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Original Article

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Testing hypotheses for male aggregations in lek and the implications for sexual selection in the White-throated manakin, *Corapipo gutturalis* (Aves: Pipridae)

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ABSTRACT

To understand male spatial aggregation in lek systems, questions have focused on whether males aggregate in areas with higher female abundance, around males that attract more females, or because of a female preference for certain male. For this, we investigated how social organization and male–male interactions are associated with female visitation in leks of the white-throated manakin (*Corapipo gutturalis*). Specifically, we evaluated whether females prefer higher-ranked males (based on the fidelity to court, display, and male age) and high-activity courts, as predicted by the hotshot hypothesis. In addition, but not mutually exclusive, we evaluated whether multi-male visitation at court and/or shorter spatial aggregation of courts attracted more females. We found that the highest-ranked males received significantly more female and male visits. However, the total activity at courts did not predict female visitation to males, but did predict male visitation to males. Furthermore, female visitation at courts was not predicted by the proportion of multi-male visitation at courts but by spatial aggregation of courts. These results suggest that the hotshot hypothesis illustrated by the male rank at court explains female visitation and male aggregation in leks of this species, generating a system in which males tend to compete for the highest rank in the court.

Keywords: Central Amazonia; courtship behaviour; female preference; hotshot; male interaction

INTRODUCTION

In lek mating systems spatially aggregated males perform ritualized courtship displays mainly for attracting females, typically without defending resources for females or contributing to parental care (Emlen and Oring 1977, Bradbury and Gibson 1983). Leks are, in part, thought to have evolved because females prefer male aggregations as they provide the opportunity to compare prospective potential mates (Bradbury and Gibson 1983, Wiley 1991). Given the substantial degree of competition among males, leks are often characterized by a strong reproductive skew (i.e. a few individuals sire many offspring) and consequently are characterized by strong sexual selection (Höglund and Alatalo 1995). Despite an extensive number of hypotheses regarding the evolution of lekking, debate has persisted on the proximate drivers and fitness benefits of male lekking behaviour.

Among the several hypotheses that have been generated to explain the evolution of lekking systems, the hotspot model suggests that male aggregation is driven by female patterns of space use in areas where leks form (Bradbury and Gibson 1983). These areas tend to have high resource availability and may be the result of the overlap of female home-ranges. The hotshot model, in turn, predicts that males will aggregate around a high-success male that attracts a greater number of females (Beehler and Foster 1988). Finally, the female preference model suggests that lek aggregation is driven by female preference to mate in large leks, where males may be easily compared (Bradbury 1981).

The factors that influence male aggregation have been studied across a diversity of lekking taxa (see Höglund and Alatalo 1995) and results obtained vary according to the study scale and species (e.g. Jones and Quinnell 2002, Young *et al.* 2009, Isvaran

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and Ponkshe 2013). A few studies addressing lekking behaviour in manakins, small neotropical birds within Pipridae, have proposed different reasons for male aggregations. The hotspot hypothesis for lekking has been tested in three species of manakins, and areas with higher fruit concentrations (hotspots) were found to have a higher number of leks (Ryder *et al.* 2006, but see Durães *et al.* 2007 on *Lepidothrix coronata*, from the same study area, for which female hotspots did not explain male aggregations). The potential fitness benefits of male aggregation include lower copulation disruption rates (Théry 1992) and higher female visitation rates (e.g. *Chiroxiphia lanceolata*; DuVal *et al.* 2018). These discrepancies suggest that specific life history traits and ecology probably influence the immediate drivers of male aggregation.

The white-throated manakin, *Corapipo gutturalis* (Linnaeus 1766), lives in the understorey of tropical rain forests and is widely distributed throughout the Guyana Shield (Kinwan and Green 2011). The breeding season lasts from late August to December, but may extend until January (Kinwan and Green 2011). Like most manakins, the species exhibits strong sexual dimorphism. The male is blue-black with a prominent white throat and white patches under the wings (Supporting Information, Fig. S1A), while females (Fig. S1B) and juvenile males are a drab grey green. The leks are classified as dispersed and formed by five to eight males, which use the court for displaying alone or in small groups of up to three males at the same time on the display courts, but most of the time in the absence of females (Prum 1986, 1990, Théry 1990, Anciães and Prum 2008). The ritualized displays occur typically in mossy fallen logs (Fig. S1C), such as in other species of *Corapipo*. Although the social organization of *C. gutturalis* has been studied by Prum (1986) and Théry (1990), no consensus has been reached regarding the role and function of multi-male displays. Théry (1990) suggested that *C. gutturalis* display courts have exclusive owners, which was based on the observation of copulation after solitary displays. However, Prum (1986) suggested that *C. gutturalis* males form mobile leks, in which males leave their exclusive leks to perform group displays, thus being able to compete for females.

Here, we investigate the social organization of *C. gutturalis* in the Central Amazon, Brazil, and test two hypotheses related to proximate drivers of male aggregations. To understand the mechanisms underlying male aggregation and female visitation rates, we studied the spatial–temporal distribution of males during three breeding seasons. We first evaluated if the hotshot model explains male spatial aggregation in the species, i.e. that low-rank males aggregate around a single high-rank individual given that it attracts more females. As such, we predicted that (i) high-ranked males should receive more visits from females and males at court; and (ii) the proportion of display activity at courts will be driven by the number of males using a court, excluding the activity of the highest-ranking male, given that males compete for the hotshot position. As such, activity should be higher at courts with males of higher activity, and hence more attractive to other males as well as females. We then tested if female preference drives lek spatial aggregation in the species, predicting that: (iii) courts with higher multi-male (resting, vocalizing, or displaying) visitation proportions (social aggregation) will also receive higher female visitation; (iv) females will prefer neighbouring courts that are closer to each other (spatial aggregation), as it would facilitate comparison among males; and (v) courts with a higher proportion of activity will receive greater female visitation.

MATERIAL AND METHODS

Sudy area

During 2016–2018, we sampled display courts of white-throated manakins within the reserve of the Biological Dynamics of Forest Fragments Project (BDFFP). The BDFFP is an experimentally fragmented landscape located in the central Brazilian Amazon, about 80 km north of Manaus, AM (2°30′S, 60°W). The BDFFP area spans ~1000 km^2 and contains large tracts of continuous, fragmented, and secondary forests (Laurance *et al.* 2018). We conducted our research in the continuous forest named Reserve KM41 (Fig. 1). This reserve is composed of ~10 000 ha of the continuous forest with a trail-grid of 1000 ha. The area is classified as a *terra firme* forest, is not seasonally flooded, and has an average elevation of 100–150 m a.s.l. Average annual rainfall in the area is ~2200 mm, and the dry season lasts from July to October (Laurance *et al.* 2002). The forest canopy is ~30–37 m tall, although some trees reach 55 m (De Oliveira and Mori 1999, Laurance *et al.* 2010).

Data collection

All mark–recapture efforts and behavioural observations were conducted at the display courts. In this study, we defined a court as an area with a fallen log where one or more males congregate to perform courtship displays. Each display court was marked with GPS (Garmin; GpsMap 60CSx) and the pairwise distance (in metres) between courts was calculated in Qgis 3.2.3 (Qgis Development Core Team).

We captured individual white-throated manakins at each display court using three 12 × 3-m ornithological nets (Ecotone Mist Nest 716/12P, Gdynia, Poland) that were placed surrounding the courts in a triangular formation. The mist nets stayed open on average between 6 a.m. and 1 p.m. for a total of at least 3 days at each display court per breeding season. We marked all individuals with unique combinations of colour bands (Avinet Color Leg Bands; Darvic; XF, Portland, ME, USA) and metal bands supplied by the National Center for Research and Conservation of Wild Birds (CEMAVE) and the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA).

We aged and sexed individuals in the field using plumage (i.e. moult limits; Ryder and Durães 2005) and additional standard criteria, such as cloacal protuberance, brood patch, and colour gape. To identify the sex of individuals with grey-green plumage, we collected 50-μL blood samples with a disposable hypodermic needle and heparinized microcapillaries via brachial venipuncture. Blood samples were stored in 95% ethanol in 1-mL microtubes. Molecular sexing was subsequently performed following the methodology of Ito *et al.* (2003), and we used individuals of known sex (i.e. males in definitive blue-black plumage) as controls.

We observed male displays during each breeding season (2016, 2017, and 2018), between August and January, thus covering the breeding season described for the species. We conducted at least

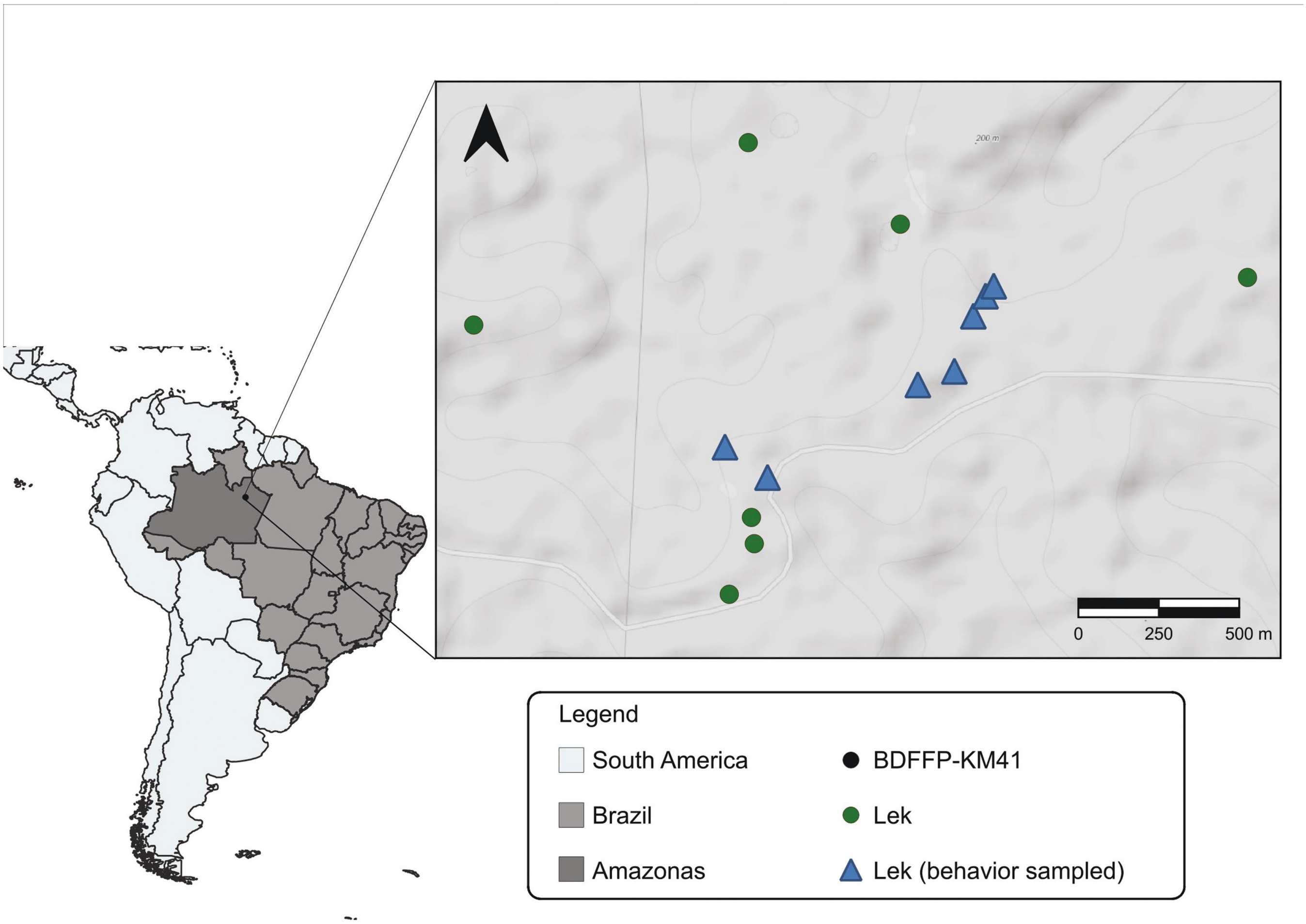

Figure 1. Location of the KM41 camp reserve, Biological Dynamics of Forest Fragments, Amazonas, Brazil.

3 days of 6-h behavioural observations ($N \cong 18$ h per court) in each breeding season. In an area of ~200 ha, we found 14 courts. Behavioural observations were conducted in the seven most central courts of the area (Fig. 1), and the total number of courts was used to calculate the spatial aggregation of the sampled courts. In 2016, five display courts were observed by M.T.; in 2017 two were added totalling seven display courts, observed by M.T. and F.A., and in 2018 the same seven were observed by F.A. To reduce interference from the observer to the site, we used binoculars and a camouflage blind placed at least 10 m from the focal display court. We recorded court activity using a video camera during observations to backup focal observations and to obtain ground truth observer data. During each 5-min interval of continuous focal observation (Altmann 1974, Bosholn and Anciães 2018), we recorded the number of birds, their sex and colour band identification, the observed display frequency, vocalizations, the number of female visits, and the respective strata of the individuals visits (i.e. on fallen logs, in the canopy, or in the understorey).

Description of variables

We calculated the key variables to evaluate our hypotheses from observational data (Table 1). Following the methodology of Bosholn *et al.* (2016) and given that we collected data in 5-min intervals, this interval formed the base unit to calculate the variables. For the predictor variables related to the hotshot hypothesis: (1) **Male Rank** (Equation 1), we generated an index that accounts for site fidelity, and the activity and age of the individual in the court, which are considered important factors for categorizing males with respect to their possible success in attracting females (i.e. Jones *et al.* 2014, Duval *et al.* 2018), which is defined as:

$$\begin{aligned} Male\ Rank = {} & Fidelity\ of\ male\,(x) \\ & \times Proportion\ of\ Male\ Display\,(x) \\ & \times Age\ class\ of\ male\ \ (x) \end{aligned} \tag{1}$$

For this, the **Fidelity of male (*x*)** was measured by Equation (2), where *number of male (x) observation intervals in the court* is the total number of intervals in which the male was observed (rest, vocalization, or display elements) at the court in the breeding season; *number of observation intervals in the court* is the total number of intervals in which the court was sampled, and *number of courts the male (x) observation* is the total number of courts where the male was observed during the breeding season:

$$Fidelity\ male\,(x) = \frac{\left(\dfrac{number\ of\ male\ \ (x) observation\ intervals\ in\ the\ court}{number\ of\ observation\ intervals\ in\ the\ court}\right)}{number\ of\ courts\ the\ male\ \ (x)\ \ observation} \tag{2}$$

Table 1. Description of the variables used to generate models to evaluate the hotshot and female preference hypotheses.

Hotshot model	
Response variable	*Description*
Proportion of female visitation to male	The number of intervals that females were observed to visit the male (x) on a court in a breeding season, divided by the total number of intervals sampled of court in a breeding season
Proportion of male visitation to male	The number of intervals that another male was observed to visit the male (x) on the same court in the same breeding season, divided by the total number of intervals sampled of court in a breeding season
Predictor variable	
Male rank (Index)	Based on the permanence (fidelity site), activity [proportion of male display (x)], and experience of male individuals [age of male (x)], we created an index to rank them. For more details see Equations (1) and (2)
Proportion of activity at court	To estimate the activity at court, we used the activity (vocalization and display) of all males (for more details see equation 3). Excluding the activity of the male (x), the focal male
Female preference model	
Response variable	
Proportion of female visitation at court	The number of intervals in the day that a female was observed visiting the court in a particular breeding season divided by the total number of intervals observed in the day for the court in a particular breeding season
Predictor variable	
Spatial aggregation of court	Average distance (m) of the three display courts nearest to the display court observed
Proportion of multi-male visitation at court	The number of intervals during which more than one male was simultaneously observed (engaged in rest, vocalization, or display elements) around the court during the day, divided by the total number of intervals sampled in the day in the court in a breeding season
Proportion of activity on the display court	To estimate activity at court, we used the activity (vocalization and display) of all males in the day divided by the total number of intervals observed in the day for the court in a particular breeding season

We extracted the variables from the observation data (interval = 5 min of observation) of the individuals in different courts in three reproductive seasons.

Proportion of Male Display (x) represents the activity of the individual at the court (displays on and above the court, without vocalization activity), calculated by the number of intervals in which the male displays divided by the total number of sampled intervals at the court; and **Age class of male (x)** represents the experience of male individuals using the court, defined as either (1) for green males, (2) for sub-adult males presenting a black mask and green body or almost entirely blue-black plumages, or (3) for males with adult plumage. We calculated male rank for all males observed in the different courts over the course of each breeding season.

(2) We calculated the **Proportion of Activity at court** in the breeding season, excluding the activity of the highest-ranking male (Equation 3), as:

$$\textit{Proportion of Activity at court} = \frac{\text{Number of activity intervals at the court}}{\text{Number of observation intervals in the court}} \tag{3}$$

where **number of activity intervals at the court** is the total number of intervals with displays or vocalization at the court by any male in the breeding season, excluding the activity of the highest-ranking male at the court; **number of observation intervals in the court** is as citated above. For the description of the variables related to the Female Preference hypothesis see Table 1. To assess the collinearity among predictor variables (Supporting Information, Table S1), we estimated their variance inflation factors (VIFs), where VIF < 3 denoted no collinearity between variables, using the car package for R v.4.2.2 (R Development Core Team 2020).

Data analysis

To evaluate the hypothesis, we used a generalized additive model for location scale and shape (GAMLSS) with a Beta zero inflated (BEZI) distribution used to correct ratio data with zeros inflated. The hotshot hypothesis model included male rank and court activity rate as effects to explain both the proportion of male visitation to males and proportion of female visitation to males. To evaluate the female preference hypothesis, the model included the proportion of multi-male visitation at court and spatial aggregation of courts as effects to explain the proportion of female visitation at court. All analyses were conducted in R 4.2.2 (R Development Core Team 2020), using the gamlss package (Rigby and Stasinopoulos 2005, v.5.4.12) and ggplot2 package (Wickham 2016, v.3.4.1) to generate figures.

RESULTS

During the 2016–2018 breeding seasons, we captured a total of 52 males, from which 26 were recaptured more than once and 20 were recaptured in different display courts, within ($N = 3$), between ($N = 10$), and both (within/between) ($N = 7$) breeding seasons. The number of males that were observed or caught in different times in the same court ranged from one to 17 in a breeding season. We conducted 342 h of observations in seven different courts distributed on average 182.41 m from each other (range 122.1–261.87 m). We observed 21 different males displaying over the three reproductive seasons and recorded 12.42 h of displays altogether. For the sum of intervals with displays, we observed that solitary displays, in which males display alone at the court without other males around the court, and displays by solo males in the presence of other males (one to three) around the court accounted for 40.3% and 59.7%, respectively. The visit of females to a solitary display was higher, but not significantly in relation to display male with the presence of another male around the court ($\chi^2 = 1.87$, d.f. = 1, $P = .1715$; Fig. 2).

In this study, we ranked males using persistence at court sites and individual display proportions at the same court. In support of the hotshot hypothesis, male rank was significantly associated with the variation in the proportion of female visits to male (Fig. 3A; Table 2). Likewise, we found that male rank was significantly associated with the variation in the proportion of male visitation to male (i.e. social interactions; Fig. 3B; Table 2). On the other hand, the total activity proportion at court did not explain the variation in the proportion of female visitation, but did explain male visitation to male (Fig. 3A, B; Table 2).

We captured and banded 11 females in different display courts. Following this, we observed 33 female visits at courts and, in none of these visits, were the females banded. For the female preference hypothesis, where the analyses were based on what happened on the court each day, the proportion of multi-male visitation around the court (resting, vocalizing, or displaying) was not related to the proportion of female visitation at court (or distance among neighbouring courts), but spatial aggregation of courts was related to the proportion of female visitation at court (Fig. 4; Table 3), demonstrating support for the female preference hypothesis for court aggregation in the dataset tested.

DISCUSSION

Before this study, the social organization and spatial dynamics of white-throated manakin leks were poorly understood. We found that in each court one male spent more time in self-maintenance and displays and was present for a longer period in the same court. As with many species of the family Pipridae, *C. gutturalis* exhibits complex social behaviour, and a male court holder receives visits from other males and females during the breeding season. Holder status may change over time (McDonald 2007, Ryder *et al.* 2008, Durães 2009), and we observed males of all ages visiting and displaying in different display courts throughout the breeding seasons of this study. Thus, male *C. gutturalis* most often use solitary displays that are either in the absence or presence of other males around the court, and each display court can be used by multiple males at different times. Displays of multiple males were observed in above-court displays, as shown in Tolentino and Anciães (2020). In Suriname, Prum (1986) observed multiple males of this species displaying at courts, apparently competing to control display sites rather than to attract females. In turn, Théry (1990) concluded that the

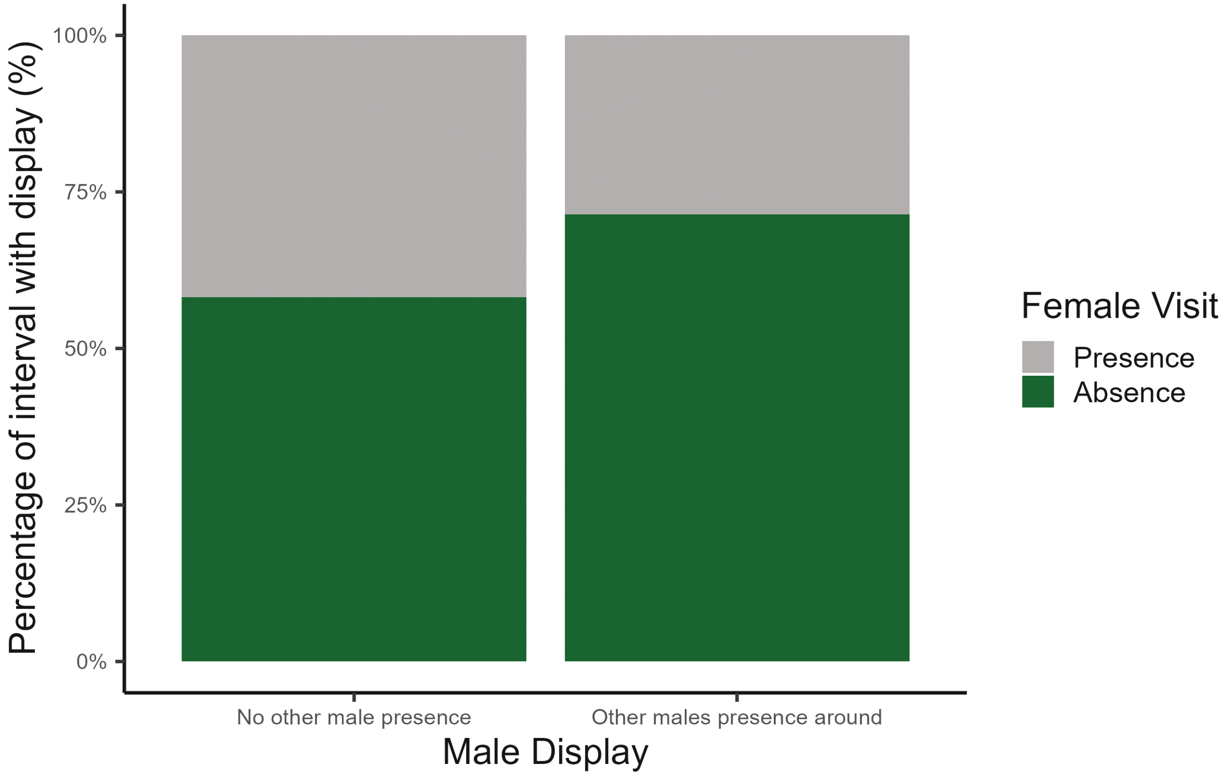

Figure 2. Percentage of intervals with display of focal male alone vs. intervals with display in the presence of other males around the focal male, with presence and absence of females ($\chi^2 = 1.87$, d.f. = 1, $P = .171$). $N = 149$ intervals observed with display.

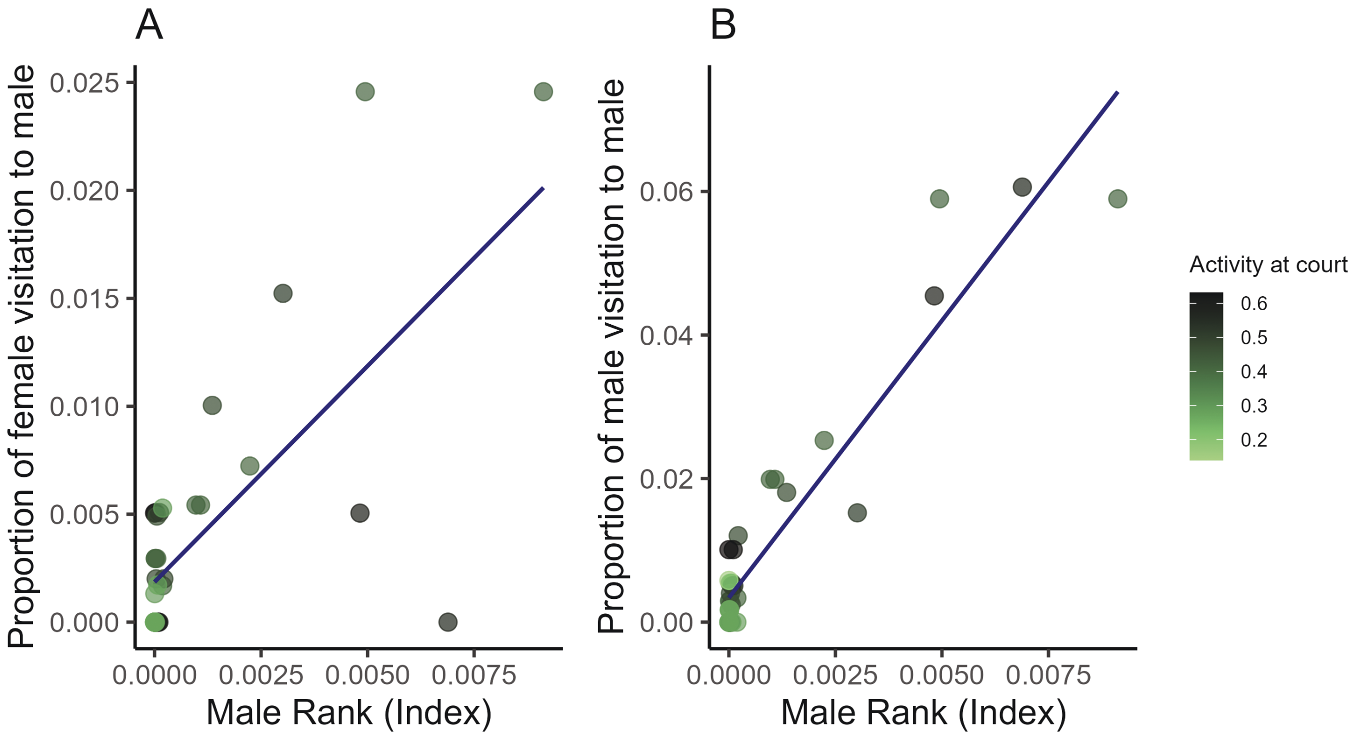

Figure 3. Relationship between: A, the proportion of female visitation to male and male rank; and B, the proportion of male visitation to male and male rank. The green colour scale represents the activity proportion in the court in relation to female visitation proportion and male visitation proportion to the male, derived from the generalized additive model with Beta zero-inflated distribution. $N = 37$, corresponding the observations of males in different courts in the different breeding seasons combined.

Table 2. Statistics of the generalized additive model explaining proportions of female visitation to males and male visitation to male.

Predictors	**Proportion of female visitation to male**				**Proportion of male visitation to male**			
	Estimate	**SE**	***t*-value**	***P***	**Estimate**	**SE**	***t*-value**	***P***
Intercept	−5.63	0.53	−10.59	**<.001**	−5.88	0.50	−11.72	**<.001**
Male Rank (Index)	208.16	30.30	6.87	**<.001**	265.73	26.19	10.14	**<.001**
Proportion of activity at court	0.44	1.16	0.38	.703	2.36	1.01	2.34	**.025**
Observations	37				37			
d.f.	5				5			

Models were generalized with Beta zero inflated distributions. Proportion of activity at courts and male rank were used as predictor variables. $N = 37$, corresponding to all male individuals observed in different courts in all breeding seasons.

observed group displays of male *C. gutturalis* in French Guiana were competitive exhibitions to attract females.

In a study by Davis (1949), *C. gutturalis* group displays occasionally ended in copulation. As we did not record copulation, we considered that female visitation is a good proxy to predict male display success. The lekking system of the congeneric *C. altera* has been reported to be one of facultative cooperation, where two males (alpha and beta) engage in coordinated displays that end in copulation in ~8% of cases (Jones *et al.* 2014). Alpha *C. altera* males remain dominant throughout a few displays in the same court. These social hierarchies can be broken by subordinate males, as shown by Boyle and Shogren (2019) for this same species. We did not observe well-defined alpha–beta pairs in *C. gutturalis* as observed for *C. altera*, but rather a single male that was present more frequently at a given court, and visiting males around courts that moved between courts, without evidence of direct cooperation or alpha and beta pair formation.

We observed that high-ranked males interacted significantly more with other males than low-ranked males. Given that high-ranked males presented higher persistence at court sites, these individuals may maintain the display courts throughout the year, which defines which individuals will persist as territorial males in the display courts during the breeding season. Females would therefore benefit from mating with high-ranked males as they are able to maintain a court, which may be a demonstration of good physical quality (Prum 1986). We also found that more male–male interactions at courts were associated with higher display proportions by male individuals.

The total display proportion at a court was also positively correlated with display proportions from higher-ranked males (Supporting Information, Fig. S2), suggesting that the

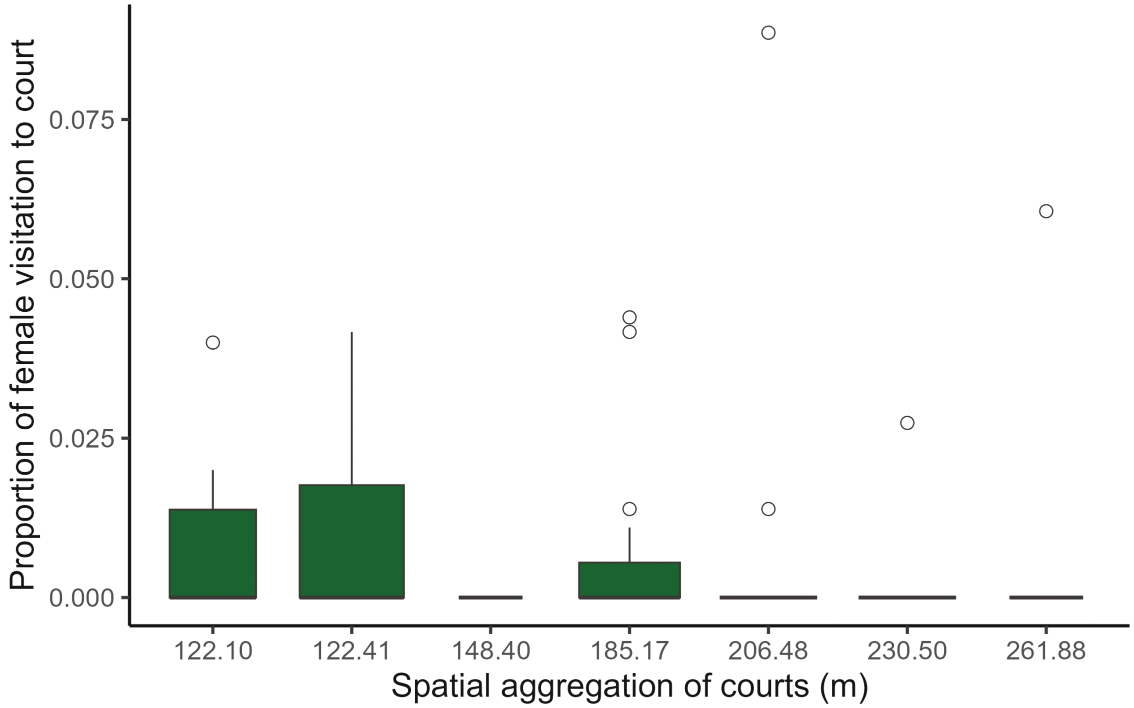

Figure 4. Relationship between rate of female visitation at courts and spatial aggregation of courts (m). *N* = 84 corresponds to the days observed in different courts in all three breeding seasons.

Table 3. Female visitation at court statistics of the generalized additive model; the model was generalized with Beta zero inflated distributions.

Predictors	**Proportion of female visitation at court**			
	Estimate	**SE**	***t*-value**	***P***
Intercept	−4.56	0.79	−5.75	**<.001**
Spatial aggregation of courts (m)	0.006	0.003	2.07	**.041**
Proportion of multi-male visitation at court	2.242	1.40	1.59	.115
Proportion of activity on the display court	−0.423	0.72	−0.58	.561
Observations	84			
d.f.	6			

As predictor variables we used: spatial aggregation of courts (mean distance to the three nearest neighbours in metres) and proportion of multi-male visitation at courts. *N* = 84 corresponding to the total number of days observed in different courts in all different breeding seasons.

high-ranked males may rule out display patterns at courts, even if males do not display at the logs concomitantly. For prairie chickens, display and aggressive behaviour are predictors of reproductive success (Nooker and Sandercock 2008). Thus, male acrobatic displays and motor skills are a sign of good quality (Barske *et al.* 2011) and for *Manacus manacus*, for example, display rate is strongly correlated with mating success (Shorey 2002). Considering these studies, our male ranking index, including both display proportions and court maintenance by males, seems to be a good proxy for the potential of males to attract females.

Interactions with high-ranked or more centrally ranked males have also been observed in other species. In marine iguanas, *Amblyrhynchus cristatus*, males were found to establish their territories around a central male and these territories did not necessarily have the highest female densities at the time of their establishment (Partecke *et al.* 2002). In an experiment with the black grouse, *Tetrao tetrix*, young males tended to aggregate in leks with multiple vocalizations, suggesting that the hotshot mechanism was at work. Females recognized leks with multiple vocalizations and visited these leks more frequently, which supports the female preference hypothesis (Hovi *et al.* 1997). These results indicate that these hypotheses are not mutually exclusive in some cases. In the present study, our results support the hotshot hypothesis. We observed that males of all ages interacted more with the higher-ranked males in each display court, a pattern also observed for females, contrary to that presented by Duval *et al.* (2018) for *Chiroxiphia lanceolata* in Panama, where no evidence of male recruitment by the alpha male was found.

Studies show that, in some species of manakins, females visit the same males repeatedly within and between breeding seasons (DuVal 2013); during our research, it was not possible to verify this repetition of visits, because we had few banded females and only one recapture. We also did not observe banded females during behavioural observations at courts, and therefore it was not possible to individualize the visits to the males. We found that female visitation is more common to males that spent more time displaying in each court. By staying in the same display court, males may increase the probability of being visited by a female because they stay longer in the same place (Castellano 2009). Likewise, displaying for longer may assist females in finding the display court (Nooker and Sandercock 2008). This result agrees with the predictions of the hotshot hypothesis that high-ranked males receive more visits from females and consequently receive visits from other males of lower rank (Beehler and Foster 1988). In contrast, Théry (1990) assumed that female *C. gutturalis* are not attracted to high-quality males, based on one observation of a female that copulated with two males from different courts of the same lek during a single breeding season. Considering the spatial scale of our analyses, in which males were ranked according to the display court in which they were observed, two males from different territories could present similar rank values. Likewise, the same male displaying at multiple courts presented different ranks on each court. Therefore, male rank was defined here at the court scale, rather than at the population level. Thus, a comparison between males of the same court and between the courts and leks within a given population can be achieved by focusing on female movements. The spatial scale at which these questions are addressed affects the patterns of female visits and male aggregations that are recovered.

When we look at the results of the female preference model, we find that the spatial aggregation of courts is a significant factor in female visits to the courts. As mentioned above, this aggregation can facilitate comparisons of the females about males, in addition to reducing female energy expenditure when searching for partners. Nevertheless, female *C. gutturalis* were not attracted by increased multi-male interactions at courts and the proximity between courts. As such, we did find partial evidence for the female preference hypothesis of Bradbury (1981). In the blue-crowned manakin, *Lepidothrix coronata*, females showed no preference for larger leks, but instead for males with higher display rates within each lek, which was then considered a reliable signal of quality (Durães *et al.* 2009). However, in other species, females were attracted to larger leks (e.g. Alatalo *et al.* 1992, Lank and Smith 1992, Young *et al.* 2009, Bosholn *et al.* 2019). In this study, females were more attracted by the presence of a high-ranked male in each display court and their spatial aggregation. In turn, high-ranked males also presented high activity, and low-ranked males aggregated around them, possibly due to the visibility that the high-ranking male had. For instance, males might join high-ranked males because high-ranked males receive more visits from females (hotshot hypothesis) or to compete for females, thus leading to more visible display courts and facilitating the comparison between males by females (female preference hypothesis), in the same courts (male aggregation) but not between courts (courts aggregation), as found in this study. As such, both models might operate and males may engage in seemingly semi-cooperative relationships, as has been reported for *C. altera* (Jones *et al.* 2014). These results therefore provide evidence that male *C. gutturalis* may interact to attract females, but that such interaction will not necessarily increase reproductive success when compared to that of males that display alone, suggesting a facultative role for this type of cooperation in the evolution of lekking within *Corapipo*.

In conclusion, our results advance the understanding of lek evolution in *C. gutturalis*, a manakin species with a poorly understood lek system. This provided cues about proximate drivers for lek mating systems. Prum (1986) suggested that this species is different from other manakins with regard to its social organization, having a mobile lek system. Based on the results presented here, several males use the same court and there is one male with greater rank in the given court and the population, but that visits other courts, and this rank can change over time, corroborating the idea of mobile leks presented by Prum (1986). In addition, males show competitive behaviour, as also found by Tolentino and Anciães (2020), where males aggregated and performed above-court competing displays (~3 m higher) without the presence of females. When displaying at court, in most cases, only one male was observed at a given court at a time. Therefore, our study represents a first step to understanding how male *C. gutturalis* interact with another one and how females and males select male court holders to visit and settle around. As such, it provides insights into the seemingly obvious grouping behaviour and male interaction within lek species. Males aggregate around males that spend more time and display at higher rates, the high-ranking individuals, that also received more female visits, supporting the hotshot hypothesis. We also show that more males using a court during the breeding season increases court activity over time and attracts females. As such, males may also increase display rates to stand out and be chosen by females, becoming high-ranking males. However, females are not attracted to increased multi-male interactions in courts. Therefore, we suggest that the lek system of *C. gutturalis* revolves around males that defend display courts through their higher permanence and display rates. Here, male–male interaction at courts evolved through some degree of competition for females rather than purely cooperation among males, in which male coalitions increase the fitness of males holding courts, as Tolentino and Anciães (2020) suggested. This agrees with the idea that males compete at courts for opportunities to display alone, but that male interaction at the court throughout the breeding season enhances the likelihood that females will visit their displays, suggesting a role for semi-cooperation among males in this system, rather than through cooperation with an alpha–beta pair during group displays.

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

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CREDIT STATEMENT

M.T., T.B.R., and M.A. conceived and developed the project. M.T and M.A. designed the methodology. M.T., F.A., and A.P.R. performed

fieldwork and collected the data. M.T. and M.A. analysed the data and wrote the manuscript. A.P.R., T.B.R., and M.A. contributed to editing the manuscript.

ETHICAL STATEMENT

The banding permit (No. 4081/1) was provided to M.T. by CEMAVE, the ethical permit was granted by the Research Ethics Committee on Animal Use (CEUA-INPA 012/2016), and the research permit (No. 44969-2) was granted by the Chico Mendes Institute for Biodiversity Conservation (ICMBIO).

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DATA AVAILABILITY

The data underlying this article will be shared on reasonable request to the corresponding author.

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