Instituto Nacional de Pesquisas da Amazônia

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Custo individual, ontogenia e visita de fêmeas como moduladores da exibição de corte de machos em *Corapipo gutturalis* **(Aves: Pipridae)**

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Manaus-AM

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Sinopse:

Estudaram-se fatores que regulam a exibição de corte dos machos da espécie *Corapipo gutturalis,* como custo individual, peso corporal, maturidade e visita de fêmeas.

Palavras-chave: Aves, agregação, comportamento reprodutivo, determinantes bióticos, exibição de corte, qualidade, preferência de fêmeas, competição de machos.

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Resumo

Segundo a teoria da Seleção Sexual, a evolução adaptativa de caracteres que favorecem a obtenção de parceiros reprodutivos é moldada por interações entre os indivíduos do mesmo sexo (seleção intra-sexual) ou de sexos opostos (seleção inter-sexual), definindo o sucesso de acasalamento entre parceiros potenciais. Assim, entender quais são, e como estas interações atuam na modulação destes caracteres permite-nos compreender a evolução destas características através de seleção sexual. Para que uma característica seja escolhida, ela precisa ser variável entre os indivíduos, para então ser estereotipada como caractere sexual secundário em uma espécie. De fato, o grau de variação em um caractere sexual secundário pode refletir, dentre outros aspectos, a variação de preferência exercida pelo sexo que escolhe parceiros, usualmente as fêmeas. Cortes nupciais são comportamentos elaborados comumente presentes em clados poligâmicos. Neste estudo avaliei se existe variação entre indivíduos nas frequências de exibição de corte de machos do tangará-de-garganta-branca, *Corapipo gutturalis*, em uma população da Amazônia Central, onde a espécie é comumente encontrada se exibindo em troncos caídos e cobertos por musgo no sub-bosque de florestas de terra-firme. A seguir, testei se as diferenças encontradas poderiam ser explicadas por fatores abióticos como a condição de iluminação no ambiente durante a exibição (ensolarado ou nublado) ou por fatores bióticos como a condição intrínseca dos machos (massa corpórea e idade) ou o contexto social extrínseco aos mesmos (total de machos e fêmeas presentes). Meus resultados indicam que existe uma diferenciação em frequência total de presença e exibição de machos nos palcos onde se exibem para as fêmeas, bem como diferenciação na frequência com que cada macho realiza os diferentes elementos que compõem os repertórios de corte da espécie. Dentre os fatores que influenciaram a frequência de exibição total e de alguns elementos separadamente estão a massa corporal do macho, sua idade e a frequência de fêmeas presentes nas proximidades dos palcos durante as observações. Uma vez que a visita de fêmeas modula as taxas de exibição dos machos, que são custosas, nossos resultados são compatíveis com o modelo de "*hotshot*" proposto para explicar a agregação de machos ao redor de machos mais ativos, os quais são selecionados pelas fêmeas.

Palavras Chave: Poliginia de lek, Neotrópico, preferência de fêmeas, competição entre machos, caracteres sexuais secundários, Pipridae.

Abstract

The theory of sexual selection predicts adaptive evolution of secondary sexual characters that favor mating through male-male competition and female preference. As such, studying how these interactions shape sexual traits allows understanding their evolution through sexual selection. In order to be selected, traits must vary phenotypically among competing individuals, before getting stereotyped as a secondary sexual trait in a species. In fact, the variability of a secondary sexual trait may reflect, among other factors, variation in preference among individuals of the choosy sex, usually females. Courtship displays are elaborate behaviors commonly present in polygamous clades. Here we addressed the within population variation in courtship display behavior among male White-throated Manakins, *Corapipo gutturalis,* from Central Amazonia, where the species is commonly found displaying in fallen mossy logs in the understory of typical "*terra-firme*" upland forest. Then, we tested whether observed variation could be explained by variation in abiotic (environmental light) or biotic factors, either intrinsic male conditions (body mass and age) or the extrinsic social context of male displays (total number of males and female visits). Our results show extensive variation in courtship displays among males, both in total presence and display rates at logs as well as among the multiple elements from the behavioral repertoire described for the species. Among the factors that affected total exhibition rates and some of the behavioral elements were age, body mass and the frequency of female visitation to or nearby the display logs. These results support the idea of costly courtships displayed by males, particularly to males in definitive, "adult-like" plumages that incorporate more complex display elements not yet presented by males in pre-definitive, "juvenile-like" plumages. This ontogeny of male behavior suggests that practicing males may learn from more experienced males. Because female visits modulate male display rates that are costly, our results are compatible with the hotshot model proposed to explain lekking around more active males, which are selected by females.

Palavras Chave: Lek polygyny, Neotropic, female preference, male-male competition, secondary sexual character, Pipridae.

Sumário

1 **Apresentação**

2 Estudos relacionados ao comportamento reprodutivo dos animais, e sobre o processo de

3 escolha de parceiros através de características morfológicas e comportamentais exibidas

4 para atração, a seleção sexual, são de grande importância para entendermos a evolução

5 das espécies através da transferência seletiva de genes, por meio da reprodução, entre

6 gerações. Esse processo consiste em adaptações de fenótipos como características

7 morfológicas e comportamentais extravagantes úteis em lutas e competições entre

8 indivíduos de um mesmo sexo pelo acesso ao outro sexo, ou para sinalizar vantagens da

9 escolha para o sexo oposto ou sua prole. Assim a seleção sexual é responsável também

10 pela evolução de características que dão aos organismos vantagens diretamente

11 associadas à capacidade reprodutiva. Estudei características apresentadas por indivíduos

12 do Tangará-de-garganta-branca (*Corapipo gutturalis*), um pássaro que apresenta danças

13 nupciais (ou de corte) para as fêmeas. O objetivo do estudo foi comparar as características

14 das danças entre machos, testando se há variação entre elas também em resposta ao

15 contexto das exibições, como a condição do macho (sua idade, massa, o tamanho de seu

16 grupo reprodutivo), a presença das fêmeas ou a condição atmosférica ambiental durante

17 a exibição (se ensolarado ou nublado). O trabalho foi realizado em uma localidade ao

18 norte da cidade de Manaus, estado do Amazonas, em ambiente de floresta de terra-firme

19 da região Amazônica. Foi evidenciado que existe uma diferenciação em taxas de exibição

20 e presença de machos nos poleiros (ou palcos) onde eles se exibem para as fêmeas, bem

21 como diferenciação na frequência em que cada macho realiza seus elementos que

22 compõem seus repertórios de corte (o que equivaleria aos passos da dança). Dentre os

23 fatores que influenciam as frequências em que os indivíduos machos se exibem, bem

24 como a taxa de ocorrência de alguns elementos de dança específicos, estão a quantidade

25 de fêmeas presentes nas proximidades dos palcos, a massa corporal (ou "peso") de cada

26 macho e sua idade (se jovem ou adulto). Este trabalho permitiu conhecer melhor a

27 biologia reprodutiva desta espécie de ave e clarificou o papel da seleção sexual na

28 exibição de corte.

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Objetivos

Objetivo Geral

Avaliar a variação no comportamento de corte nos locais de exibição (Leks) de *Corapipo gutturalis,* em uma população localizada em uma região de floresta de terra-firme na Amazônia Central.

Objetivos Específicos

1 A – Avaliar se existe variação na taxa total de presença e exibição entre indivíduos machos de *Corapipo gutturalis.*

1 B – Caso haja variação na taxa de presença e exibição, testar ela é explicada por fatores ambientais (luminosidade), características individuais (massa e idade) e contextos sociais (presença de fêmea ou de outros machos).

2 A – Avaliar se existe variação na exibição dos diferentes elementos do repertório de corte entre indivíduos machos de *Corapipo gutturalis.*

2 B – Caso haja variação em repertório, testar se ela é explicada por fatores ambientais, características individuais e contextos sociais.

Individual cost, ontogeny and female visitation modulate the courtship behaviour of male White-throated Manakins, *Corapipo gutturalis* (Aves: Pipridae)

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Abstract. The theory of sexual selection predicts adaptive evolution of secondary sexual characters that favor mating through male-male competition and female preference. As such, studying how these interactions shape sexual traits allows understanding their evolution through sexual selection. In order to be selected, traits must vary phenotypically among competing individuals, and might be stereotyped as a secondary sexual trait in a population. In fact, the variability of a secondary sexual trait may reflect variation in preference among individuals of the choosy sex, usually females. Here we addressed the within population variation in courtship display behavior among male White-throated Manakins, *Corapipo gutturalis,* from Central Amazonia. We then tested whether observed variation could be explained by variation in abiotic or biotic factors, either intrinsic male conditions or the extrinsic social context of male displays. Our results show extensive variation in courtship displays among males, both in total presence and display time at courts, as well as among the multiple elements from the behavioral repertoire described for the species. Among the factors associated to male attendance to courts and display rates of one element, but not total display time, were age, body mass, the number of males and females at or nearby display courts. These results

support the idea of costly courtships displayed by adult males, driven by the social context experienced at courts. The observed ontogenetic changed in male display behavior suggests that practicing males may learn from more experienced males, or refrain from displaying them in order to avoid competition with territorial males. Because female visits somehow also modulate male displays that are costly, our results are compatible with both the proximate "*female preference*" and "*hotshot*" models proposed to explain lekking around more active males.

Key-words: Female preference, male-male competition, Neotropics, lek polygyny, Pipridae, secondary sexual character.

INTRODUCTION

Lek mating systems offer great models for studying sexual selection, given the high opportunity for sexual selection (Duval 2008). In lek polygyny, females visit male display courts for comparing among potential mates, who provide only genes for their offspring (Bradbury 1981). Sexual selection may operate through male-male competition or female choice, or both, and the relevance of such processes to fitness affects the behavioral strategies in which males engage in order to breed successfully (Duval 2008). Within manakins, females usually prefer older or more experienced territorial males (or alfas, in hierarchies) in displaying courtships, followed by non-territorial younger males (or betas, in hierarchies), who practice and improve courtships at visited leks (Foster 1977). In fact, male mating success at a lek increases when alfa males are present at display courts (Duval 2008). However, there are still few studies describing male traits preferred by females, or which characteristics provide higher success to males during male-male interactions (e.g. Trainer & McDonald 1995, Lukianchuk & Doucet 2014). This might be, among other factors, due to a lack of information on the degree of existing variation in traits that are potentially subjected to selection, such as male courtship displays in lekking clades. For instance, Barske et al. (2015) showed that female presence influences male performance in *Manacus*. In turn, Durães et al. (2009) and Bosholn et al. (2016) showed significant associations between male-male interactions and individual male display rates in *Lepidotix coronata*. Variation in display activity by males at different ages have also intrigued researchers, because young males also exhibit

116   courtships, engaging frequently either in solo or group displays in multiple species within

117   Pipridae. These displays are usually considered training and learning practices (Cestari

118   2000; Boyle & Shogren 2019). Yet, in order to estimate the potential of a trait to affect

119   mate choice, its associated production cost should be considered, given that it intrinsically

120   affects the ability to produce and maintain variability in the expression of traits potentially

121   subjected to strong sexual selection, which ultimately relies on regulatory mechanisms of

122   complex genetic interactions (see The Lek Paradox, Lek, Kirkpatrick 1991; reviews in

123   Kokko 2006; Byers 2010). Because low cost traits might be presented by most

124   individuals, they would not be good candidates for selection of mating partners, their

125   variation being proportional to their selection potential (Duval 2007). Changes in body

126   condition and physiological alterations in *Manacus* after displays in captivity, for

127   example, indicates that courtships in Pipridae are quite costly to males (Barske 2014),

128   suggesting that variations in these behaviors permeates female choice.

129   Display behaviors have been compared among species within Pipridae in multiple

130   studies (e.g. Prum 1992, 1994; Prum & Johnson 1996; Prum 1998; Bostwick 2000;

131   revision in Anciães et al. 2009), which have shown that behavioral repertoires are

132   extensively shared among closely related taxa, thus usually presenting strong

133   phylogenetic component in their evolution. As such, display behaviors in manakins are

134   inherited across generations within species as a result of female choice and male-male

135   competition for mating. However, despite our current knowledge on the variation in

136   display repertoire among species, consistent with their phylogenetic affinities and thus

137   suggestive of a role for sexual selection in shaping their evolution, we still know little

138   about their variability in natural populations, which factors modulate the potential

139   variation, and their consequences to male fitness (but see Trainer & McDonald 1995;

140   Lukianchuk & Doucet 2014). Uncovering such information may reveal proximate factors

141   leading to the evolutionary patterns observed within and between species, either shared

142   similarities or divergences accumulated through the evolutionary history of the family.

143   Thus, studies addressing intra-population variation in male courtship behaviors are

144   relevant for estimating the degree of variation in these traits and their selection potential.

145   With that we may inquire about factors potentially modulating the evolution of these

146   phenotypes, which will allow revealing sexual selection mechanisms by female choice or

147   male-male competition explaining, ultimately, the phenotypic diversity currently

148   observed among species (Prum 1997). For instance, the relationship observed between

149 brain size and display complexity among species within piprids suggests the importance

150 of strong sexual selection for the evolution of displays, with display elaboration

151 associated with high physiologic investment for mating acquisition (Lindsay et al. 2015).

152   Here, we address the variation and factors modulating the display behaviors of

153 male White-throated Manakins (*C. gutturalis*, Aves: Pipridae), in order to better

154 understand the role of sexual selection in their evolution. For this, we compared total

155 display rates among males, besides the display frequency of seven elements from the

156 behavioral repertoire of the species, and investigated whether observed variations could

157 be explained by environmental (abiotic) factors or by biotic individual characteristics

158 intrinsic from males or related to the social contexts during displays. We present below

159 tested hypotheses and respective predictions, considering alternative scenarios and

160 interpretations in light of sexual selection theory: First, we test (1) whether abiotic factors

161 extrinsic to the system - the light conditions reaching courts during displays, affect male

162 display rates, and predict that, if they do, ambient light drives the opportunities for

163 selection towards the evolution of the observed phenotypes, as previously suggested for

164 this and other species in the family (Endler & Théry 1995; Théry & Vehrencamp 1996;

165 Anciães & Prum 2008). However, if we do not find such association, we presume that

166 other characteristics from males and courts may affect male display activity in the species,

167 which would contradict previous studies that, nevertheless, did not account for biotic

168 factors in comparing display rates among individuals. As such, (2) if we observe

169 considerable variation among males, either in total display rate or in specific elements of

170 their repertoire, such characteristics will present high selection potential and might be

171 used for mate choice by females or through male-male interactions. In turn, low

172 variability in displays would indicate behaviors that are currently stereotyped in the

173 population, which we would expect for low cost displays that would, however, no longer

174 be useful in female choice or male-male competition for females, being already fixed in

175 the population. Likewise, (3) if variation in display rates are affected by body mass, we

176 may conclude that display behaviors are indeed costly to males, in case they are inversely

177 related to body mass or, in case they are positively related to body mass, that they reflect

178 male condition, suggesting a *"handicap"* effect (Zahavi 1975; Lindsay et al. 2015).

179 Furthermore (4) if variation in display behaviors is related to male age, we will verify that

180 display elaboration is ontogenetic, following a development through learning or

181 regulatory mechanisms in their expression, particularly for differences in male

repertoires. Such changes might be linked to physiological (e.g. hormonal) changes affecting male condition with aging or immediate responses to the social context during displays, such as the presence of females or other males, which would demonstrate that courtship behaviors would also present a delay in respect to gonad maturation, as described for male plumages in Manakins (Foster 1980). Then, (5) if we observe that display behaviors are modulated by the frequency of female visits to display courts, we may conclude that the composition (quality) and amount (frequency) of male displays are important for selection (Barske et al. 2015). Otherwise, we would conclude that measured display traits would not be primary sources of information and evaluation by females, possibly interacting with other signals such as plumage coloration, lek size or light condition during displays (Durães et al. 2009; Bosholn et al. 2016, 2019; Anciães & Prum 2008). In turn, (6) if the total number of males at courts are positively related to the total attendance and display rates of focal males, we may conclude that male aggregations at courts increases male-male competition for females (Durães et al. 2009; Bosholn et al. 2016) favoring comparison by females (Foster & Beehler 1988; Bosholn et al. 2016). In the other hand, male display rates not related to the number of males at courts would be suggestive of other factors, such as female preferences for specific displays attributes not related to male quality or social interactions at leks are prevailing in the evolution of display behaviors (Prum 1997, 2017).

Material and Methods

Study Area

The study was conducted in a continuous forest located ca. 80 km North of Manaus (2° 30' S, 60° O), at the Km-41 reserve, from the Biologic Dynamics of Forest Fragmentation Project, BDFFP. The region includes an experimental landscape composed by fragments surrounded within continuous forests in Central Amazonia, Brazil, including the km-41 reserve, stablished in 1984 with ca. 1000 ha of open trails for wildlife monitoring throughout a topographic gradient (Lovejoy et al. 1986; Soule 1986), where the study was conducted. Vegetation is typical upland *terra-firme* forest where average tree height ranges from 30-37 m, and altitude reaches 100-150 m above sea level (Chauvel et al. 1987; Laurance et al. 1999). Mean annual temperature is 26°C and

213   precipitation 2200 mm. The raining season lasts from November through April and the
214   dry season from May through October (Laurance 2001).

215

216   **Study System and Focal Species**

217   Manakins are restricted to forest habitats within the Neotropics and are well-
218   known by their usually striking sexually dimorphic plumages, with adult males holding
219   colorful ornaments and females retaining the juvenile-like greenish plumages. As for
220   most species in the family, White-throated Manakins feed on fruits and small arthropods
221   and may be seen foraging in fruiting trees from the medium strata to the canopy together
222   with other manakins or in mixed flocks. The species is distributed from Venezuela
223   through the Guianas and northern Brazil from 200 to 1100 m (Prum 1985; Meyer de
224   Schauensee 1970; Meyer de Schauensee & Phelps 1978). It is one of the smallest species
225   in the family, with ca. 8 g. Males in definitive adult-like plumage are glossy blue-black
226   with a white-throat extending to their breasts in a "V" shaped patch. They also present a
227   white patch hidden within their wing primaries, visible only when wings are open.
228   Females are olive green and light gray underneath and do not present white patches. Males
229   in juvenile-like plumage resemble females but are easy to identify during molt, because
230   of the onset of the black face mask around the eyes (Prum 1985) in their second year (MT,
231   *unpublished data*).

232   In most manakins, males engage in elaborate courtship displays in spatially
233   aggregated territories, or courts, grouped in leks. Leks are usually classified according to
234   spatial distribution (concentrated or disperse) affecting communication (visual or
235   auditory, respectively) among individuals at leks. Males may display in solitary (solo
236   displays) or in groups (multi-male displays) (Bradbury 1977, 1981; Oring 1982), which
237   might have cooperative or competitive purposes. Cooperative displays are synchronized
238   among males to increase fitness of a group member (Prum 1994), including body
239   movements and postures coordinated among males (Duval 2007). Competitive group
240   displays, in the other hand, are not coordinated, and males will rather chase each other
241   during multi-male displays (Prum 1994). White-throated Manakins lekking in Suriname
242   were described as competitive, with adult and juvenile males using the same mossy fallen
243   logs for displays (Prum 1986).

Manakin displays include vocalizations, mechanical sounds, stereotyped flights, jumps, ritualized steps and other maneuvers (Snow 1963; Sick 1967; Prum 1990, 1998). The behavioural repertoire of the courtship display described for Male White-throated Manakins is composed by seven elements displayed at or nearby courts (fallen logs), including postures, body movements, flights, vocalizations and mechanical sounds, not necessarily in a predictable order (Prum 1986; Théry 1990): "*Bill-pointing*", "*Advertisement-call*", "*About-face*", "*To-and-fro*", "*Hunched-posture*", "*Wing-shiver*" and "*Pop-tickee-yeah*". Males also engage in the "*Log-approach-display-calls*", when they fly from up in the canopy towards the log, emitting successive *"tsee"* notes that are subtle and thus difficult to detect our audio-recording. In French Guiana, Théry (1990) observed advertisement-calls described by Prum (1986) displayed by multiple and single adult males, but never during female presence, which the author attributed to dominance-related displays. More recently, Anciães & Prum (2008) studied the species in Central Brazilian Amazonia, near Manaus, addressing the relationship between either male displays and female visitation rates and the variation in available light conditions at courts, following previous studies showing an association between these factors at leks of the species elsewhere (Endler & Théry 1995; Théry & Vehrencamp 1996) and, in agreement with these studies, found that males prefer to display when sunlight reaches directly, but only partially, the court.

Altogether, these studies produced behavioural information that allow more detailed inferences regarding the variation in display behaviour and female visitation rates at leks of the species. Here, we focus on display elements presented by males at their main courts, i.e. the fallen logs and up to the midstorey immediately above it (Prum, 1986; MT, *unp. data*). Thus, all measured observations and variables are related to focal courts and areas immediately surrounding it, as further described below.

Sampling Design

The display behaviour of male White-throated Manakins was sampled during the breeding seasons of 2017 and 2018, from July through December, except by July 2018 due to the very low activity recorded at leks. Display courts had been marked and monitored previously in the study area (Tolentino & Anciães, *in review*.; TEAM Aves, Manaus). They are mossy fallen logs, usually located in relatively open understory

276 regenerating from forest gaps open by fallen trees (Prum, 1986). Before behavioural

277 observations individuals were identified with unique combinations of two-color bands

278 (Avinet Inc.) and one metallic band from CEMAVE (ICMBIO/SNA permit n° 4081/1).

279 Birds were caught in mist nets (36 mm mash, 12 x 2m) placed around courts at least three

280 days prior to focal observations. Captured individuals were weighted with 20 g spring

281 scales (Pesola Inc.), aged and sexed through inspection of skull ossification, gape and

282 molt (Johnson & Wolfe 2017). Sex of green plumaged individuals was verified through

283 molecular markers following Ito et al. (2013), using the adapted protocol described in

284 Bosholn et al. (2016).

285   A total of 10 courts (logs) were sampled but, because activity was very low or

286 absent in three of them during the first field season, we collected information

287 subsequently only in 7 courts. Observations last from six to seven hours on each court

288 separately, conducted from 10-12 non-consecutive days per month within the breeding

289 season, resulting in the observation of two focal individual (males) for about five days

290 each per month, and a total of five days of observation per male during the study, for 16

291 males; from which 11 were in definitive plumage and five in pre-definitive plumage,

292 classified as adults and juveniles, respectively. Behavioural data were recorded every five

293 minutes using animal focal sampling (Altmann 1974; revision in Bosholn & Anciães

294 2018) with binoculars (Nikon 10 x 42 mm), and all displays were video-recorded (Sony

295 highHDR-PJ200 and Nikon D7100 with 50 mm-300 mm lens) from 10 to 20 m to the

296 court behind a camouflage blind to ground truth behavioral observations and subsequent

297 analyses. During observations, the identity (color bands) of individuals; their age and sex

298 were registered; as well as their behavioural activities; both vocalizations and courtship

299 displays, including the frequency in which the court was visited by the focal individual

300 and the elements displayed; and whether displays were solo or in presence of multi-males

301 around the log, recording the number of males present on or around courts during displays

302 by the focal male, for each observation interval. The presence of females, i.e. green-

303 plumaged birds without the typical pre-definitive juvenile-like plumage including black

304 facial mask and not engaging in displays, nearby (10-20 m) the court were also recorded

305 at each observation interval. Ambient light condition was recorded following Anciães &

306 Prum (2008), indicating if the weather was mostly cloudy or sunny (sky mostly clear from

307 clouds) and, in this last case whether the court received direct sun light (sunny gaps) or

308 not (forest shade). Because males of this species have been observed to display preferably

309　under a mix of forest shade and small sun flecks reaching the display log (Endler & Thér,

310　1995; Théry & Vehrencamp 1996; Anciães & Prum 2008), we recorded light condition

311　as sunny gaps when the log was at least 80% covered by direct sunlight.

312　　　　Detected displays included all display events recorded for the focal male,

313　considering every time that it arrived at the main court or above it and started a display,

314　regardless of its duration or number of elements displayed during the event, which ceased

315　with the bird flying off the log and re-started upon a new arrival. This would include

316　male-male chase flights in which males engaged approaching or leaving the log. All

317　elements and their display frequencies were then quantified through inspection of the

318　video recordings. Only FA conducted the behavioural observations and video-recordings

319　analyzed here.

320

Data Analysis

322　　　　We first estimated total display time considering all elements together, and the

323　display frequencies per each sampled element, for each observed male. Because sampling

324　effort varied among individuals, we standardized the total display time of each individual

325　by both (i) the total sampling effort of observation (in minutes) at the court; and (ii) the

326　total time in which focal males were present at courts (either displaying or not, or male

327　attendance); whereas display frequencies for each element was standardized by (iii) the

328　total time in which the focal male displayed at the court, for each individual. With that,

329　we generated three behavioral indices for each focal individual: (a) total male attendance,

330　given by the proportion [(ii) total time present at court/(i) total observation effort at court];

331　(b) total displays during observations, or the proportion [(iii) total display time at court/(i)

332　total observation effort at court]; and (c) total displays during attendance, herein total

333　display time, given by (iii) total display time at court/total time present at court (Table

334　S1).

335　　　　Because male displays in this species was described to be modulated by prevalent

336　ambient light conditions at courts (Endler e Théry 1995; Théry & Vehrencamp 1996;

337　Anciães & Prum, 2008), we analyzed the effect of this environmental (abiotic) factor in

338　the rates of male presence and display at courts prior to testing for the effects of the biotic

339　factors intrinsic or extrinsic to the focal males. Then we tested for the biotic effects

through multimodel comparison with generalized linear models, including factors intrinsic to focal males – their age (juvenile or adult), as a proxy to maturation, and body mass (g) during mist netting a few days prior to observations; or extrinsic to them – female visitation rates (as the frequency of visits standardized by sampling effort) and total number of males present around logs (as the sum of the number of males present around courts during all observation time, standardized by total observation time, for each individual), for each focal male.

We tested for associations between total presence and display time, separately, and the rate of display of individual elements sampled from the courtship repertoire of the species described above through comparison of VIF (*Variance Inflation Factors*) values (Zuur et al. 2010). Fort this we generated a generalized linear model (GLM) to test for the contribution of each element in the total display time, thus addressing their collinearity and independence in explaining the total display time. Finally, we tested for effects of the same biotic variables in the display rate of each individual element, considering for this only those elements that passed the VIF analysis (values < 3). In all comparisons we used generalized linear models (GLM) with a Gaussian error distribution and VIF, implemented in packages lme4 and stats4 in R 3.5.2 (R Development Core Team, 2019). Best models were selected through the lowest AIC (Akaike Information Criterium, Akaike, 1975) values and similar models were considered for delta AIC values equal or smaller than two (Burnham & Anderson 1998).


Results

Table S1 summarizes the total sampling efforts by individual, individual and their behavioural activities, for all the 16 males observed, 11 of which were adults and five juveniles according to plumage patterns. In all seven courts, males were observed displaying either in solo (adult males) or in multi-male displays of up to three juvenile males, and some males of either age class displayed in up to three different display courts. There was variation among individuals in their attendance and display times at courts, as well as in the rates in which each element of the courtship repertoire was displayed (Figure 1). Two of the 16 observed individuals were present at courts and displayed considerably more than other males, and four males displayed during the entire time while present at the courts. Only adult males (i.e. those in definitive plumage) received female

visits during observations. The frequency in which each element was displayed also varied among males. There was also variation in the number of elements displayed by individuals, from two or three elements to five or six per individual, and only one male (number 7, adult) displayed all elements included in the sampling protocol during the study (Figure 2).
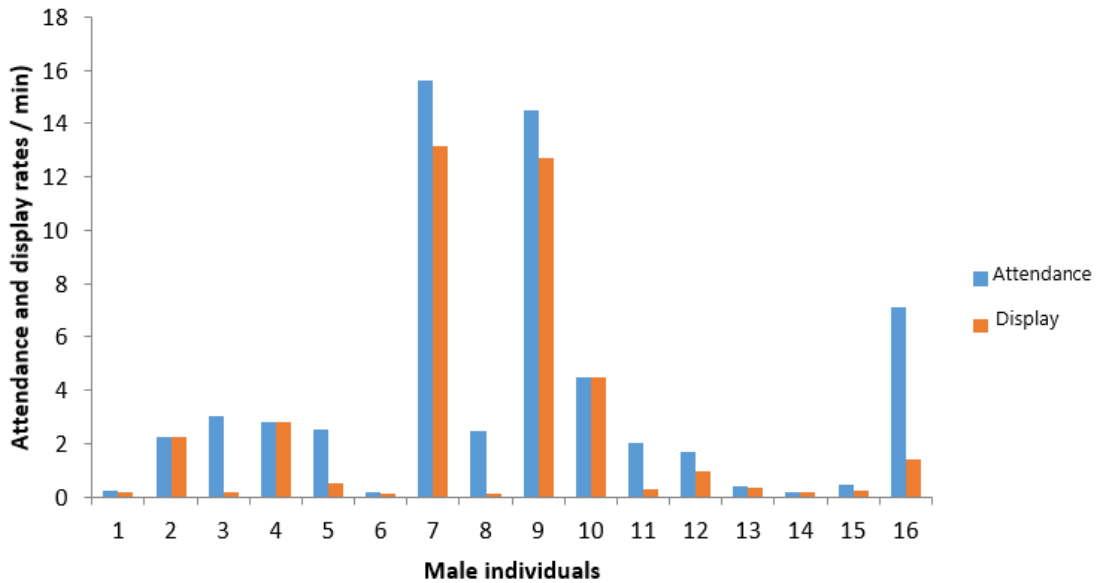
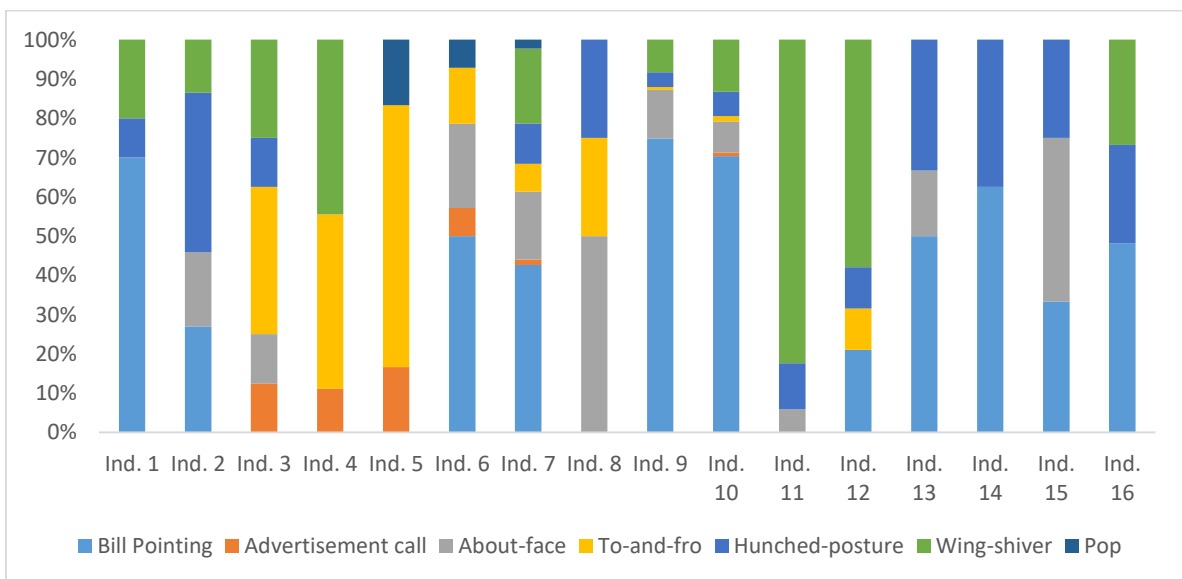Figure 1: Male presence and display rates for the 16 male *Corapipo gutturalis* observed. Adults males: 1,2,3,5,7,9,10,11,12,14 and 16 / Juvenile males: 4,6,8,13 and 15.

Figure 2: Display frequency for each element of the courtship repertoire sampled for the 16 male *Corapipo*

gutturalis.

385

386   Male attendance was positively associated to female visitation at courts (GLM: *t-*

387 *value* = 5.23, *P* < 0,05, Figure 3) and marginally associated with the total number of

388 males at courts (GLM: *t-value* = 1.99, *P* = 0,07), but these variables did not explain total

389 display time (*t-values > 0,23*; all *P > 0.05*). In turn, male age and body mass were not

390 associated to male attendance nor total display time at courts (*t-values > 1.37*; all *P >*

391 *0.05*) and, likewise, available light conditions during observations did not affect male

392 attendance nor total display time at courts (*t-values > X*; all *P > 0.05*). All models for

393 male attendance and total display time at courts are summarized in Table 1.
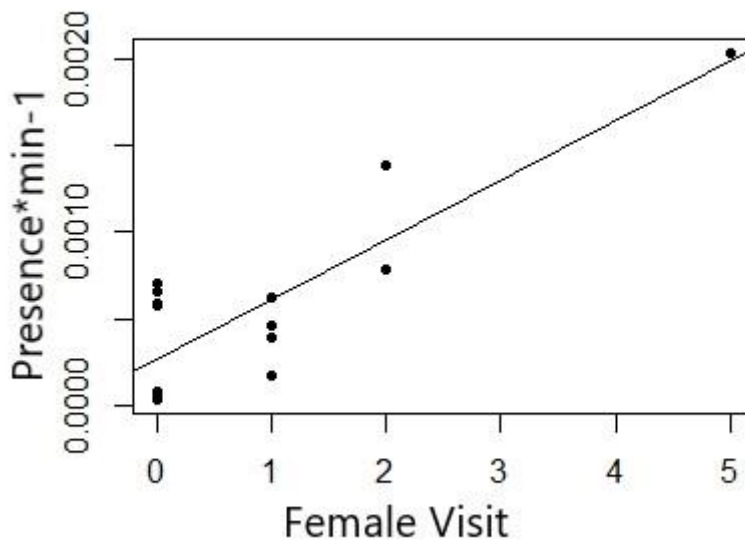
394

395 Figure.3: Associations between male presence and female visits to courts.

396

397   Only three behavioural elements from the courtship repertoire presented

398 independent VIF values (*"About-face"* VIF = 1.60; *"Wing-shiver"* VIF = 1.20; e

399 *"Hunched-posture"* VIF = 1.41). Among these, "*To and Fro*" and "*Wing Shiver*" were

400 displayed at rates inversely related to male attendance and total displays at courts (GLM

401 *t-value = -3.03* and *-2.99*, respectively; *P < 0.05*), whereas the "*Hunched Posture*" was

402 displayed at rates marginally and inversely related to male attendance to courts (GLM: *t*

403   *value = -1.96, P = 0.086*) (Figures 4a,b). In turn, the element "*About-face*", in which

404   males flip backwards, was the only element associated with male age, body mass and the

405   number of males during displays; as it was displayed at higher rates by adults and lighter

406   males (GLM: *t value* = 3.54 and -3.94, respectively; *P* < 0.05), that displayed in the

407   presence of more males (GLM: *t value = 2.36 , P = 0.05*), and tended to display in the

408   absence of females (GLM: *t value = -2.09 , P = 0.075*) (Figure 5a,b). This element was

409   also displayed at higher rates when vegetation shade illuminated courts, (GLM: *t-value =*
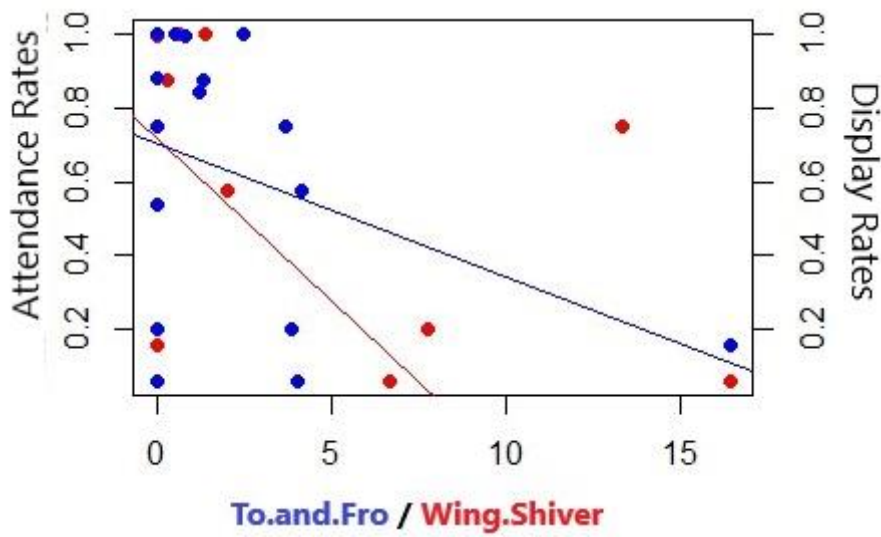
410   *X, P = X*, Figure 6).

411

412   a)
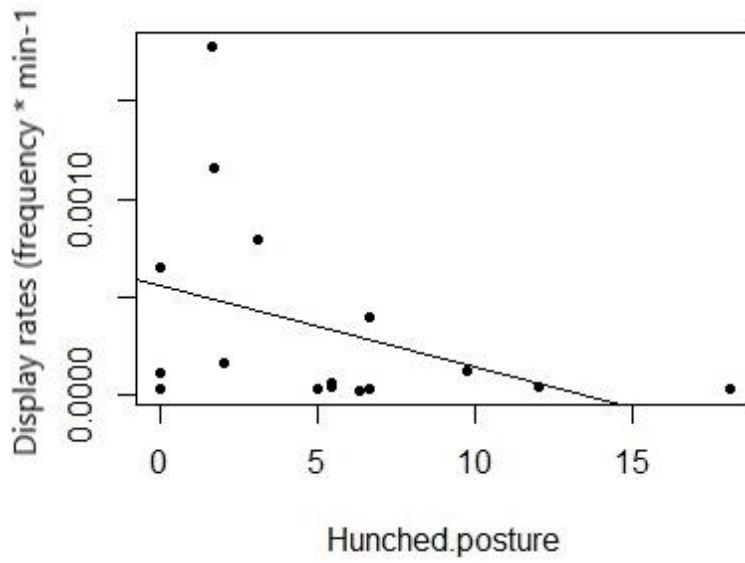
413

414   b)

415

416   Figure 4: Association between total display time and the display rate of (a) "*Hunched-Posture*" and (b) "*To*
417   *and Fro*" (in blue) and "*Wing Shiver*" (in red) with male attendance (right axis) and total display time (left
418   axis) at courts.
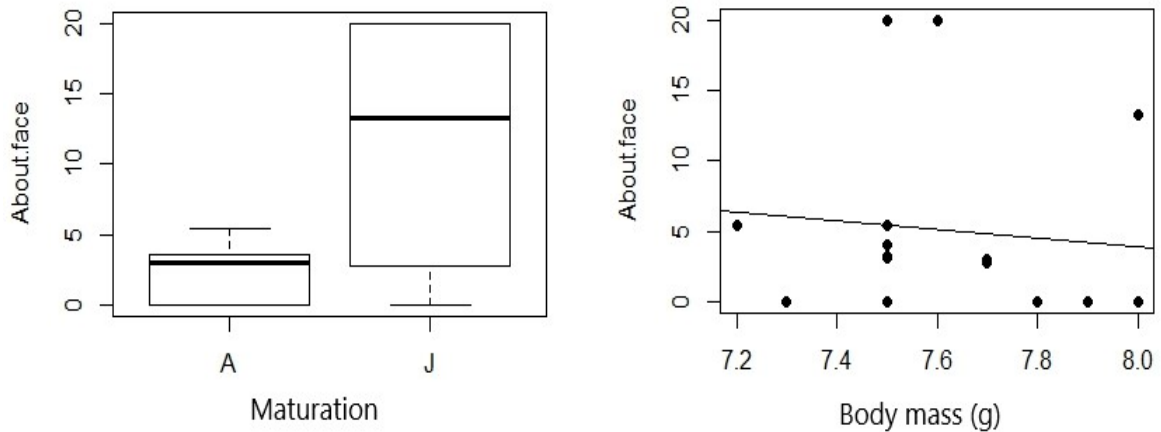
419

420

421

422

423

23

424   a)

425

426

427   Figure 5: Associations between display rate of the element "*About Face*" with (a) male age (adults in black
428   and juveniles in gray); body mass the social context (other males in black and females in grey) during
429   displays, and under the available light conditions (cloudy in black and vegetation shade with sunny gaps in
430   grey) during observations.

431

432   **Discussion**

433   　　We found marked variation in male attendance and display rates at courts in the

434   studied population of *Corapipo gutturalis*, which extends to individual behavioural

435   elements of the courtship repertoire described for the species (Prum 1986; Théry 1990).

436   Considering that selection requires trait variability among individuals, these results

437   corroborate the role of male courtships predicted in sexual selection (Prum 1992, 2012).

438   Because some of the behavioural elements of the courtship repertoire were considerably

439   variable among males, our results suggest yet variability of preferences among females,

440   as predicted by sexual selection models based on female preferences (Kirkpatrick & Ryan

441   1991; Anderson 1994; Prum 2010, 2012). The stereotypy of secondary sexual traits in

442   populations (or species) might result from strong directional sexual selection, while

443   differentiation among traits under selection would be explained by the maintenance of the

444   genetic variability associated to their expression, which is a central idea of "*The Lek*

445   *Paradox*" (Kirkpatrick 1982; Pomiankowski 1995; Tomkins 2006; revision in Kokko

446   2006).

447   　　The ambient light quantified during observations did not explain total display

448   rates, meaning that changes in the prevailing light conditions around courts did not affect

449   total activity rates (either total attendance or displays) at courts. This result opposes

associations found in previous studies showing that males prefer to display during forest shade with small sun flecks reaching directly the courts, which enhances plumage conspicuity (Endler & Théry 1996; Tori et al. 2008; Anciães & Prum 2008), including the studied population. Such variation among results might reflect differences in data analysis and sampling design, given that our study focused on the attributes of individual courtship displays sampled for each individual as sampling unity, without comparing light conditions among all observation intervals sampled, which likely rendered reduced accuracy and power to the analysis than in previous studies designed specifically for this goal. Only large variation in the proportion of available time under each light condition would potentially lead to an association of this variable to male activity rates. As such, we did not control for effects of ambient light in subsequent analysis, warranting us the interpretation of our results according solely to the variation in measured biotic variables, either intrinsic (body mass and age) or extrinsic (female visits and total males at courts) to observed males. In fact, we applied a framework of behavioral comparison that could change interpretation of the previous studies mentioned above, which did not consider biotic factors affecting male display behavior. The significant effects of shady light conditions on the display rate of one specific element, the *About Face*, nevertheless, suggests that males rely on habitat cues for displaying specific subsets of their behavioral repertoire at leks, which is also compatible with non-significant results when the general repertoire is evaluated.

Males that attended and displayed at higher rates at courts were, in general, adults during the study, whereas only the oldest males, banded in 2009, displayed all behavioural elements described for the species. These data suggest higher investment of adult males in courtships, as would be expected considering that juveniles would not be able to copulate, being restricted to training these behavioural elements. Nevertheless, in polygynous lek systems studied among manakins, males in pre-definitive plumage that are considered juveniles, are frequently sexually mature, a phenomenon described also for other birds as "*delayed plumage maturation*", suggested to prevent retaliation from older males towards younger males attempting to copulate (Rohwer et al 1983; Foster 1987, Chen et al. 2018). Even in the event that green-plumaged males studied here were sexually mature and potentially could copulate, their reduced display rates suggest lower investment or opportunity to copulate (direct displays to females), as it would be expected for individuals during training at courts. In fact, these males received no female visits

during the study, which would be typical of satellite courts (Cestari 2003), despite the fact that in our study the courts were held by definitive plumaged males, not only green-plumaged males, although these could receive visits and opportunistically copulate, as recently observed in the congeneric *C. altera* (Boyle & Shogren 2019).

Female attendance to courts tended to be positively associated to male attendance, as it would be expected when female choice is considered a central part of the social interactions taking place in sexual selection (Fisher 1932; Kirkpatrick & Ryan 1992; Prum 2012). Considering that male presence at display logs precedes courtships, our findings suggests that female presence drive male attendance to courts, in order to compete for females, suggesting that male displays are then used by females to select males in the breeding season. This is reinforced by the observation that female visits seem to modulate male activity rates for adults, but not for juvenile males (which did not receive female visits). The total number of males at courts was also associated to the activity patterns of focal males. Together, these results support a role of both the "*hotshot*" model of lek evolution, in which the shape and amount of male displays would be favored by female choice and explain male aggregations around males that are more visited by females (Beehler & Foster 1988), and the "*female preference*" model (Bradbury 1981; Bradbury & Gibson 1983) predicting social aggregations that favor male comparison by females, as expected if females preferred to visit larger aggregations to ease comparison and selection, and indeed observed in our study and elsewhere (Durães et al. 2009; Bosholn et al. 2016). This is also corroborated by recent data for the same population in which other information about male crowding affects individual male activity rates, such as the total number of males that share the court non-concomitantly within the breeding season (Tolentino et al. *in review*).

Three out of the seven behavioural elements described for the species (Prum 1986; Théry 1990) were displayed at rates not inflated by the others, i.e. provided independent information about male displays in comparison to remaining elements, they were: "*Wing-Shiver*", "*About-Face*" and "*Hunched-Posture*". Considering that the first two elements are more complex or elaborate (Lindsay et al. 2015), as they include walking backwards opening wings alternately in a coordinated motion towards females (if present); flipping forward and backwards, respectively, and are displayed when females are present (but non-exclusively) we can infer that they are relevant in female choice for mates. The observation that one of these elements, *About-face* (in which males flip forward and

backwards), was also associated with reduced body masses and, as such, could be energetically costly to males, corroborates their probable relevance for male choice (Darwin 1871; Fisher 1930; revisions in Anderson 1994; Prum 2010). The same element is displayed at higher rates by adult males, indicating an ontogenetic component in the elaboration of display behaviour in the species. Furthermore, this suggests that only adult males invest in displaying more complex and costly displays, which are displayed towards females likely in response to their own preferences.

Because increased display rates of specific elements are positively associated with total male display time in two elements (*Wing-shiver* and *To-and-fro*), and to male attendance at courts in another (*Hunched-posture*) our data indicates that the behavioural repertoire of the species involves less complex elements displayed at reduced energetic costs by both juveniles and adults, towards more elaborate complex elements displayed only by adults (*About-face*), which nevertheless is displayed regardless of total display effort in which males engage. Higher investment by adult males in displaying this element would be compensated by increased chances to mate and increase individual fitness, explaining their evolution through female choice (Kirkpatrick & Ryan 1991; Anderson 1994; Herron & Freeman 2014). As this display is apparently energetically costly to males, as the more the males displayed it at courts, the lower their body mass are, it furthers corroborates the role of sexual selection on it, because low cost traits would not provide information on the quality of individuals bearing it (Zahavi 1975), as most individuals would be able to present similar trait values and as such not being useful for comparison and selection among potential mates (Darwin 1871; Anderson 1994). It also agrees with previous data showing that courtships displayed by manakins are indeed costly (Lindsay et al. 2015; Barske et al. 2015). The role of differential repertoire among males of different age classes, however, still requires further investigation to address e.g. whether juvenile-like plumaged birds refrain from displaying part of the species repertoire as a result of cooperative coalitions, in which multi-male crowding would maximize individual fitness of territorial males, and thus lead to increased female visitation to multi-male coordinated displays (Duval 2007; Jones et. al. 2014), or whether they represent ontogenetic changes in the display repertoire related to male ability to compete, rather than cooperate, for mating.

We observed variation in total attendance to courts and display rates among males and that the relative frequency in which they display each element of the repertoire

549   described for the species also varies considerable among males. We also showed that

550   biotic factors such as male body mass and female attendance are associated to the

551   observed variation. The variation in total display rate was nevertheless associated to the

552   variation in the display rate of part of these elements, one of which was associated to male

553   age. The observed variation may affect male body mass, suggesting a high cost associated

554   to displays. Because female presence and male age modulate courtship displays of male

555   White-throated Manakins, and that they are energetically costly for males, we conclude

556   that those are important attributes used for mate choice through female preference, and

557   likely for *hotshots*, in this species. The observation that male attendance to courts relates

558   to the number of males present at courts suggests further a role of male-male competition

559   and, as such, for *female preference* for male crowding in lek evolution.

560

Conclusion

562   The present study showed male display traits that are potentially advantageous for

563   male selection by females in *Corapipo gutturalis*, i.e. that are directly associated with

564   mating ability, in contrast to benefits for survival (Darwin 1871; Prum 2012). Despite not

565   finding influence of ambient light conditions on general male activity at courts, we found

566   that one element of the repertoire was displayed at higher rates during the same light

567   conditions associated with higher display activities by males of this species previously

568   observed. Our data also show that the social context of displays modulates male displays

569   at courts, particularly the number of males present at courts during male displays and, to

570   a lesser extent, female presence. These results corroborate that both intra- and intersexual

571   selection shapes the evolution of elaborate phenotypes such as the complex displays of

572   manakins. Given the marked differences in the composition of elements and the amount

573   of displays exhibited by individual males at courts, modulated by multi-male and female

574   presence at or nearby courts, with associated costs to body mass, we conclude that these

575   displays might be functional cues of male quality for females, representing their effort to

576   obtain partners. Furthermore, we verified ontogenetic changes in both display

577   composition and intensity, varying from less elaborate in juvenile to more complex

578   displays exhibited in higher frequencies in adult males. As such the recorded displays are

579   likely particularly costly for adults, who would make higher investment in increasing

580   individual fitness through mating with multiple females, while juveniles spent their time

581   likely training less elaborated displays.

Overall, our data support the role of female choice as a proximal driver in the evolution of courtship displays in *Corapipo gutturalis*, and that the social dynamics of males at leks likely results from female preferences for larger aggregations favoring comparison among competing males and their display features *per se*. These conclusions would thus support a role of both the "*hotshot*" model of lek evolution favoring crowding around quality males, and the "*female preference*" model for increased aggregations, to begin with. Nevertheless, our study does not allow for direct conclusions on alternative roles of group displays nor female search strategies in the species, at least not at the spatial scale of the analysis currently employed. The fact that these factors modulate individual male displays at courts, particularly male crowding, is compatible with intrasexual selection driving mate choice, such as in dominance hierarchies and spatially dynamic cooperation systems, when individual males use multiple courts as observed here. Intersexual selection would then compare among males sharing courts. Additional data would be needed to investigate alternatives such as male-male competition acting among multiple courts and leks, and direct data on female preferences for individual display elements and their role in male-male coalitions among adult- and juvenile-like plumaged birds.

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Suplementary Information

Table S1: Age, body mass, absolute frequency of each element and summed for all elements or individuals (T), sampling observation effort (Obs), total presence and display time in minutes and respective presence and display minute-rates at courts, proportion of presence time with displays, total female visits (F) and total males present (M) during displays for each male individuals (Ind.) observed.

Ind.	Age	B. Mass (g)	Bill point	Adv call	About face	To and fro	Hunched posture	Wing shiver	Pop	T	Obs (min)	Presence (min)	Display (min)	Presence rate	Display rate	F	M
1	A	8	7	0	0	0	1	2	0	10	5755	0.266	0.2	4.62E-05	3.47E-05	0	1
2	A	7.5	10	0	7	0	15	5	0	37	5695	2.266	2.26	3.98E-04	3.96E-4	1	3
3	A	7.5	0	1	1	3	1	2	0	8	4310	3.016	0.183	7.00E-04	4.24E-05	0	4
4	J	8	0	1	0	4	0	4	0	9	4310	2.83	2.83	6.57E-04	6.56E-14	0	3
5	A	7.8	0	1	0	4	0	0	1	6	4310	2.55	0.516	5.92E-04	1.19E-4	0	1
6	J	7.6	7	1	3	2	0	0	1	14	4310	0.2	0.15	4.64E-05	3.48E-05	0	1
7	A	7.7	96	3	39	16	23	43	5	225	11315	15.616	13.166	1.38E-03	1.16E-3	2	9
8	J	8	0	0	2	1	1	0	0	4	4310	2.5	0.15	5.80E-04	3.48E-05	0	1
9	A	7.2	417	0	69	4	21	46	0	557	7145	14.5	12.7	2.03E-03	1.77E-3	5	2
10	A	7.5	159	2	18	3	14	30	0	226	5695	4.5	4.5	7.90E-04	7.9E-4	2	4
11	A	7.5	0	0	1	0	2	14	0	17	11450	2.016	0.316	1.76E-04	2.75E-05	1	1
12	A	7.3	4	0	0	2	2	11	0	19	5755	1.7	0.983	4.66E-04	1.71E-4	1	1
13	J	7.7	3	0	1	0	2	0	0	6	5695	0.416	0.366	7.30E-05	6.42E-05	0	1
14	A	7.9	5	0	0	0	3	0	0	8	4230	0.166	0.166	3.92E-05	3.92E-05	0	1
15	J	7.5	4	0	5	0	3	0	0	12	5695	0.466	0.25	8.18E-05	4.38E-05	0	3
16	A	7.5	27	0	0	0	14	15	0	56	11450	7.116	1.433	6.21E-04	1.25E-4	1	4
T			739	9	146	39	102	172	7	1214							

Table S2: Elements matriz correlacion.

	Bill.pointing	Advertisement.call	About.face	To.and.fro	Hunched.posture	Wing.shiver	Pop
Bill.pointing	1.00000000	0.2078538	0.2672025	-0.05601229	0.08690982	-0.21673829	0.4409071
Advertisement.call	0.20785380	1.0000000	0.4285049	0.91617551	-0.31352141	-0.10034896	0.7551091
About.face	0.26720252	0.4285049	1.0000000	0.38625928	0.04057370	-0.23170631	0.5184748
To.and.fro	-0.05601229	0.9161755	0.3862593	1.00000000	-0.31091889	-0.12884367	0.5775620
Hunched.posture	0.08690982	-0.3135214	0.0405737	-0.31091889	1.00000000	0.02011808	-3730567
Wing.shiver	-0.21673829	-0.1003490	-0.2317063	-0.12884367	0.02011808	1.00000000	0.2040200
Pop	0.44090712	0.7551091	0.5184748	0.57756197	-0.37305666	-0.20401996	10.000.000

Table S3: Data analysis GLM variables correlations with Presence and Display by Presence.

	GLM - Presence		GLM - Display/Presence	
	t value	P	t value	P
Age	0,372	0,717	0,594	0,565
Body mass	1,28	0,226	0,861	0,407
Total number of males	1,99	0,072	0,233	0,82
Female visitation	5,234	**0,000279**	1,374	0,197

Table S4: Data analysis GLM elements of display correlation with Presence, Display and Display/Presence rates.

	GLM - Presence		GLM - Display		Display/Presence	
	t value	P	t value	P	t value	P
Bill.Pointing	0,707	0,499	1,095	0,305	0,398	0,7
Advertisement.call	0,28	0,786	0,41	0,692	2,253	**0,054**
About.Face	0,362	0,726	0,467	0,653	-0,484	0,641
To.and.Fro	-0,481	0,643	-0,604	0,562	-3,025	**0,016**
Hunched.Posture	-1,956	0,086	-2,636	**0,029**	-1,148	0,284
Wing.Shiver	-0,565	0,587	-0,787	0,453	-2,938	**0,018**
Pop	-1,02	0,337	-1,513	0,168	-0,833	0,428

Table S5: Data analysis GLM variables in correlation with all elements of display

	GLM - Bill Pointing		GLM - Advertisement call		**GLM - About Face****		GLM - To and Fro		GLM - Hunched Posture		GLM - Wing Shiver		GLM - Pop	
	t value	P	t value	P	t value	P	t value	P	t value	P	t value	P	t value	P
Age	-0,516	0,621	0,277	0,79	3,535	**0,00954**	0,423	0,685	-1,399	0,205	-0,483	0,644	1,471	0,184
Body mass	-1,142	0,29	-1,994	0,0864	-3,94	**0,0056**	-1,5	0,177	-0,473	0,651	0,114	0,912	-1,783	0,117
Total number of males	1,812	0,112	1,194	0,271	2,362	**0,05017**	1,018	0,342	0,127	0,902	-1,337	0,223	1,35	0,219
Female visitation	-0,763	0,47	-1,857	0,105	-2,086	0,075	-1,514	0,174	-1,424	0,198	0,543	0,604	-1,138	0,292

Table S6: VIF (Variance Inflation Factors) correlations with Display/Presence rates and frequency elements of presence and display.

```
vif(Display/Presence - B)
   bill.p_B adv.call_B  ab.face_B   to.fro_B   h.post_B    wi.sh_B      pop_B
   3.012445 119.504004   2.921239  65.737035   2.403788   1.785130  71.526995
vif(Display/Presence - C)
   bill.p_C adv.call_C  ab.face_C   to.fro_C   h.post_C    wi.sh_C      pop_C
   2.123681  16.479763   1.608931  12.640033   1.411324   1.204492   4.156337
```