy and Stutchbury 2005), in the zenaïda dove (*Zenaida*  
86 *aurita*; Quinard and Cézilly 2012) and in the rufous hornero (*Furnarius rufus*; Diniz et al.  
87 2018), where males engaged more in defensive interactions than females. In addition, whilst  
88 intensity of territorial defence can be positively correlated within pairs in some species  
89 (especially on those that duet e.g. Logue 2005; Hall and Peters 2008), in others the opposite  
90 relationship is true (e.g. zenaïda dove; Quinard and Cézilly 2012). Therefore, the generality of  
91 sex-specific territorial defence as well as its intensity from both members of a pair remains  
92 poorly understood in species that are socially monogamous and territorial year-round.  
93 Furthermore, it also remains largely unknown whether the same observed behavioural variables  
94 characterize the latent variable territorial defence in males and females and across different  
95 breeding contexts. For instance, it is still an open question whether territorial defence is equally  
96 characterized by physical and vocal behaviours in both sexes and across contexts. Studies  
97 describing territorial defence as a latent variable using SEM and explaining broader patterns of  
98 territorial defence across sexes or contexts, will help to shed light on these questions and further  
99 our understanding of the evolution of male and female defence of territory.

100 While physical displays are considered the main defensive responses, the role of vocal  
101 displays as defensive signals remains under discussion (see Searcy and Beecher 2009; Naguib  
102 and Mennill 2010). Among the vocal displays that take place during agonistic interactions,  
103 perhaps the most fascinating one is duetting – occurring in around 18% of avian species  
104 worldwide (Tobias et al. 2016). Duets are defined as coordinated vocal interactions between  
105 two individuals - usually a male and female of a pair - that occur with a given temporal precision  
106 (Farabaugh 1982; Hall 2004). Duets are hypothesised to represent an important component of  
107 territorial defence (Langmore 1998; Hall 2004). In particular, the “joint territorial defence”  
108 hypothesis, proposed as one evolutionary driver of duetting behaviour (Wickler and Seibt  
109 1980), postulates that duets allow pairs to cooperatively defend resources from conspecific  
110 intruders (Robinson 1949; reviewed by Hall 2004). A central prediction of the “joint territorial  
111 defence” hypothesis is that duets are threatening signals, stronger than solo songs (Hall 2004).  
112 To date, few studies investigated duetting in the context of territorial defence across different  
113 life-history stages (Topp and Mennill 2008; Odom et al. 2017; Quirós-Guerrero et al. 2017;  
114 Sosa-López et al. 2017; Diniz et al. 2018). The few that did so used mainly three methods: i)  
115 context criterion (i.e. which compares responses towards acoustic stimuli that represent  
116 different contexts, like only male/female solo songs, only duet songs or only heterospecific  
117 songs; e.g. Dowling and Webster 2016), ii) response criterion (i.e. which compares responses

118 with and without a playback stimulus e.g. Hall and Peters 2008), and iii) correlation methods  
119 (i.e. which applies correlation techniques and principal component transformations on  
120 behavioural data, e.g. Kolof and Mennil 2013). However, none of the abovementioned methods  
121 allow to test the role that duets play in the context of territorial defence while embracing the  
122 multivariate nature of this traits as a latent variable.

123 We conducted simulated territorial intrusions (STI) in the territory of focal pairs of  
124 rufous horneros during two contexts in the breeding season: nest building and chick  
125 provisioning. The rufous hornero, hereafter hornero, is a single brooded furnarid bird species  
126 that is widely distributed throughout southern South America (Fraga 1980). Horneros are  
127 territorial year round, socially monogamous (Fraga 1980; Diniz et al. 2018) and both members  
128 of the pair are involved in defending their territory (Fraga 1980; Diniz et al. 2018). Indeed, all  
129 breeding behaviours studied in horneros so far are performed in an equitable and coordinated  
130 manner between sexes, such as incubation, parental care-related activities and even territorial  
131 defence in non-breeding context (Fraga 1980; Massoni et al. 2012; Diniz et al. 2020). Also,  
132 previous studies on this species suggest that duets have a territorial function (Diniz et al. 2018,  
133 2019, 2020). However, these studies were either acoustic-centered (Diniz et al. 2018, 2019) or  
134 carried out during a non-breeding season (Diniz et al. 2020), and none of them considered the  
135 multivariate nature of territorial defence.

136 The main goals of our study were first to characterize the multivariate nature of  
137 territorial defence in male and female horneros, and to test whether duets were indeed part of  
138 the defence displays during a territorial intrusion. Our second goal was to quantify phenotypic  
139 variation across sexes, breeding contexts and pair members. Our third goal was to evaluate the  
140 level of coordination between sexes during territorial defence. To do so, we constructed a series  
141 of structural equation models where we tested three hypotheses of potential associations among  
142 the behavioural variables: model 1 hypothesised that each territorial defence behaviour is  
143 independent and not part of a functional unit or evolutionary character; model 2 hypothesises  
144 that one latent variable, “territorial defence”, underlies the relationships between all behavioural  
145 variables; and model 3 hypothesises that all behavioural variables except number of duet songs  
146 are linked by the latent variable “territorial defence”. These models were therefore specifically  
147 constructed to test the “joint territorial defence” hypothesis (Hall 2009). According to this  
148 hypothesis, for our first aim, we predicted duets to be part of the latent trait ‘territorial defence’  
149 and to be more relevant than solo songs. We also predicted that territorial defence will be  
150 characterized by the same behavioural traits (i.e. number of duets, number of flights over the  
151 decoy, times spent within 5m of the decoy, number of solo songs, time spent on nest) in males

152 and females. Second, we predicted that in our STIs males would defend more their territories  
153 than females. This was based on the notion that, although in neotropical birds there is mixed  
154 evidence for the sexual difference in territorial defence, a recent study reported that male  
155 horneros engaged more in defending their territories than females (Diniz et al. 2018). Further,  
156 because in horneros territory take-over is expected to be a stronger driver of aggression than  
157 paternity loss (i.e. extra-pair paternity levels are ~ 3%; Diniz et al. 2019), we predicted higher  
158 levels of territory defence earlier in the nest building than in the provisioning context (see also  
159 Demko and Mennill 2018). Finally, we predicted both members of the pair to positively  
160 correlate their territory defence behaviors (e.g. Diniz et al. 2020).

161

## 162 **Materials and Methods**

### 163 **Field site and experimental procedures**

164 We studied pairs of horneros in two periods during 2016 on the campus of INIA “Las Brujas”  
165 (National Institute of Agricultural Research), department of Canelones, Uruguay (34°40’ S,  
166 56°20’ W; 0-35 m a.s.l.). Behavioural assays were carried out during “nest-building” (i.e. when  
167 pairs were observed finishing their nests and females were in their fertile period; August 23<sup>rd</sup> –  
168 September 27<sup>th</sup>), and “provisioning” periods (i.e. when pairs were observed feeding their young;  
169 November 7<sup>th</sup> – December 6<sup>th</sup>). Overall, we observed 39 males and 38 females during nest  
170 building and 25 males and 24 females during provisioning. Each pair was tested only one time  
171 (i.e. either during the nest-building or during the provisioning period). It was not possible to  
172 record data blind because our study involved focal animals in the field. All the behavioural  
173 assays were performed between 07h00 and 13h00. We quantified territorial defence behaviours  
174 by performing simulated territorial intrusions (STI) in the territory of a focal pair. Once the  
175 focal pair was identified, a stuffed decoy of a hornero together with playback sounds was  
176 presented 10 metres away from the pair’s nest. Using two decoys could have been more  
177 realistic; however, we could not do this for ethical reasons. Every STI playback lasted 20  
178 minutes and consisted of randomly selected stimuli from a pool of ten male solo songs, ten  
179 duets and ten audio files containing 7-15 seconds of silence. The auditory stimuli for each STI  
180 were randomly selected to avoid pseudo-replication of the acoustic component across territories  
181 (e.g. Apfelbeck et al. 2011), to avoid a behavioural bias towards specific songs or duets, and to  
182 elicit comparable behavioural responses across territories. Our approach hinged on the notion  
183 that horneros are suboscines and do not learn their vocalizations (Freeman et al. 2017). This is,  
184 compared to oscines, the acoustic variability of songs and duets across individuals is low  
185 (Freeman et al. 2017). We played silence tracks of different length to avoid habituation in the

186 focal birds. All playback sounds were “wav” files recorded in Uruguay and were obtained from  
187 the database of Xeno-canto ([www.xeno-canto.org](http://www.xeno-canto.org)) and normalized in amplitude. All the sounds  
188 were broadcasted from a single speaker (Douglas and Mennil 2010). Although a multiple-  
189 speaker approach would have been more realistic, because horneros frequently perform their  
190 duets while close to each other, it is unlikely that our set-up introduced a bias in the STIs. We  
191 simultaneously recorded the behaviour of each individual of the pair during the 20 minutes of  
192 STI (mean  $\pm$  SE;  $19.96 \pm 0.23$  min). Two observers performed the observations from a distance  
193 of 15 metres using digital voice recorders (Philips VoiceTraicer DVT1200 and Olympus Digital  
194 Recorder VN-733 PC). The focal bird was randomly assigned to each observer. The following  
195 measures were recorded: 1) response latency (time between start of playback and first approach  
196 within 10 metres from the dummy), 2) time spent within five metres of the decoy, 3) average  
197 time spent on the nest during a visit, 4) number of solo songs, 5) number of duet songs, and 6)  
198 number of flights over the decoy (i.e. flights directed to and over the decoy). Regarding the  
199 variable ‘number of duets’, we initially considered the fact that both males and females can  
200 initiate the duet (Diniz et al, 2018). However, during our STIs there were seldom cases in which  
201 the female initiated the duet, and none were during nest building. For this reason, we only  
202 considered the number of duets as a joint variable across sexes in our models. Additionally, the  
203 solo songs in males represent instances in which females decided not to join in the duet. The  
204 sex of each bird could be determined from the acoustic signature of each individual because the  
205 vocal contribution of each sex in the duet is dimorphic (Roper 2005). As part of a different  
206 project, birds were captured after the STI and the sex was verified by PCR (sex was correctly  
207 assigned by the observers in 96.3% of the cases for those individuals to whom the sex could be  
208 assigned acoustically and were trapped in the nets; for details see Adreani et al. 2018).

209

## 210 **Statistical analyses**

### 211 *(i) Structural equation modelling*

212 First, we applied a structural equation modelling (SEM) approach to study three *a priori*  
213 hypotheses of relationships among the six behavioural variables quantified during the simulated  
214 territorial intrusion (i.e. response latency, time spent within five metres of the decoy, time spent  
215 on the nest, number of solo songs, number of duet songs, and number of flights over the decoy;  
216 Fig. 1). Of the three models for each sex and context, model 1 represents a (biologically  
217 unrealistic) “null” expectation (i.e. each defensive behaviour is independent and not part of a  
218 functional unit or evolutionary character); model 2 hypothesises that one latent variable,  
219 “territorial defence”, underlies the relationships between the six behavioural variables; and

220 model 3 hypothesises that all behavioural variables except number of duet songs are linked by  
221 the latent variable “territorial defence”. While more complex structural models could be  
222 constructed (i.e. including trade-offs between behavioural variables), the present framework is  
223 the one that allows for a straightforward testing the “joint territorial defence” hypothesis (Hall  
224 2009). We estimated each structural equation model separately for males and females because  
225 we only have one measure of the number of duet songs from a single pair and, therefore, it is  
226 not possible to disentangle the sex-differences in number of duets on the latent variable  
227 territorial defence. We also estimated each model separately for the two breeding contexts (i.e.  
228 nest building vs. provision context). The formulation of these four different sets of models  
229 allowed us to qualitatively assess whether there were differences between sexes and breeding  
230 contexts (nest building and provisioning) in the structure and strength of the hypothesized latent  
231 variable. Therefore, besides characterizing the latent variable structure, we were also interested  
232 in qualitatively investigating differences between sexes and contexts in path loadings across  
233 models (i.e. whether behavioural traits maintain their rank differences among path loadings).  
234 We also constructed a single model for each sex in both breeding contexts, where the 12  
235 different behavioural variables were modelled simultaneously. However, we decided to present  
236 here the separated models, one for each breeding context, because the full model (i.e., with the  
237 12 variables) is likely over-parametrized (i.e., there was a compromise between the complexity  
238 of the SEM models fitted and the number of observations given the number of variables tested  
239 in each SEM). See Supplementary Material for further details on the full model (Table S1-2  
240 and Fig S1).

241 To test the relative fit of each alternative biological hypotheses, we first estimated the  
242 matrix of phenotypic correlations of all the behavioural variables for each combination of sex  
243 and breeding context. The correlation matrix was constructed using Spearman coefficients  
244 obtained with the R package “stats” in R v. 3.3.3 (R Core Team 2013). Data on “response  
245 latency” were missing for one out of 38 individual females during nest building and data for  
246 “time spent on the nest” were missing for two out of 24 females during provisioning. We  
247 assigned the average population phenotypic value of each trait to those individuals with missing  
248 values (note that a “complete-case analysis” did not change our findings, results not shown).  
249 We then implemented each among-trait correlation matrix in the R-package “sem” and tested  
250 the different SEM hypotheses. We statistically compared each model’s fit using the Akaike  
251 Information Criterion for small sample sizes (AICc; Burnham and Anderson 2004) and  
252 evaluated their relative support based on AICc differences relative to the best-fitting model  
253 ( $\Delta$ AICc). We also present values for the Goodness of Fit Index (GFI), which represents the



254 proportion in the improvement of the overall fit of a given hypothesised model compared to the  
255 independence model. GFI values range from 0 (poor fit) to 1 (perfect fit), being considered as  
256 satisfactory when it is higher than 0.9.

257

258 *(ii) Univariate mixed-effect models*

259 As a second step, we investigated sources of variation in territorial defence behaviour in our  
260 population of horneros using a series of univariate mixed models. This step was necessary  
261 because we were also interested in investigating sex-differences in territorial defence. However,  
262 as we only had a single measure of number of duets per pair, we could not test for sources of  
263 variation in territorial defence using our multivariate SEM approach. Thus, we ran two  
264 univariate mixed-effect models fitting number of flights over the decoy and number of duets as  
265 the response variables, respectively. Though we had measured various potential proxies of  
266 territorial defence (detailed above), we used number of flights over decoy and number of duet  
267 songs because they consistently had the highest value in path loading across all models (for a  
268 further discussion on the rationale of this approach, see Araya-Ajoy and Dingemanse 2013).  
269 Breeding context (nest building vs. provisioning), sex (male vs. female) and their interaction,  
270 time of the day (i.e. moment of the day when the territorial intrusion was simulated, expressed  
271 in decimal fractions of hours after sunrise and mean centred), and observer identity (observer 1  
272 vs. 2) were included as fixed effects in the univariate mixed-effect models. Time of day was  
273 mean centred, such that the fixed-effect intercept of the model was estimated for the behavioural  
274 trait on the average time (following Dingemanse and Dochtermann 2013). In the model with  
275 “number of flights over the decoy” as a response variable, we fitted random intercepts for pair  
276 identity (“Pair identity”;  $n = 63$  levels). In the model with “number of duet songs”, we did not  
277 include this random effect because we did not have repeated measures of duet song frequency  
278 for the same pair identity. Both response variables, number of flights over the decoy and number  
279 of duet songs, were modelled with Poisson errors with a log-link function. In both models, we  
280 included an observation level random effect to account for over-dispersion (Harrison 2014).  
281 The analyses were performed using the R packages “lme4” (Bates et al. 2014) and “arm”  
282 (Gelman and Yu-Sung 2015). We used the “sim” R function to simulate posterior distributions  
283 of the model parameters. Based on 5000 simulations, we extracted the mean value and 95%  
284 Credible Intervals (CrI) of the posterior distributions. Model fit was assessed by visual  
285 inspection of the residuals. Assessment of statistical support was obtained from the posterior  
286 distribution of each parameter (Zuur 2016). We considered an effect “strongly supported” if  
287 zero was not included within the 95% CI, and “moderately supported” if the point estimate was

288 skewed away from zero while its 95% CI simultaneously overlapped zero. Estimates centred  
289 on zero were viewed as strong support for the absence of an effect.

290

291 *(iii) Correlation between male and female contribution to territorial defence*

292 We studied the correlation pattern between male and female territorial defence to investigate  
293 whether defence response within a pair was positively correlated. To do so, we estimated the  
294 Spearman correlation coefficient of “number of flights over the decoy” between males and  
295 females from a single pair. This correlation was calculated by including in our analysis all pairs  
296 observed during both contexts ( $n = 91$  pairs), given that we found no differences in the number  
297 of flights over the decoy between the nest building and provisioning contexts (see below). The  
298 correlation test was performed using the R-package “stats” in R v. 3.3.3 (R Core Team 2013).

299

## 300 **Results**

301 (i) Territorial defence as a latent trait and the role of duetting

302 The behavioural variables assayed during the simulated territorial intrusion (i.e. response  
303 latency, time spent within five metres of the decoy, time spent on the nest, number of solo  
304 songs, number of duet songs, and number of flights over the decoy) were, to a varying extent,  
305 correlated with each other; both across sexes and contexts (Table S3, S4). Overall, horneros  
306 with shorter latency of response to the territorial intrusion spent more time within five metres  
307 of the decoy and on the nest, sang more solo and duet songs, and flew more often over the  
308 decoy, suggesting the existence of the hypothesised latent variable “territorial defence” linking  
309 the six behavioural variables.

310 AICc model comparison identified the SEM model 2 as the best one (among the models  
311 we fitted) explaining the structure of the phenotypic variables across the four different set of  
312 models (Table 1). Model 2 represented an overarching latent variable (“territorial defence”) linking  
313 the expression of all behavioural variables, including the number of duet songs (Fig.  
314 1A). Furthermore, the number of duet songs together with the number of flights over the decoy  
315 had consistently the highest values of path loading in males and females for both breeding  
316 context (Fig. 1B, Table S5). We thus considered them both equally good predictors for territory  
317 defence in horneros. Furthermore, a standard index of model fit (“Goodness of Fit Index”) considered  
318 satisfactory our best fitting model across all models (i.e., GFI values for Model 2  
319 were around or above 0.90 across all models, Table 1).

320

321 *(ii) Effect of sex, breeding context and time of the day on territorial defence*

322 We did not find strong evidence that horneros differed in the number of duet songs between the  
323 nest building and provisioning context. While the effect size is moderately supported, the  
324 evidence is weak due to large uncertainty (Table 2; Fig. 2A). We did not find differences in the  
325 number of duets explained by time of the day (Table 2). Regarding the number of flights over  
326 the decoy, males were on average defending more (i.e. flew more times over the decoy) than  
327 females during both breeding contexts (Table 2; Fig. 2B). However, we again found weak  
328 evidence that horneros differed in the number of flights over the decoy between the nest  
329 building and provisioning context, and there were also no sex-specific differences between the  
330 two breeding contexts (i.e. the effect sizes are relatively large but estimated with large  
331 uncertainty, therefore the support is moderate; Table 2, Fig. 2B). Furthermore, we observed  
332 moderate effects of time of day and observer identity in our model (the estimates include zero  
333 in their 95% CrI, but the effect sizes are considerable).

334

335 *(iii) Defending as a unit: correlation between male and female territorial defence*

336 We investigated whether the defensive response to a territory intrusion of an individual was  
337 correlated with the response expressed by its partner. We found that territorial defence of males  
338 and females within pairs was strongly positively correlated ( $\rho = 0.67$ ,  $p < 0.0001$ ). Thereby,  
339 within a single pair, male and female had matching levels of defensive response (Fig. 3).

340

341 **Discussion**

342 We studied territorial defence in both male and female horneros and the role of duets during  
343 nest building and provisioning contexts. By using structural equation modelling, we were able  
344 to demonstrate that six observed behavioural variables (i.e. response latency, time spent within  
345 five metres of the decoy, average time spent on the nest during a visit, number of solo songs,  
346 number of duet songs, and number of flights over the decoy) were linked by an unmeasured  
347 latent trait “territorial defence”, both across sexes and contexts (Fig. 1). We also found that the  
348 number of flights over the decoy and duet songs were the variables with highest path loading  
349 to territorial defence. We then proceed to study independently those two traits with highest path  
350 loadings and showed that males were defending territories more strongly than were females  
351 during both breeding contexts, even though we only found weak evidence for differences  
352 between contexts within each sex (owing to large uncertainty in our estimate, Fig. 2). Lastly  
353 and as expected, we observed a strong positive correlation in territorial defence between males  
354 and females within the pair (Fig. 3).

355           The correlation structure of the latent variable territorial defence was similar in males  
356 and females, providing for the first time a sex-comparison of the latent variable “territorial  
357 defence” in birds. We also observed that the sign and magnitude of the path loadings between  
358 breeding contexts (i.e. nest building and provisioning) were very similar (Fig. 1B). Our results  
359 thus suggest the existence of a common structure in defensive behaviour during territorial  
360 intrusion in horneros, potentially underlined by a sex- and context-independent mechanism that  
361 is affecting all behavioural variables in a similar manner. However, to draw general  
362 evolutionary patterns of territorial defence it would be necessary to investigate whether the  
363 described latent variable is under selection as an integrated trait (i.e. functional module) and  
364 whether the same structure among traits is observed in other life-history stages (e.g. outside the  
365 breeding season) or in different ecological contexts (e.g. as territorial defence against predators  
366 or nest-parasitic species). Importantly, by using a structural equation modelling approach we  
367 were able to reveal complex relationships for multiple traits that would have otherwise not been  
368 possible to capture. Traditional statistical approaches such as multiple regression analysis or  
369 principal component analysis (PCA) are not suitable to evaluate different *a priori* defined  
370 hypotheses while accounting for trait correlation. PCAs are defined purely on the basis of  
371 mathematical associations between the traits and so their biological meaning can be challenging  
372 to interpret or even nonexistent. However, SEM provides a more interpretable method of  
373 viewing variation among correlated variables. Although SEM will ultimately be defined by  
374 mathematical associations like PCAs, with SEM, one makes use of biological information to fit  
375 the correlation structure to be tested among variables. Therefore, SEM has a clear advantage  
376 over PCA in terms of making biological inferences from the data. Lastly, another advantage of  
377 using a structural equation modelling approach is related to data collection methods. The fact  
378 that the number of flights over the decoy and duets songs were the variables with the highest  
379 path loadings to territorial defence indicates that by measuring only these two observable  
380 behaviours, and not all six, researchers should have a good estimation of territorial defence – at  
381 least in those studies that aim to quantify territorial defence towards conspecifics in horneros.  
382 Nonetheless, a good biological use of the approach would require a validation of the method  
383 for each new species where territorial defence is to be characterized.

384           In the context of territorial defence, duets have been mostly studied as a single trait  
385 independently of other complementary or related behaviours in multiple bird species (e.g. Hall  
386 and Peters 2008; Dowling and Webster 2016; Odom et al. 2017; Quirós-Guerrero et al. 2017).  
387 Here we explicitly tested for the first time whether duets are a behavioural variable linked by a  
388 latent trait, “territorial defence”. We did so by combining a classical STI approach with

389 structural equation modelling. One of the predictions of the “joint territorial defence”  
390 hypothesis is that duets should play a more important role than solo songs (Hall 2009). As  
391 expected, in our study duets represented an important response during territorial defence for  
392 both sexes and breeding contexts. They were stronger than solo songs and were as relevant as  
393 other physical traits like the number of flights over the decoy. Our results are in line with  
394 previous findings in the species suggesting the territorial function of duets in hornero, overall  
395 providing evidence for the “joint territorial defence” hypothesis (Diniz et al. 2018, 2019, 2020).  
396 While previous studies tested this hypothesis by means of different approaches, the strength of  
397 our study resides in the application of a comprehensive method that accounts for the  
398 multivariate nature of territorial defence behaviours.

399 Males defended more their territories than females during both breeding contexts. At  
400 first glance, this is not surprising given that an unequal sex contribution of territorial defence  
401 has been previously reported in bird species that are socially monogamous and maintain  
402 territories year round (e.g. Willis 1972; Morton and Derrickson 1996; Bard et al. 2002; Fedy  
403 and Stutchbury 2005; Quinard and Cézilly 2012). In the specific case of horneros, however,  
404 male and female have been reported to contribute equally in most of the behaviours studied to  
405 date (Fraga 1980; Massoni et al. 2012; Diniz et al. 2020). However, there is strong evidence for  
406 sexual differences in singing-related traits independent of season (Diniz et al. 2018).  
407 Additionally, the observation that males engaged more in aggressive interactions than females  
408 has only been recently described (Diniz et al. 2018). Thus, our findings confirm and expand  
409 this observation with a standardized field test applied to a multivariate framework beyond song  
410 production. One explanation for the observed sex-differences might be a division of labour  
411 between members of a pair (e.g. Morton et al. 2000). For instance, males might invest more  
412 resources (i.e., time and energy) in actively defending their territory or nest (e.g. physical  
413 attacking the intruder), whereas females might focus on different activities (e.g. predator  
414 vigilance, guarding the nest against parasitic species). Another factor potentially explaining our  
415 results is that males and females might face different physiological (breeding) costs (e.g.  
416 Nilsson and Råberg 2001). In fact, during nest building (when females are close to egg laying)  
417 females have a poorer oxidative condition than males and are more sensitive to STIs, suggesting  
418 a sex-specific physiological cost of territorial defence (Mentesana and Adreani 2020). Lastly,  
419 our findings could also be influenced by the way the territorial intrusions were performed (i.e.  
420 with one single dummy). While plausible, this explanation seems unlikely given that horneros  
421 are monomorphic in body size and plumage colouration (Diniz et al. 2016) and the playbacks  
422 consisted of vocalizations from both sexes.

423 We did not find strong support for our prediction that the levels of territorial defence  
424 were higher during the nest building than in the provisioning context (Table 2). Given that  
425 extra-pair levels are very low in this species (~3%, Diniz et al. 2019), one of the main  
426 assumptions of our prediction was that territory take-over was higher during the fertile period  
427 of the females, i.e., during nest building than during provisioning (Gill et al. 2007; Demko and  
428 Mennill 2018). It is possible that for horneros it is more beneficial to maintain constant levels  
429 of territorial defence in order to hold the territory year-round than the potential benefits of extra-  
430 pair paternity (Warner and Hoffman 1980). This might be especially the case when population  
431 densities are high, where comparable territorial defence can be expected across different life-  
432 stages as we observed in the horneros. Further research will help to shed light on these context-  
433 specific patterns.

434 Male and female aggression were strongly and positively correlated within the pair  
435 despite sex-specific differences in territorial defence. Our results are in line with previous  
436 findings of coordinated territorial defense on rufous horneros outside the breeding season  
437 (Diniz et al. 2020) and more generally with other studies showing that duetting birds were more  
438 collaborative within the pair than non-duetting species (see Logue 2005). Although our study  
439 cannot directly address the evolutionary relevance of pairs being positively correlated in their  
440 behaviours (e.g., fitness consequences), our findings suggest that exhibiting a joint territorial  
441 defence might be an important mechanism of pair bonding or pair stability (Wickler and Seibt  
442 1980). In this direction, our study raises the question of whether pairs of horneros that show  
443 similar territorial defence levels would experience increased reproductive benefits (Schuett et  
444 al. 2010). Indeed, it is known from other bird species that pairs exhibiting comparably high  
445 levels of territory defence towards conspecifics attain higher reproductive success (e.g. in  
446 eastern blue birds, *Sialia sialis*; Harris and Siefferman 2014). Therefore, investigating patterns  
447 of selection on assortative mating in pairs of horneros poses an exciting avenue for future  
448 research.

449

## 450 **Conclusion**

451 This work expands upon a classical body of research on territorial defence. We demonstrated  
452 that six observed behavioural variables quantified during a simulated territorial intrusion were  
453 linked by an unmeasured latent trait “territorial defence”. In particular, the number of flights  
454 over the decoy and the number of duet songs were the variables with highest path loadings to  
455 the latent variable “territorial defence”. Furthermore, this study fills an important gap in our  
456 knowledge about the role of duets. We provided support for the hypothesis that avian duets are

457 a key component in the joint territory defence. Indeed, we showed that duets represented a  
458 stronger response of territory defence than solo songs, and that their importance was  
459 comparable to physical traits. Our study also highlights the importance of using more  
460 integrative, multivariate approaches to study behavioural traits. By applying a structural  
461 equation modelling framework, we were able to evaluate *a priori* hypotheses of how different  
462 behavioural variables were linked by an unmeasured latent trait. Such complex patterns would  
463 have not been possible to capture using traditional statistical approaches such as principal  
464 component analyses Hence, the combination of a classical behavioural approach like simulated  
465 territorial intrusions with structural equation modelling brings new exciting possibilities into  
466 the field of behavioural ecology.  
467

468 **Authors' contributions**

469 NMA, LM and MM share first authorship and names are ordered at random. NMA and LM  
470 conceived the study and designed the study. BT provided logistic support. NMA, LM, EG and  
471 EC collected the data. NMA, LM, and MM analyzed the data. NMA, LM, and MM wrote the  
472 manuscript with input from all authors.

473

474 **Acknowledgments**

475 We thank Klaus Pichler for his help to prepare the STI and all the “INIA Las Brujas” staff for  
476 supporting us with accommodation and equipment during fieldwork. We also thank Facultad  
477 de Ciencias and the Ethology lab from Universidad de la República and Juan Carlos Reboreda  
478 and the “Laboratorio de Ecología y Comportamiento Animal” at the Universidad de Buenos  
479 Aires for the logistical support, and Pablo Tubaro from the Museo Argentino de Ciencias  
480 Naturales ‘Bernardino Rivadavia’ (MACN) for providing us with the mounted hornero. We are  
481 grateful to Manfred Gahr and Michaela Hau for their valuable support. We also thank Yimen  
482 Araya-Ajoy, Glenn Cockburn, Luke Eberhart-Phillips and Wolfgang Wickler for constructive  
483 criticism on previous versions of the manuscript. Finally, we want to thank the anonymous  
484 reviewers for constructive feedback on the manuscript.

485

486 **Availability of data**

487 The datasets generated and/or analysed during the current study are available in the open  
488 repository: Mendeley Data (<https://data.mendeley.com/datasets/7ztwn539jd/1>).

489

490 **Compliance with ethical standards**

491 **Ethical approval**

492 The experimental procedures of this study have approval by the Ethics Committee of Animal  
493 Experimentation (CEUA) of the Facultad de Ciencias of the Universidad de la República,  
494 Uruguay (Protocol number 186, file 2400-11000090-16).

495 **Conflict of interest**

496 The authors declare they have no conflicts of interest.

497 **Funding**

498 This work was funded by the International Max Planck Research School (IMPRS) for  
499 Organismal Biology, and by Idea Wild that provided field equipment.

500

501



502 **References**

- 503 Adreani NM, Goymann W, Montesana L (2018) Not one hormone or another: Aggression  
504 differentially affects progesterone and testosterone in a South American ovenbird. *Horm Behav*  
505 105:104–109  
506
- 507 Apfelbeck B, Goymann W (2011) Ignoring the challenge? Male black redstarts (*Phoenicurus*  
508 *ochruros*) do not increase testosterone levels during territorial conflicts but they do so in  
509 response to gonadotropin-releasing hormone. *Proc R Soc Lond B* 278:3233–3242  
510
- 511 Araya-Ajoy YG, Dingemanse NJ (2013) Characterizing behavioural “characters”: an  
512 evolutionary framework. *Proc R Soc B* 281:20132645  
513
- 514 Bard SC, Hau M, Wikelski M, Wingfield JC (2002) Vocal distinctiveness and response to  
515 conspecific playback in the spotted antbird, a neotropical suboscine. *Condor* 104:387-394  
516
- 517 Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear Mixed-Effects Models using  
518 lme4, <https://cran.r-project.org/web/packages/lme4/index.html>  
519
- 520 Bollen KA (2002) Latent variables in psychology and the social sciences. *Annu Rev Psychol*  
521 53:605–634  
522
- 523 Burnham KP, Anderson DR (2004) Multimodel inference. *Sociol Methods Res* 33:261–304  
524
- 525 Carter AJ, Feeney WE (2012) Taking a comparative approach: Analysing personality as a  
526 multivariate behavioural response across species. *PLoS ONE* 7:e42440  
527
- 528 Card NA, Little TD (2007) Studying aggression with structural equation modeling. In: Flannery  
529 DJ, Vazsonyi AT, Waldman ID (eds) *The Cambridge handbook of violent behavior and*  
530 *aggression*. Cambridge University Press New York, NY, pp 727-739  
531
- 532 Clutton-Brock TH, Vincent ACJ (1991) Sexual selection and the potential reproductive rates  
533 of males and females. *Nature* 351:58–60  
534
- 535 Demko AD, Mennill DJ (2018) Male and female signaling behavior varies seasonally during

- 536 territorial interactions in a tropical songbird. *Behav Ecol Sociobiol* 72:84  
537
- 538 Dingemanse NJ, Dochtermann NA (2013) Quantifying individual variation in behaviour:  
539 mixed-effect modelling approaches. *J Anim Ecol* 82:39–54  
540
- 541 Diniz P, Júnior EF da S, Webster MS, Macedo RH (2018) Duetting behavior in a Neotropical  
542 ovenbird: sexual and seasonal variation and adaptive signaling functions. *J Avian Biol* 49:jav-  
543 01637  
544
- 545 Diniz P, Macedo RH, Webster MS (2019) Duetting correlates with territory quality and  
546 reproductive success in a suboscine bird with low extra-pair paternity. *Auk* 136:1-13  
547
- 548 Diniz P, Rech G, Ribeiro PH, Webster MS, Macedo RH (2020) Partners coordinate territorial  
549 defence against simulated intruders in a duetting ovenbird. *Ecol Evol* 10:81-89  
550
- 551 Diniz P, Ribeiro PHL, Rech GS, Macedo RH (2016) Monochromatism, cryptic sexual  
552 dimorphism and lack of assortative mating in the Rufous Hornero, *Furnarius rufus albogularis*.  
553 *Emu* 116:294–300  
554
- 555 Dowling J, Webster MS (2016) An experimental test of duet function in a fairy-wren (*Malurus*)  
556 with moderate cuckoldry rates. *Behav Ecol* 27:228–236  
557
- 558 Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems.  
559 *Science* 197:215–223  
560
- 561 Farabaugh SM (1982) The ecological and social significance of duetting.  
562 In: Kroodsma DE, Miller EH (eds) *Acoustic Communication in Birds*, vol. 2. Academic Press,  
563 New York, pp 85–124  
564
- 565 Fedy BC, Stutchbury BJM (2005) Territory defence in tropical birds: are females as aggressive  
566 as males? *Behav Ecol Sociobiol* 58:414–422  
567
- 568 Fraga RM (1980) The breeding of Rufous Horneros (*Furnarius rufus*). *Condor* 82:58–68  
569

- 570 Freeman BG, Montgomery GA, Schluter D (2017) Evolution and plasticity: Divergence of song  
571 discrimination is faster in birds with innate song than in song learners in Neotropical passerine  
572 birds. *Evolution* 71:2230-2242  
573
- 574 Garcia JT, Arroyo BE (2002) Intra- and interspecific agonistic behaviour in sympatric harriers  
575 during the breeding season. *Anim Behav* 64:77–84  
576
- 577 Gelman A, Yu-Sung S (2015) arm: Data analysis using regression and multilevel/hierarchical  
578 models. R package version 1.8-5, <https://cran.r-project.org/web/packages/arm/arm.pdf>  
579
- 580 Gill SA, Alfson ED, Hau M (2007) Context matters: female aggression and testosterone in a  
581 year-round territorial neotropical songbird (*Thyrothorus leucotis*). *Proc R Soc Lond B*  
582 274:2187–2194  
583
- 584 Greenberg R, Gradwohl J (1983) Sexual roles in the dot-winged antwren (*Microrhoptias*  
585 *quixensis*), a tropical forest passerine. *Auk* 100:920–925  
586
- 587 Hall ML (2004) A review of hypotheses for the functions of avian duetting. *Behav Ecol*  
588 *Sociobiol* 55:415–430  
589
- 590 Hall ML (2009) A review of vocal duetting in birds. *Adv Stud Behav* 40:67–121  
591
- 592 Hall ML, Peters A (2008) Coordination between the sexes for territorial defence in a duetting  
593 faire-wren. *Anim Behav* 76:65–73  
594
- 595 Harris MR, Siefferman L (2014) Interspecific competition influences fitness benefits of  
596 assortative mating for territorial aggression in eastern bluebirds (*Sialia sialis*). *PLoS ONE*  
597 9:e88668  
598
- 599 Harrison XA (2009) Using observation-level random effects to model overdispersion in count  
600 data in ecology and evolution. *PeerJ* 2:e616  
601
- 602 Houle D, Pélabon C, Wagner GP, Hansen TF (2011) Measurement and meaning in biology. *Q*  
603 *Rev Biol* 86:3-34

604  
605 Huntingford FA (1976) An investigation of the territorial behaviour of the three-spined  
606 stickleback (*Gasterosteus aculeatus*) using principal components analysis. Anim  
607 Behav 24:822-834  
608  
609 Koloff J, Mennill DJ (2013) The responses of duetting antbirds to stereo duet playback provide  
610 support for the joint territory defence hypothesis. Ethology 119:462–471  
611  
612 Korner-Nievergelt F, Roth T, von Felten S, Guélat J, Almasi B, Korner-Nievergelt P (2015)  
613 Bayesian data analysis in ecology using linear models with R, BUGS, and Stan. Academic  
614 Press, New York  
615  
616 Langmore NE (1998) Functions of duet and solo songs of female birds. Trends Ecol Evol  
617 13:136–140  
618  
619 Massoni V, Reboreda JC, López GC, Aldatz MF (2012) High coordination and equitable  
620 parental effort in the Rufous Hornero. Condor 114:564–570  
621  
622 Mentésana L, Adreani NM (2020) Is aggression costly? Acute aggressive behavior increases  
623 oxidative stress independently of testosterone. bioRxiv,  
624 <https://doi.org/10.1101/2020.04.06.027029>  
625  
626 Morton ES, Derrickson KC (1996) Song ranging by the dusky antbird, *Cercomacra tyrannina*:  
627 ranging without song learning. Behav Ecol Sociobiol 39:195–201  
628  
629 Morton ES, Derrickson KC, Stutchbury BJM (2000) Territory switching behavior in a  
630 sedentary tropical passerine, the dusky antbird (*Cercomacra tyrannina*). Behav Ecol 11:648–  
631 653  
632  
633 Naguib M, Mennill DJ (2010) The signal value of birdsong: empirical evidence suggests song  
634 overlapping is a signal. Anim Behav 80:e11-e15  
635  
636 Nilsson JÅ, Råberg L (2001) The resting metabolic cost of egg laying and nestling feeding in  
637 great tits. Oecologia 128:187–192

638

639 Odom KJ, Logue DM, Studds CE, Monroe MK, Campbell SK, Omland KE (2017) Duetting  
640 behavior varies with sex, season, and singing role in a tropical oriole (*Icterus icterus*). Behav  
641 Ecol 28:1256–1265

642

643 Owens IPF, Thompson DBA (1994) Sex differences, sex ratios and sex roles. Proc R Soc Lond  
644 B 258:93–99

645

646 Quinard A, Cézilly F (2012) Sex roles during conspecific territorial defence in the Zenaida  
647 dove, *Zenaida aurita*. Anim Behav 83:47–54

648

649 Quirós-Guerrero E, Janeiro MJ, Lopez-Morales M, Cresswell W, Templeton CN (2017)  
650 Riverside wren pairs jointly defend their territories against simulated intruders. Ethology  
651 123:949–956

652

653 R Core Team (2013) R: A language and environment for statistical computing. R Foundation  
654 for Statistical Computing, Vienna, Austria, <http://www.R-project.org>

655

656 Robinson A (1949) The biological significance of bird song in Australia. Emu 48:291–315

657

658 Roper JJ (2005) Sexually distinct songs in the duet of the sexually monomorphic Rufous  
659 Hornero. J Ornithol 76:234–236

660

661 Schuett W, Tregenza T, Dall SRX (2010) Sexual selection and animal personality. Biol Rev  
662 85:217–246

663

664 Searcy WA, Beecher MD (2009) Song as an aggressive signal in songbirds. Anim  
665 Behav 78:1281–1292

666

667 Smith BR, Blumstein DT (2008) Fitness consequences of personality: a meta-analysis. Behav  
668 Ecol 19:448–455

669

670 Sosa-López JR, Mennill DJ, Renton K (2017) Sexual differentiation and seasonal variation in  
671 response to conspecific and heterospecific acoustic signals. Ethology 123:460–466

672

673 Sprenger D, Dingemanse NJ, Dochtermann NA, Theobald J, Walker SP (2012) Aggressive  
674 females become aggressive males in a sex-changing reef fish. *Ecol Lett* 15:986-992

675

676 Stamps JA, Krishnan VV (1997) Functions of fights in territory establishment. *Am Nat*  
677 150:393–405

678

679 Tobias JA, Sheard C, Seddon N, Meade A, Cotton AJ, Nakagawa S (2016) Territoriality, social  
680 bonds, and the evolution of communal signaling in birds. *Front Ecol Evol* 4:74

681

682 Topp SM, Mennill DJ (2008) Seasonal variation in the duetting behaviour of rufous-and-white  
683 wrens (*Thryothorus rufalbus*). *Behav Ecol. Sociobiol* 62:1107–1117

684

685 Warner RR, Hoffman SG (1980) Population density and the economics of territorial defence in  
686 a coral reef fish. *Ecology* 61:772–780

687

688 Wickler W, Seibt U (1980) Vocal dueting and the pair bond. *Z Tierpsychol* 52:217–226

689

690 Willis EO (1972) The Behavior of ocellated antbirds. *Ornithol Monogr* 10:1–162

691

692 Wingfield JC (1994) Regulation of territorial behavior in the sedentary song sparrow,  
693 *Melospiza melodia morphna*. *Horm Behav* 28:1–15

694 **Table and Figure captions**

695

696 **Table 1** Results of model comparison using Akaike Information Criterion for small sample  
697 sizes (AICc) values to compare our three candidate models. Smaller AICc values are given to  
698 models that better fit the data. Models whose AICc values differ from that of the top model  
699 ( $\Delta\text{AICc}$ ) by more than 2 are considered to lack explanatory power relative to the top model.  
700 We also present values for the Goodness of Fit Index (GFI). The best-supported hypothesis is  
701 printed in boldface

702

703 **Table 2** Sources of variation in “number of flights over the decoy” and “number of duets” in  
704 horneros. Breeding context (nest building vs provisioning), sex (female vs male) and their  
705 interaction; time of the day (hours after sunrise, mean centred); and observer identity (Observer  
706 1 vs 2) were fitted as fixed effects. Pair identity and an observation-level parameter were fitted  
707 as random effects. Both response variables were modelled with Poisson error. We present  
708 estimates of fixed ( $\beta$ ) and random ( $\sigma^2$ ) parameters with their 95% Credible Intervals (CrI) in  
709 brackets. The reference category for the categorical variable sex is “female”; for breeding  
710 context, “nest building”; and for observer identity is “observer 1”

711

712 **Fig. 1** (A) Three models (hypotheses) explaining the correlation structure among behavioural  
713 variables assayed during a simulated territory intrusion in the nest building and provisioning  
714 context in wild horneros. Model 1 hypothesises trait independence (null model); model 2  
715 hypothesises a latent variable (“territorial defence”) linking all behavioural variables, whereas  
716 model 3 hypothesises a latent variable (“territorial defence”) linking all behavioural variables  
717 except “number of duets”. Unidirectional arrows represent directional relationships between  
718 traits. Solid lines represent relationships present across all models; and the dashed line  
719 represents a relationship expressed in a specific model structure. Path “a” is only active in model  
720 2. (B) Path loadings of model 2 for males and females in both breeding contexts. Squares and  
721 circles represent the estimated mean, and error bars represent the standard error of the mean

722

723 **Fig. 2** Number of (A) duets and (B) flights over decoy of hornero pairs during nest building  
724 and provisioning context. Grey symbols represent raw data. The mean estimates of the posterior  
725 distributions (black symbols) as well as the 95% credible intervals (error bars) are also shown

726

727 **Fig. 3** Female-male correlation of territorial defence, using number of flights over the decoy as  
728 proxy. The black line represents the regression line and the dashed line is the reference line  
729 with a slope of 1



730 **Figures and Tables**

731

732 **Table 1**

	<b>SEM models</b>								
	<b>Model 1</b>			<b>Model 2</b>			<b>Model 3</b>		
<b>Sex – breeding context</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>GFI</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>GFI</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>GFI</b>
female - nest building	72.64	44.53	0.60	<b>28.11</b>	<b>0.00</b>	<b>0.90</b>	51.11	23.00	0.79
female - provisioning	55.74	19.43	0.58	<b>36.31</b>	<b>0.00</b>	<b>0.89</b>	54.06	17.75	0.78
male - nest building	30.53	11.60	0.81	<b>18.93</b>	<b>0.00</b>	<b>0.95</b>	30.99	12.06	0.87
male - provisioning	62.17	16.11	0.54	<b>46.06</b>	<b>0.00</b>	<b>0.84</b>	49.40	3.34	0.80

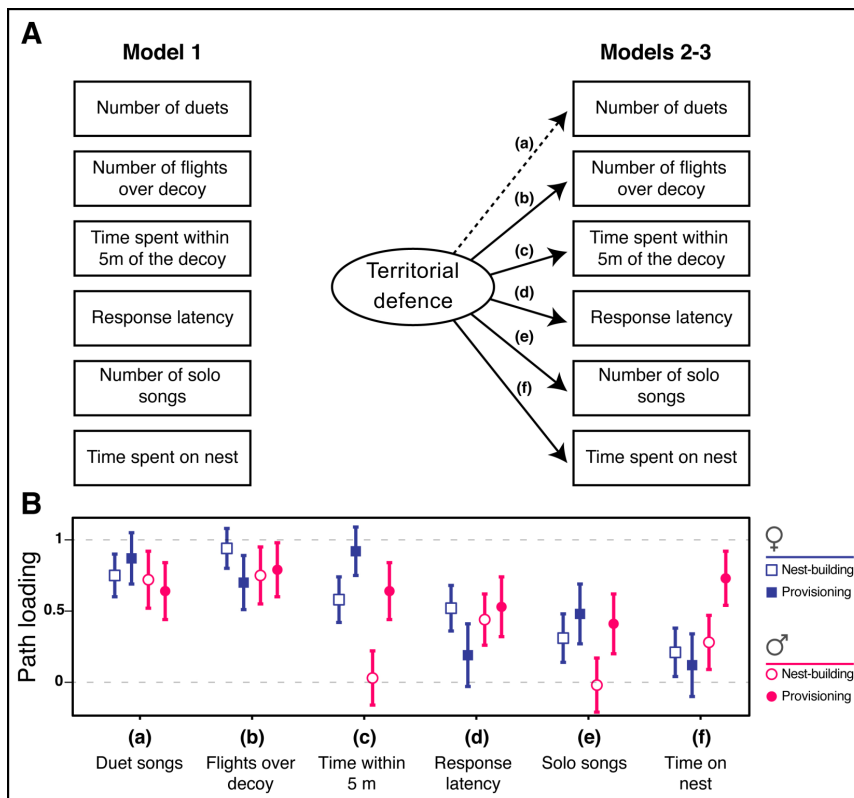
733

734

735 **Figure 1**

736

737



738

739

740

741

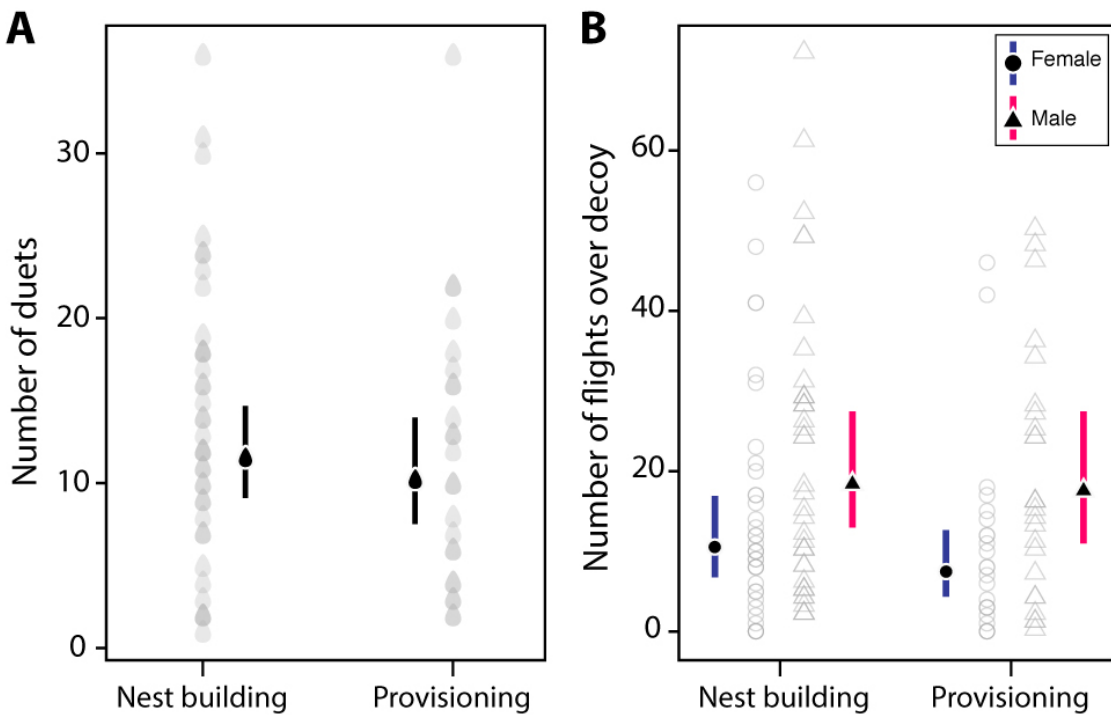
742 **Table 2**

Fixed effects	Flights over decoy	Duets
	$\beta$ (95% CrI)	$\beta$ (95% CrI)
Intercept	2.33 (1.87, 2.78)	2.44 (2.21, 2.69)
Sex	0.58 (0.32, 0.83)	--
Breeding context	-0.28 (-0.88, 0.31)	-0.11 (-0.52, 0.28)
Sex $\times$ Breeding context	0.22 (-0.19, 0.64)	--
Time of day	-0.19 (-0.45, 0.05)	-0.07 (-0.26, 0.13)
Observer Identity	-0.16 (-0.36, 0.04)	--
Random effects	$\sigma^2$ (95%CrI)	$\sigma^2$ (95%CrI)
Pair Identity	1.02 (0.75, 1.36)	--
Observation-level parameter	0.18 (0.14, 0.24)	0.44 (0.33, 0.60)

743

744

745 **Figure 2**



746

747

748 **Figure 3**

749

