Instituto Nacional de Pesquisas da Amazônia – INPA
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Determinantes sociais e espaciais da agregação de machos do Dançarino-de-garganta-branca (*Corapipo gutturalis*, Aves: Pipridae) em leques na Amazônia Central

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Manaus, AM
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Orientador: Marina Anciães

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Sinopse: Nessa tese, investigou-se quais fatores sociais e espaciais podem explicar a agregação de machos do Dançarino-de-garganta-branca em leques. Foram testadas hipóteses propostas para a evolução de leques, descritos comportamentos pouco observados anteriormente e analisada a dinâmica espacial dos indivíduos entre os leques e as estações reprodutivas na atração de fêmeas.

Palavras-chave: Comportamento Animal; Pipridae; Seleção Sexual; Sistema de leque

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E a você que lê.

Sou muito grata.

O apanhador de desperdícios

“Uso a palavra para compor meus silêncios.
Não gosto das palavras
fatigadas de informar.
Dou mais respeito
às que vivem de barriga no chão
tipo água pedra sapo.
Entendo bem o sotaque das águas
Dou respeito às coisas desimportantes
e aos seres desimportantes.
Prezo insetos mais que aviões.
Prezo a velocidade
das tartarugas mais que a dos mísseis.
Tenho em mim um atraso de nascença.
Eu fui aparelhado
para gostar de passarinhos.
Tenho abundância de ser feliz por isso.
Meu quintal é maior do que o mundo.
Sou um apanhador de desperdícios:
Amo os restos
como as boas moscas.
Queria que a minha voz tivesse um formato
de canto.
Porque eu não sou da informática:
eu sou da invencionática.
Só uso a palavra para compor meus silêncios”
Manoel de Barros

Resumo

Seleção sexual é um processo no qual os indivíduos competem para atrair parceiros reprodutivos. Ao longo desse processo, as espécies desenvolveram diferentes mecanismos e estratégias para incrementar seu sucesso reprodutivo. Como podemos observar no sistema de acasalamento de leques poligínico, onde machos se agregam com o intuito de atrair fêmeas, sendo o sucesso reprodutivo entre os machos bastante variado. Os indivíduos desse sistema estão constantemente sob forte seleção sexual. Assim, os custos e benefícios dessa agregação têm sido amplamente estudados em várias espécies com sistema de leques, sendo encontrados diferentes resultados dependendo das espécies estudadas, o que mostra uma grande diversidade e complexidade para esse sistema. Nessa tese, investiguei fatores sociais e espaciais para explicar a agregação de machos do Dançarino-de-garganta-branca (*Corapipo gutturalis,* Aves: Pipridae) em leques em uma população da Amazônia Central. Para isso, monitorei uma população, dessa espécie, localizada na reserva do Km 41 do PDBFF, aproximadamente 80 km de Manaus, Brasil. Durante três estações reprodutivas capturei, anilhei, coletei amostras de sangue e, posteriormente, observei esses indivíduos em suas arenas de exibição. No **primeiro capítulo** testei as hipóteses de *hotshot,* que postula que machos com um alto rank atraem tanto mais fêmeas quanto machos de menor rank, e preferência de fêmeas, onde fêmeas são atraídas por leks maiores. Encontrei uma associação entre machos de alto rank com a atração de fêmeas e machos corroborando com a hipótese de *hotshot*. Além disso, observei uma maior visitação de fêmeas aos palcos mais próximos, o que indica também uma preferência de fêmeas. Assim temos uma associação entre a hipótese de *hotshot* e preferência de fêmeas para explicar a agregação de machos. No **segundo capítulo**, adicionei novas informações às exibições que acontecem em galhos acima das arenas, entre 5-10m de altura. Essas exibições ocorreram em quatro das sete arenas observadas.

Adicionalmente, observei que alguns machos realizam voos estereotipados e exibem elementos nunca registados para a espécie ou registrados apenas nos palcos do chão da floresta. A partir dessas observações, testei se essas exibições acima das arenas tinham o intuito de atrair fêmeas. No entanto, não encontrei relação entre as exibições acima das arenas e o número de visita de fêmeas comparada aos displays nas arenas. Assim discuto que essas exibições são uma competição entre os machos a fim de determinar quem irá se exibir na arena e/ou disputar quem tem o maior rank. Essa tese acrescenta conhecimentos para a história natural da espécie no que se refere a descrição da organização social e espacial, e novos caminhos para entender a evolução de leques através da agregação de machos.

Social and spatial determinants of male White-throated Manakin (*Corapipo gutturalis*, Aves: Pipridae) male aggregation at leks in Central Amazonia

Abstract

Sexual selection is a process in which individuals compete to attract reproductive mates. Throughout this process, species have developed different mechanisms and strategies to increase their reproductive success. As we can see in the polygynous lekking mating system, where males aggregate to attract females, the reproductive success among males is quite varied. The individuals in this system are constantly under strong sexual selection. Thus, the costs and benefits of this aggregation have been widely studied in several species with a lek system. Since different results are found depending on the species under study, which shows great diversity and complexity for this system. In this thesis, I investigated social and spatial factors to explain the aggregation of White-throated Manakin (*Corapipo gutturalis*, Aves: Pipridae) males in leks in a Central Amazonian. For this, I monitored a population of this species, located in the BDFFp, Km 41 Reserve, approximately 80 km from Manaus, Brazil. During three breeding seasons, I captured, banded, collected blood samples, and later observed these individuals in their display court. In the first chapter, I tested the hypotheses of hotshot, which postulates that higher-ranking males attract more females and lower-ranking males, and female preference, where females are attracted to larger leks. I found an association between high-ranking males with the attraction of females and males corroborating the hotshot hypothesis. In addition, I observed a greater visitation of females to the nearest courts, which also indicates a female preference. Thus, we have an association between the hotshot hypothesis and female preference to explain male aggregation. In the second chapter, I added new information to the exhibits that take place on perch above the log display, between 3 and 10m high, these exhibits occurred in four of the seven observed display court. Additionally, I noticed that some males perform stereotyped flights and display elements never recorded for the species or recorded only on log display. From these observations, I tested whether these above-log displays were intended to attract females. However, I found no relationship between the above-log displays and the number of female visits compared to the log displays. So, I argue that these displays are a competition between males to determine who will perform in the log display and/or to compete for the highest ranking. This thesis adds knowledge to the natural history of the species regarding the description of social and spatial organization, and new ways to understand the evolution of leks through male aggregation.

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https://drive.google.com/file/d/1JGpOzvijLpFMuXpDF-WpNUqvuiq0rWGg/view?usp=sharing

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Síntese

Figura 1. Uma síntese dos resultados encontrados no capítulo 1, onde com relação a hipótese de *Hotshot*: as linhas cheias apontando para o macho mais atraente significa que ele interagiu com mais machos e teve mais visitas de fêmeas, já as setas cheias voltadas mais a atividade dos arenas significa que as arenas como mais atividade também tiveram mais machos interagindo e mais visitas de fêmeas. A hipótese de *Female Preference* teve uma associação entre a proximidade das arenas e a visita de fêmeas. As linhas pontilhadas representam relações que não foram testadas nesse estudo e que fica como sugestão para estudos futuros.

Figura 2. O capítulo 2 sintetizado na figura acima, onde em preto represento as observações das exibições: quadro 1 exibições no tronco, quadro 2 exibições acima dos troncos em galhos, o sinal de maior que representa que observei um maior número de exibições nos troncos. Em azul é representado o número de machos, onde observei mais machos participando de uma mesma exibição acima dos troncos. Em vermelho é representado a visita de fêmeas, onde as análises não mostraram diferenças significativas na visita de fêmeas nos dois locais.

Introdução geral

Indivíduos de uma população relacionam-se de diferentes formas entre si e com o ambiente em que vivem (Krause, Croft, & James, 2007). Essas relações entre indivíduos – que podem ser do tipo cooperativa, sexual, agressiva, dentre outras (McDonald, 2009; Pinter-wollman et al., 2013) – criam uma interação social com intensidades e níveis de associações diferentes entre os envolvidos. Assim, essa rede de interações pode determinar a escolha de parceiros, transmissão de doenças, fluxo gênico e evolução de estratégias comportamentais (Krause et al., 2007).

Em geral, os comportamentos sociais variam de acordo com a idade e o sexo dos indivíduos de um dado grupo, como a dependência de cuidado parental, a maturidade sexual dos indivíduos, as interações entre os sexos e as dominâncias hierárquicas relacionadas à idade (Faust, 2011). Assim, as interações indicam as funções dos indivíduos dentro da organização social da sua espécie. Já suas variações resultam de mudanças ambientais ou quesitos espécie-específicos (Whitehead, 2008), os quais determinam a estruturação hierárquica do grupo (de Silva, Ranjeewa, & Kryazhimskiy, 2011), o status social na vida adulta (McDonald, 2007) e as decisões do grupo mediante a posição do indivíduo na população (Lusseau, 2007). Por isso, uma espécie pode apresentar diferentes estruturas sociais ao longo de sua distribuição geográfica, gerando variações em processos reprodutivos, transferências de informações e transmissão de doenças (Krause et al., 2007).

Os animais desenvolveram diferentes estratégias e mecanismos para atrair seus parceiros sexuais, garantindo o sucesso reprodutivo para manter seus genes na população. Nesse contexto, a seleção sexual é um processo de seleção natural em que os indivíduos competem por acasalamentos (Darwin 1871, Andersson 1994). Dois tipos de seleção sexual são elucidados. A seleção intrasexual inclui interações entre indivíduos do mesmo sexo, principalmente em forma de competição (Moore, 1990; Andersson, 1994). Por outro lado, a seleção intersexual trata da escolha do sexo oposto por um parceiro que demonstre boas condições, que usualmente denotam uma boa qualidade genética (Moore, 1990; Andersson, 1994; Prum, 2012). Dessa forma ambos os sexos estão envolvidos no processo de conseguir parceiros. Assim, os indivíduos passaram a investir energia para manter ornamentos e armamento em exibições, interações, além de procura e competição por parceiros reprodutivos (Andersson, 1994; Morales, Alonso, Martín, Martín, & Alonso, 2003; Sardà-Palomera, Puigcerver, Vinyoles, & Rodríguez-Teijeiro, 2011).

Os sistemas de acasalamento de leque poligínico são caracterizados por uma forte seleção sexual (Höglund & Alatalo, 1995). Dado o grau substancial de competição entre os machos, os leques são frequentemente caracterizados por um forte desvio reprodutivo (poucos machos detêm grande parte das cópulas e assim um maior sucesso reprodutivo) (Höglund & Alatalo, 1995). Nesses leques, machos espacialmente agregados realizam exibições com o principal intuito de atrair fêmeas, normalmente sem defender recursos para elas ou contribuir no cuidado parental (Bradbury & Gibson, 1983; Emlen & Oring, 1977). Sugere-se que os leques teriam evoluído primariamente devido à preferência feminina por agregações masculinas, pois essas oferecem oportunidade de comparar possíveis parceiros de acasalamento (Bradbury, 1981; Wiley, 1991).

No entanto, as fêmeas podem utilizar diferentes estratégias para selecionar os parceiros reprodutivos dentro dos leques (Kirkpatrick and Ryan 1991; Andersson 1994), as quais podem ser associadas às boas características físicas ou genéticas dos machos (Foster, 1983), ou não (Prum, 1997). Com isso, elas usam traços secundários para fazer suas escolhas, como a conspicuidade da cor da plumagem (Stein and Uy 2006) ornamentos e desempenho de exibição (Gibson and Bradbury 1985; Höglund et al. 1990; Mcdonald et al. 2001); vocalização e exibição (Trainer and Mcdonald 1995; Gibson 1996; Trainer et al. 2002) e comportamento territorial (R. Durães, Loiselle, Parker, & Blake, 2009; Théry & Vehrencamp, 1995). Essas características podem denotar uma boa condição do macho (Andersson 1994; Morales et al. 2003; Sardà-Palomera et al. 2011) ou representar caracteres “Fisherianos”, em que preferências puramente estéticas estão sob seleção (Fisher 1930; Prum 1997).

Ao longo do tempo muitas hipóteses vêm sendo propostas e discutidas para entender a evolução do sistema de leque e, assim, a agregação de machos. Dentre as principais hipóteses, destacam-se (a) o modelo de *hotspot*, que postula que os machos estabelecem seus leques em áreas de grande densidade de fêmeas, onde há uma grande quantidade de recursos, por exemplo alimento ou territórios para nidificação (Bradbury & Gibson, 1983); (b) O modelo de *hotshot*, no qual fêmeas e machos são atraídos por um macho considerado de maior rank na população (Beehler & Foster, 1988); e (c) o modelo de preferência de fêmeas, como citado acima, que sugere que a agregação de machos nos leques funciona como um atrativo para as fêmeas, uma vez que essa agregação facilita a comparação dos machos pelas fêmeas (Bradbury, 1981). Essas hipóteses vêm sendo testadas muito frequentemente em espécies da família Pipridae (Loiselle et al. 2007, Barske et al. 2011, Duval 2019), que agrega pequenos pássaros neotropicais (Kinwan & Green, 2011), cuja maioria das espécies apresentam sistema de leques poligínicos (Richard O. Prum, 1990a, 1994a). Tem-se observado que diferentes espécies e escalas espaciais levam a diferentes resultados com relação as hipóteses que elucidam a evolução de leques (Ex. DuVal, 2018; Ryder, 2006; Théry, 1992), demonstrando uma grande complexidade e diversidade nesse sistema.

Nessa tese investiguei os determinantes sociais e espaciais para a agregação de machos em sistema de leque. Para isso testei hipóteses de evolução de leque e adicionei informações às descrições de exibição da espécie do Dançarino-de-garganta-branca (*Corapipo gutturalis*). Usei essa espécie como modelo levando em consideração que, embora a organização social de *C. gutturalis* tenha sido estudada por Prum (1986) e Théry (1990), não houve um consenso sobre a função de várias exibições dos machos. Théry (1990) sugere que as arenas de exibição de *C. gutturalis* têm um macho dominante, baseando-se na observação das cópulas após exibições solitárias. Prum (1986), por outro lado, sugere que os machos de *C. gutturalis* formam leks móveis, nos quais os machos se exibem em grupos e as fêmeas escolhem o macho dominante. Essa espécie, portanto, trata-se de um bom modelo onde seria possível acrescentar informações às espécies com sistema de leque.

Espécie modelo

O Dançarino-de-garganta branca (*Corapipo gutturalis*) é uma espécie da família Pipridae que vive no sub-bosque de florestas tropicais, sendo encontrado na Venezuela, Guianas e Brasil (Meyer de Schauensee 1970, Snow 2004). São principalmente frugívoros, mas também são vistos em bandos misto se alimentando de insetos, principalmente fêmeas em época reprodutiva (Kinwan e Green 2011). Como a grande maioria das espécies de piprídeos, machos de *C. gutturalis* formam leques para atrair as fêmeas. Apresentam acentuado dimorfismo sexual, em que machos são pretos azulado com uma mancha branca na garganta e nas asas quando abertas (figura 1A), enquanto os machos juvenis e as fêmeas são verdes acinzentados (figura 1B-C), ambos pesando em média oito gramas (Prum 1986). Esses leques são compostos por cinco a oito machos que se apresentam em arenas (figura 2A). As arenas são feitas em troncos caídos na floresta (figura 2B) estando distantes uma das outras por 30 metros e de poleiros em galhos no alto (figura 3, Prum 1986). Os leques são dispersos com machos juvenis e alguns machos adultos que não possuem palcos próprios interagindo com machos que dominam alguns palcos (Prum 1986; Théry 1990). Essa espécie escolhe períodos do dia para se exibir utilizando a luz que chega à arena para aumentar o contraste entre suas cores e o palco utilizado (Anciães & Prum, 2008; Endler & Thery, 1996; Théry & Vehrencamp, 1995).

O primeiro registro publicado de comportamento dessa espécie foi feito por Davis em 1949, onde ele descreve uma observação de poucos dias em uma reserva da Guiana Inglesa. Posteriormente em 1986, Prum publicou um artigo com uma descrição mais completa, onde ele descreve a vocalização e os elementos de exibição. Com relação a vocalização o *C. gutturalis* apresenta dois cantos de forrageamento que ambos os sexos executam “*seeu*” e “*seeu-see*”, um canto de advertência que é executando quando os machos estão nas arenas de exibição “*seeu-see-ee-ee-ee*” e um som mecânico “*pop-tickee-yeah*” que é atribuído as asas, mas que não é confirmado (Prum 1986). Um dos elementos peculiares exibidos por *C. gutturalis* é o voo acima do dossel, onde os machos voam acima das arvores e mergulham em direção ao tronco que usam como arena de exibição executando o som mecânico. Os elementos mais comumente observados são bico para cima (figura 4a), agachado (figura 4b) e sacudida das asas (figura 4c). Em uma compilação de dados dos elementos de exibição para várias espécies de Pipridae, *C. gutturalis* apresenta um total de 12 elementos (Prum 1990), mais recentemente um novo artigo também compilando os elementos de exibição, diz que a espécie em questão apresenta 15 elementos (Anciães et al. 2009).

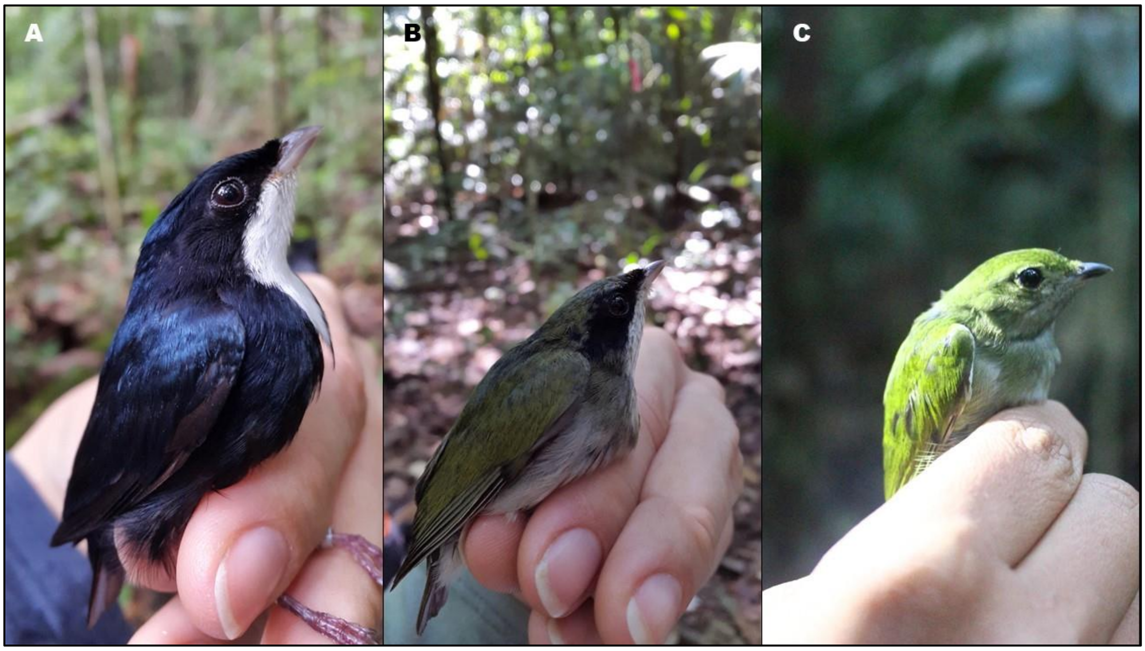

Figura 1. Indivíduos Dançarino-de-garganta-branca (Corapipo gutturalis). A. Macho adulto, B. Macho jovem, C. Fêmea. Fotos: Aline Rampini

Figura 2. Exemplo de palco de exibição. A. visão geral, B. Detalhe mostrando a camada de musgo que sempre cobre os palcos que são utilizados para exibição.

Figura 3. Galhos de exibição acima do tronco caído com dois machos adulto se exibindo.

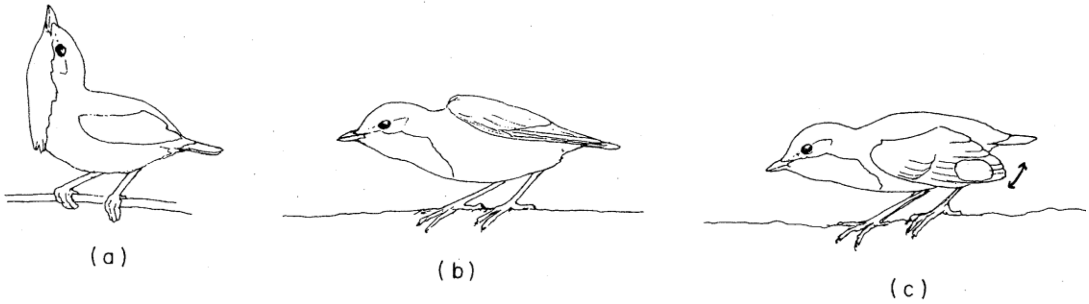

Figura 4 Representação dos elementos de exibição de Corapipo gutturalis: (a)bico para cima, (b)agachado, (c)sacudida de asas. Retirada de Prum 1986.

Objetivos

Objetivo geral

Nesta tese investiguei fatores sociais e espaciais para explicar a agregação de machos do Dançarino-de-garganta-branca (*Corapipo gutturalis*, Aves: Pipridae) em leques em uma população da Amazônia Central.

Objetivos específicos

A tese possui dois objetivos específicos que são apresentados nos dois capítulos a seguir:

Capítulo 1: Investigar a organização social do Dançarino-de-garganta-branca, onde testei as hipóteses de *Hotshot* e Preferência de fêmea, relacionando fatores determinantes para a agregação de machos.

Capítulo 2: Adicionar informações sobre as exibições do Dançarino-de-garganta-branca no alto da floresta e testar se essas exibições são uma forma de atrair fêmeas comparada com as exibições nos palcos no chão da floresta.

CAPÍTULO 1

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

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

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Short running title: Testing Hypotheses for Male Aggregation

ABSTRACT

The reasons for male spatial aggregation in lekking systems have been the subject of substantial debate over the last decades. Questions have largely focused on whether males aggregate in areas with higher female abundance, around high-ranked males that attract more females, or as the result of female preference for easy comparison among potential mates. Under this framework, we investigated how the social organization and male-male interactions are associated with female visitation in the lekking system of the white-throated manakin. Specifically, we tested whether females prefer higher-ranked males and courts with greater activity, as predicted by the hotshot hypothesis. In addition, but not mutually exclusive, we tested whether larger leks and/or shorter spatial distances among neighboring courts attracted more females. We found that highest-ranked males at courts received significantly more female visits, and that total display activity at courts also predicted female visitation. Furthermore, male visitors were also attracted to highest-ranked males and more active display courts. Moreover, female visitation rates at court were not predicted by multi-male attendance around courts, but by their spatial aggregation. These results suggest that both hotshots rather and female preference for higher male aggregations explain the proximate evolution of male aggregation in leks of the white-throated manakin.

KEYWORDS: Central Amazonia - courtship behavior - female visitation – high rank male -Hotshot - lek polygyny - male interaction – female preference

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 (Bradbury & Gibson, 1983; Emlen & Oring, 1977). Leks are thought to have primarily evolved because of female preference for male aggregations, as they provide opportunity to compare prospective mating partners (Bradbury & 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 & Alatalo, 1995). Despite an extensive number of hypotheses for the evolution of lekking, debate has persisted regarding the proximate drivers and fitness benefits of male lekking behavior.

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 & 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-ranked male that attracts a greater number of females (Beehler & Foster, 1988). Finally, the female preference model suggests that lek aggregation is driven by female preference to mate in large leks, in which 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 and Ponkshe 2013). Few studies addressing lekking behavior in manakins, small neotropical Pipridae birds, 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, Blake, & Loiselle, 2006, but see Durães, Loiselle, & Blake, 2007 on *Lepdothrix 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 likely influence the immediate drivers of male aggregation.

The white-throated manakin, *Corapipo gutturalis* (Linnaeus, 1766) lives in the understory of tropical rain forests and is widely distributed throughout the Guyana Shield (Kinwan & Green, 2011).The breeding season last from late August to December, but may extend until January (Kinwan & Green, 2011; Tolentino *unpublished data*). Like most manakins, the species exhibits strong sexual dimorphism. Males are blue-black with a prominent white throat and white patches under the wings, while females and juvenile males are a drab gray-green. Leks are classified as dispersed and formed by 5-8 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 (Anciães & Prum, 2008; Richard O. Prum, 1986, 1994b; Théry, 1990). Ritualized displays occur typically in mossy fallen logs, 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 multiple 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 exhibit themselves in groups and females choose the dominant male.

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 spatio-temporal distribution of males during three breeding seasons. We first tested if 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 1) high-ranked males should receive more visits at court; 2) Degree of social aggregation will be biased towards the highest-rank male that, as such, interact with more males throughout the breeding season; and 3) rate of display activity at courts will be driven by the number of males using a court, given that males compete for the hotshot position. As such, activity should be higher at courts with higher-rank male in the populations, 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: 1) courts with higher male-male interaction rates will also receive higher female visitation, and 2) females will prefer neighboring courts that are closer from each other, as it would facilitate comparison among males.

MATERIAL AND METHODS

Study 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 approximately 1,000 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 km 41. This reserve is composed of approximately 10,000 ha of the continuous forest with a trail-grid of 1,000 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. The average annual rainfall in the area is ~2,200 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 & Mori, 1999; Laurance et al., 2010).

Data collection

All mark-recapture efforts and behavioral 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 meters) 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 x 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 7:00 am-1:00 pm for a total of at least 3 days at each display court per breeding season. We marked all individuals with unique combinations of color bands (Avinet Color Leg Bands - Darvic – XF, Portland, Maine, 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). The banding permit (No. 4081/1) was provided to MT of

CEMAVE and the research permit (No. 44969-2) was granted by the Chico Mendes Institute for Biodiversity Conservation (ICMBIO).

We aged and sexed individuals in the field using plumage (i.e., molt limits; Ryder and Durães 2005) and additional standard criteria, such as cloacal protuberance, brood patch, and color gape. To identify the sex of individuals with gray-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- January, thus covering the breeding season described for the species. We conducted at least three days of 6-h behavioral observations (n ≅ 18 h per court) in each breeding season. In 2016, five display courts were observed by MT; in 2017 two were added totaling seven display courts, observed by MT and FA and in 2018 the same seven were observed by FA. To standardize male behavior and avoid observer bias, we used binoculars and a camouflage blind placed at least 10 m from the focal display court. We recorded arena activity using a video camera during observations in order to backup focal observations and to obtain ground truth observer data. During each 5-min interval of continuous focal observation (Altmann, 1974a; Bosholn & Anciães, 2018), we recorded number of birds, their sex and color band identification, the observed display frequency, vocalizations, number of female visits, and respective strata of the individuals visits (i.e., on fallen logs, in the canopy, or in the understory).

Data analysis

We calculated key variables to test our hypotheses from both observational and capture data (table 1). We transformed all response variables to the arcsine of the square root of original values, appropriated for ratios and proportions (Sokal & Rohlf, 1995). To assess the collinearity among predictor variables (table S1), we estimated their variance inflation factors (VIF), where VIF < 3 denoted no collinearity between variables, using the car package for R version 3.5.2 (R Development Core Team 2019). In order to rank males, we generated an index following the methodology of Jones et al. (2014) that accounts for site fidelity, the activity and experience of the individual in the court, which is defined as:

$$Male\ Rank = \left(\frac{\Sigma\ obs\ male\ (x)\ in\ court\ (y) + male\ (x)\ display\ rate}{\Sigma\ day\ obs\ in\ court\ (y) + \Sigma\ all\ obs\ male\ (x)}\right) age\ class\ of\ male\ (x) \qquad (1)$$

Where **obs male (x) in court (y)** represents the fidelity of the individual to the court, in number of days that the male was either captured or observed at the display court; **male (x) display rate** represents the activity of the individual at the court, in number of observation intervals in which the male displayed divided by the total number of observational intervals conducted at the court; **day obs in court (y)** is the number of days in which the display court was sampled with mist nets and that observations were carried out during the breeding season; **all obs male (x)** is the number of days that the male was captured and observed in all display courts during the season, which penalizes individuals visiting multiple courts in the same breeding season, reducing their fidelity to each courts where it was observed,; and **age class** represents the experience of male individuals using the court, defined as either (1) for green young males, (2) for sub-adult males presenting black mask and green body or almost fully blue-black plumages, or (3) for adult male with adult plumage. We calculated male rank for all males captured and observed in different courts and immediate surroundings (above the log or within a radius of about 5-10 m from it) over the course of each breeding season.

Following the methodology of Bosholn et al. (2016) and considering that we collected data in 5-min intervals, we calculated the display rate at each court, excluding the activity of the highest-ranking, as:

$$Display\ rate\ at\ court\ = \frac{\sum \text{Number of intervals with displays at the court}}{\sum \text{Number of observation intervals in the court}} \quad (2)$$

Where **number of displays intervals in display court** is the total number of observation intervals with displays at the court, excluding the activity of the highest-ranking male at the court; **number of observation intervals in display court** is the total number of intervals in which the court was observed.

To test the hotshot hypothesis, we used a generalized linear mixed model (GLMM) with a Poisson error distribution. The GLMM model included male rank and court display rate as fixed effects to explain both the male interactions to other males and female visits to males. We used male id and year as random effects. To test the female preference hypothesis, we used a generalized linear model (GLM) with a Poisson error distribution with the spatial aggregation and multi-male presence at courts as fixed effects and female visitation at courts as response variables. All analyses were conducted in R 3.5.2 (R Development Core Team 2019), using the functions glmer and glm in the lme4 package (Bates et al, 2015, version 1.1.20) and ggplot2 in the grid package (Wickham, 2009 and Murrell, 2005, respectively) to generate figures and the sjPlot package (Lüdecke, 2019) to generate tables.

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) or both (n=7) breeding seasons. The number of males that used a court ranged from 1-17 in the same breeding season. We conducted 342 h of observations in seven different courts distributed on average at 182.41m from each other (<min-max range> 122.1-261.87). We observed 23 different males displaying over the three reproductive seasons and recorded 6.83 h of displays altogether. Solitary displays, in which males display in solo at the court without other males around the court and displays by solo males in the presence of other males (1-3) around the court accounted for 37.8% and 62.2% of the total time in which males displayed, respectively. Female presence was significantly higher in solitary display than display with presence of another male around the court (*chi-square* = 7.36; *d.f.* = 1; *p-value* = 0.006, figure S1).

In this study, we ranked males using persistence at court sites and individual display rates at the same court. Among the males with the highest ranks, 45% were observed interacting with other males. Male rank significantly explained the variation in females visits to males (Fig. 1a, Table 2). Likewise, the total display rate at court explained the variation in female visits to males (Fig. 1b, Table 2). In support of the hotshot hypothesis, we found that male rank and display rate at courts were significantly associated with the variation in the rate of male interaction to other male (i.e., social interactions; Fig. 1c-d respectively, Table 2).

We captured and banded 11 females in different display courts. After this, we observed 33 female visits at courts and, in none of these visits, were the females banded. The presence of multiple males around a court was not related to female visitation (Fig. 2a, Table 3). In the other hand, the spatial aggregation (or distance among neighboring courts) was related to female visitation at courts (Fig. 2b, Table 3), in support of the female preference hypothesis.

DISCUSSION

Before this study, social organization, and spatial and temporal 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, *Corapipo gutturalis* presents complex social behavior, and a male court holder receives visits from other males and females during the breeding season. Holder status may change over time (Durães, 2009; McDonald, 2007; Ryder et al., 2008), 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* presents solitary displays that are either in absence or in presence of other males around the court, and each display court can be used by multiple males in different times. In Suriname, Prum (1986) observed multiple males of this species displaying at courts apparently for competing for the control of display sites rather than to attract females. In turn, Théry (1990) concluded that the 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 a facultative cooperation, where two males (alpha and beta) engage in coordinated displays that end in copulation in ~8% of cases. Alpha *C. altera* males remain dominant over the course of a few displays in the same court. We did not observe well-defined alpha-beta pairs in *C. gutturalis* as observed for *C. altera* (Jones et al., 2014), but rather a single male that was present more frequently at a given court and visiting males around courts that traveled between courts, without evidence of direct cooperation or alpha and beta pair formation.

We found that high-ranked males interacted significantly with more males than low-ranked males. Given that high-rank males presented higher court site persistence, it is possible that these individuals 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 rates by male individuals.

The total display rate at a court was also positively correlated with display rates from higher-ranked males (fig. S2), suggesting that the 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 behavior are predictors for reproductive success (Nooker & Sandercock, 2008). Thus, male acrobatic displays and motor skills are a sign of good quality (Barske, Schlinger, Wikelski, & Fusani, 2011) and for *Manacus manacus*, for example, the display rate is strongly correlated with mating success (Shorey, 2002). Considering these studies, our male ranking index, including both display rates 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 that a these territories did not necessarily have the highest female densities at the time of their establishment (Partecke, Von Haeseler, & Wikelski, 2002). In an experiment with the black grouse, *Tetrao tetrix*, young males tended to aggregate in leks with multiple vocalizations suggesting that a hotshot mechanism was at work. The females recognized leks with multiple vocalizations and visited these leks more frequently, which supports the female preference hypothesis (Hovi, Alatalo, Halonen, & Lundberg, 1997). These results indicate that these hypotheses are not mutually exclusive in some cases. In the present study, our results support both the hotshot hypothesis and female preference models. We observed that young males and males of all ages interacted more with the higher-ranked males in a given display court, a pattern also observed for females and males from nearest courts, which received more female visits to the contrary of what Duval et al. (2018) found for *C. lanceolata* in Panama.

Although studies show that, in some species of manakins, females visit the same males repeatedly within and between breeding season (DuVal, 2013), during our study we did not find evidence for that, as we had only one female recapture throughout the study that, nevertheless occurred in different courts and breeding season. Furthermore, we did not observe banded female during behavioral observations at courts. Hence, we found that female visitation is more common to males that spent more time displaying in each court, which likely can be attributed to different females. 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 longer may also assist females in finding the display court (Nooker & 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 & Foster, 1988). Théry (1990), on the contrary, assumes 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. During the breeding season, there are several courts within the home range of a female (Rampini et al 2019, in preparation). This enables females to compare males not only in a display court but between multiple display courts. Thus, by focusing on female movements, a comparison between males of the same court and between the courts and leks within a given population can be achieved. Thus, the spatial scale in which these questions are addressed likely affects the patterns of female visits and male aggregations that are recovered.

Nevertheless, female *C. gutturalis* were not attracted by increased multi-male interactions at courts, but rather by the proximity between courts. As such, we found 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 & 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. In turn, high-ranked males also presented increased activity, and low-ranked males aggregated around them , possibly due to their increased activity. For instance, males might join high-ranked males because high ranked receives more visits from females (hotshot hypothesis) or in order to compete for females, thus leading to more visible display courts and facilitating the comparison between males by females (female preference hypothesis) as shown by the results of spatial aggregation. As such, both models might operate and males may engage in seemingly semi-cooperative relationships, as has been reported for *Corapipo altera* (Jones et al 2014). These results provide therefore evidence that male *C. gutturalis* may cooperate to attract females, but that such cooperation does not necessarily increase reproductive success when compared to that of males that display in solitary, 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 *Corapipo gutturalis,* a species of manakin with a poorly understood lek system, providing cues about proximate drivers for lekking mating systems. Prum (1986) discuss that this specie is different from other manakins with regard to its social organization, having a mobile lek system. Therefore, our study represents a first step to understanding how male *C. gutturalis* interact with one another and how females and males select male court holders to visit and settle around. As such, it provides insights into the seemingly obvious grouping behavior and male interaction within lekking species. Males aggregate around males that spend more time and display at higher rates, the high-rank individuals, that also received more female visits, supporting the hotshot hypothesis. We also showed that more males using a court during the breeding season increases court activity over time and attract females. As such, males may also increase display rates to stand out and be chosen by females, becoming high-rank males. However, females are not attracted to increased multi-male interactions at courts. Therefore, we suggest that the lek system of *C. gutturalis* revolves around males that defend display courts through their higher permanence and displays rates. Because females visited more often neighboring males, our results highlight the role of multiple models in driving the proximate evolution of lekking, which likely operates according to specific lek systems. 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. At the same time, spatial crowding also determined female visitation rates, indicating that comparison among males by females occur at a larger spatial scale (among courts or leks) than male-male competition, which happens within each court (or lek). This agrees with the idea that males compete at courts for opportunities to display in solo, but that male interaction at the court throughout the breeding season enhance 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.

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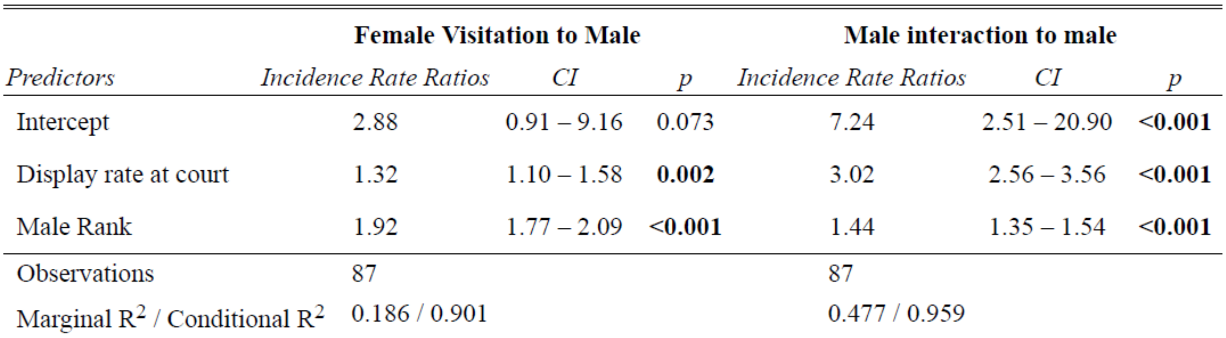
Table 1. Description of the variables used to generate models to test the hotshot and female preference hypotheses. We extracted the variables from the observation and capture data of the individuals in different courts in three reproductive seasons.

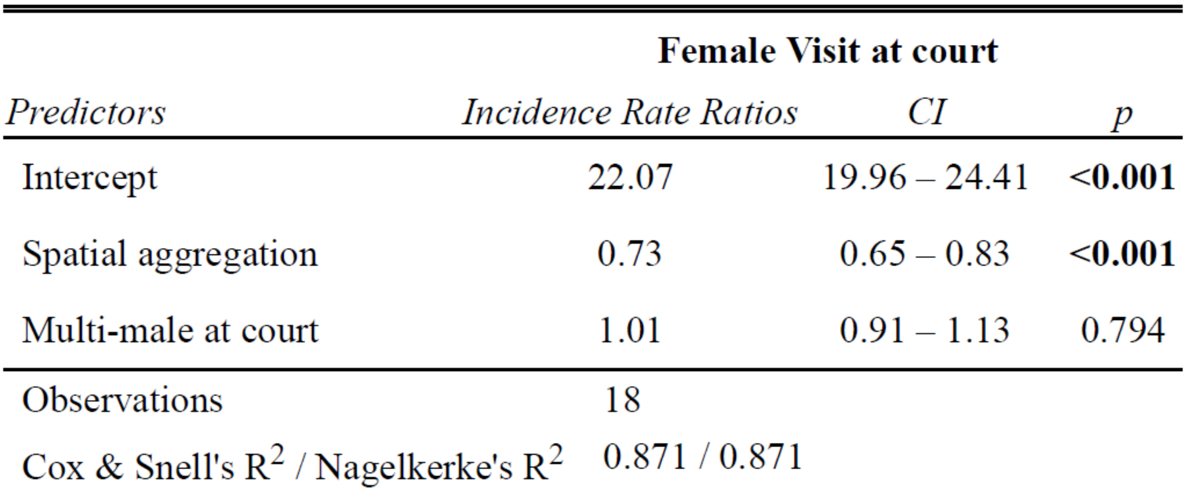
Hotshot model	
Response variable	Description
Female visitation to male	The number of times a female was captured or observed together with the male on a court in a breeding season, divided by the number of samples of court.
Male interaction to other males	Total number of different males observed or captured with each male on the same court in the same breeding season, divided by the number of samples of court.
Predictor variable	
Male rank	Based on the permanence, activity and experience of male individuals, we created an index to rank them. More details see equation 1
Display rate at court	To estimate the activity at court, we used the activity of all males, excluding the activity of the highest-ranking male of each court. More details see equation 2
Female preference model	
Response variable	
Female visitation at court	The number of times a female was captured or observed on a court in a breeding season, divided by the number of samples of court.
Predictor variable	
Spatial aggregation	Average distance (m) of the three display courts closest to the display court observed.
Multi-male interaction at court	Number of intervals in which more than one male was observed in around the court divided by the number of intervals sampled in the court.

Table 2. S*tatistics of general linear mixed models* for explaining female visitation to males and male interaction to other males. Models were generalized with Poisson distributions. Display rates at courts and male rank were used *as predictor variables*. Display court id and breeding season were used as *random effects*. N= 87, corresponding to all male individuals observed in different courts in all breeding seasons.



	Female Visitation to Male			**Male interaction to male**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
Intercept	2.88	0.91 – 9.16	0.073	7.24	2.51 – 20.90	**<0.001**
Display rate at court	1.32	1.10 – 1.58	**0.002**	3.02	2.56 – 3.56	**<0.001**
Male Rank	1.92	1.77 – 2.09	**<0.001**	1.44	1.35 – 1.54	**<0.001**
Observations	87			87		
Marginal R^2 / Conditional R^2	0.186 / 0.901			0.477 / 0.959		

Table 3. Female visitation at court statistics of general linear models, the model was generalized with Poisson distributions. We used as predictor variables: Spatial aggregation (distance to nearest neighbors in meters) and multi-male interaction at courts. N= 18 corresponding to the total of courts observed in the different breeding season.



	Female Visit at court		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Intercept	22.07	19.96 – 24.41	**<0.001**
Spatial aggregation	0.73	0.65 – 0.83	**<0.001**
Multi-male at court	1.01	0.91 – 1.13	0.794
Observations	18		
Cox & Snell's R^2 / Nagelkerke's R^2	0.871 / 0.871		

Figure legends

Figure 1. Relationship between: a) female visitation to males and the male rank; b) female visitation to males and the display rate at courts to which these males belong; c) male interaction to male and the male rank; d) male interaction to male and the display rate at courts to which these males belong, derived from the generalized linear model with Poisson distribution. *N*= 87, corresponding the observations of males in different courts in different breeding season for all results.

Figure 2. Relationship between a) female visitation at courts and multi-male at court; b) female visitation at courts and spatial aggregation, derived from the generalized linear model with Poisson distribution. *N*= 18 corresponding to the total of courts observed in the different breeding season for all results.

SUPPORTING INFORMATION

Table S1. VIF for all the variables included in the regressions.

Predictor	VIF Female visitation to male	VIF Male interaction to other males	VIF Female visitation at court
Display rate at court	1.05	1.05	-
Male Rank	1.05	1.05	-
Spatial aggregation	-	-	1.00
Multi-male interaction at court	-	-	1.00

Figure S2. Percentage of display solitary vs. display on presence of another male around the court, with presence and absence of female (x^2=7.36, df=1, p=0.006). N= 80 interval observed with display.

Figure S2. Relationship between Display rate of court without high-rank males and High-rank male display rates (R =0.64; *p*= 0.004). *N*= 18 corresponding to the total of courts observed in the different breeding season.

Figure S3. Association between display rate at court and total male display rate (blue dots and lines) and without females (red dots and lines). N= 18 corresponding to the total of courts observed in the different breeding season.

Figure 1.

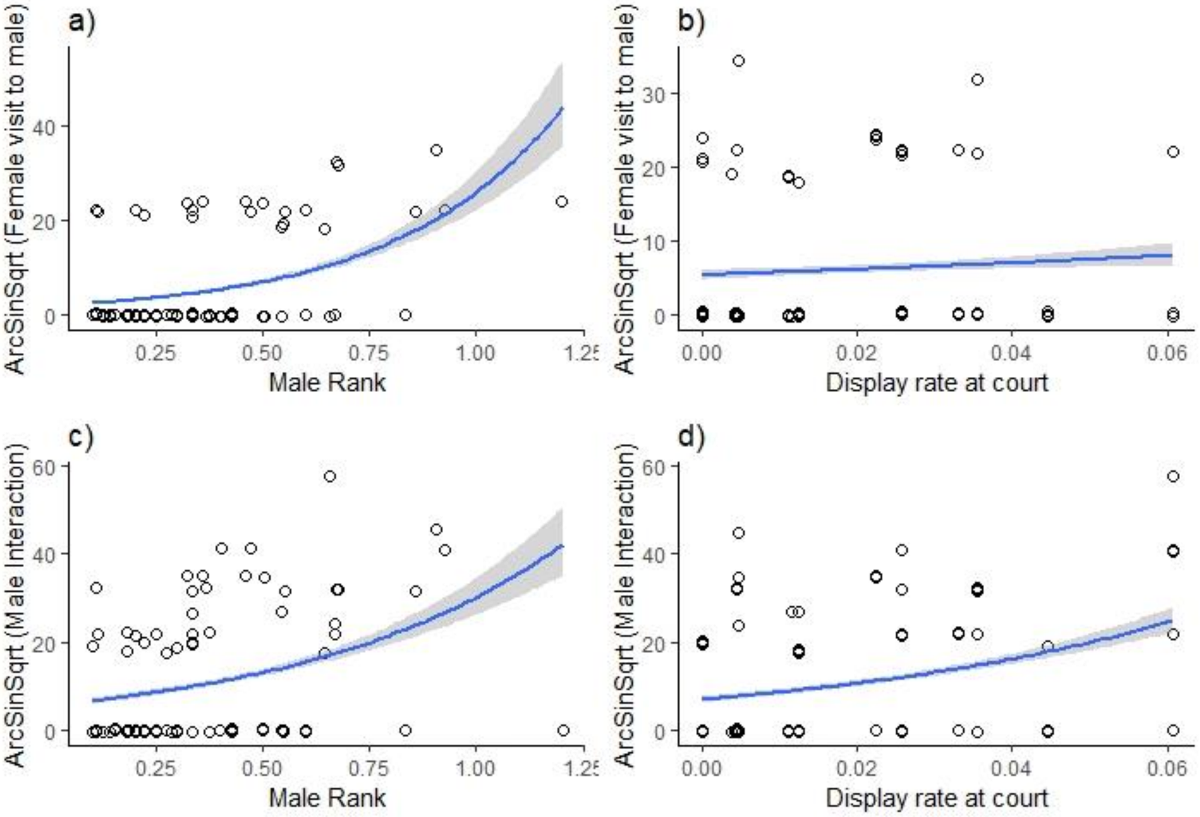


Figure 2.

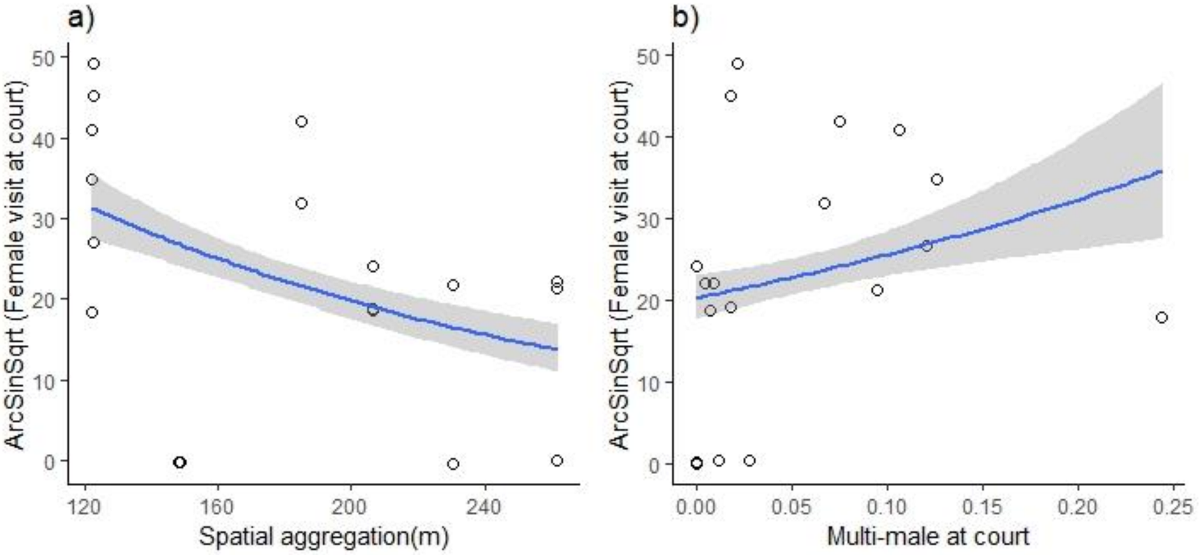


Figure S1.

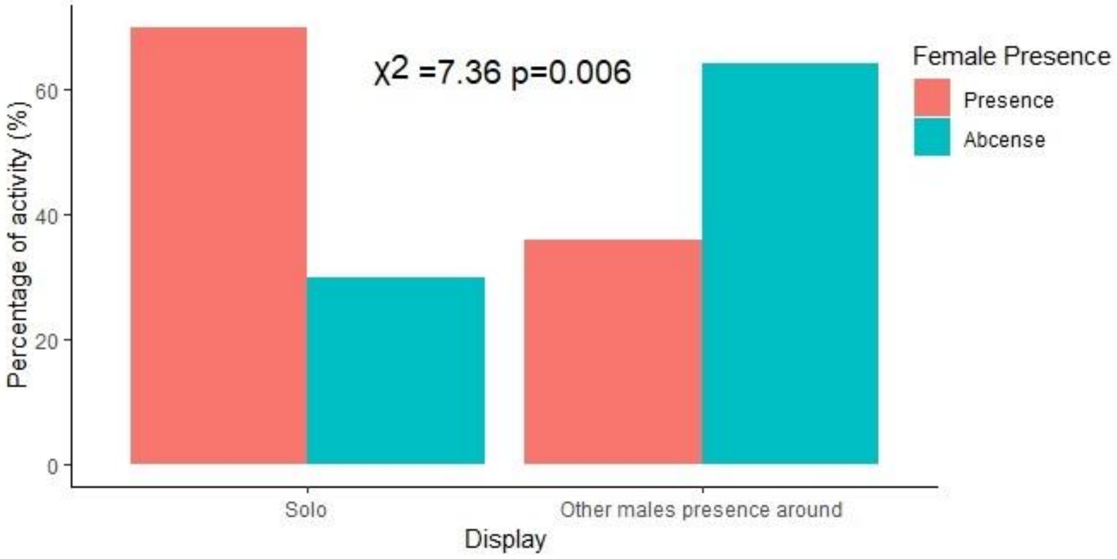


Figure S2.

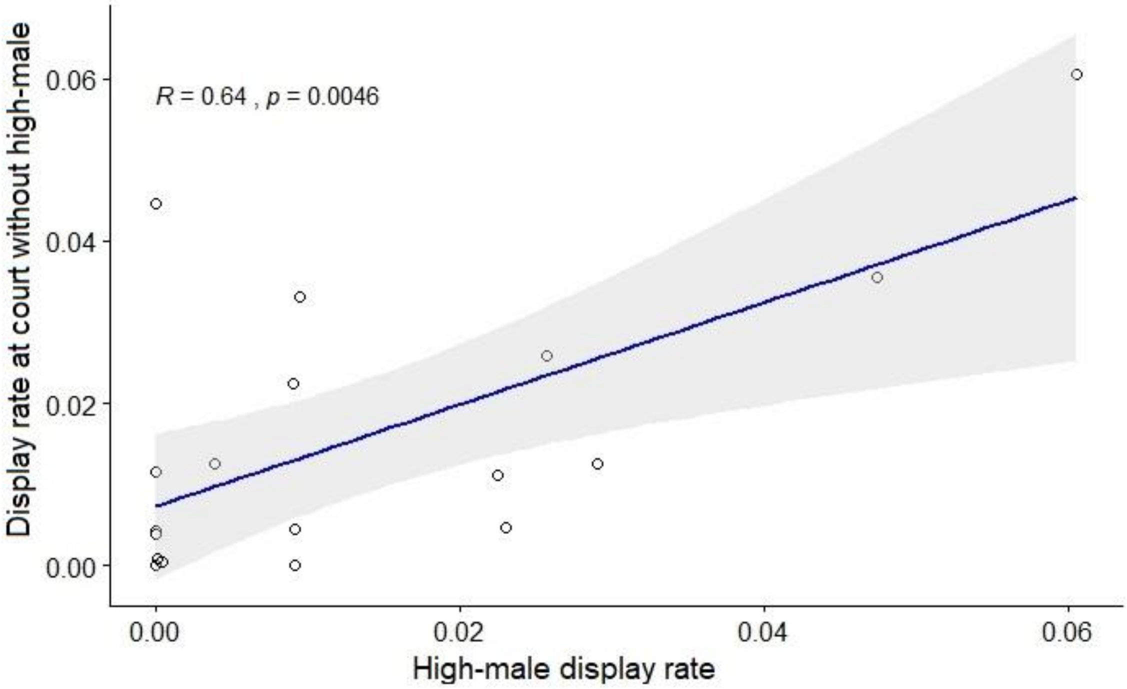
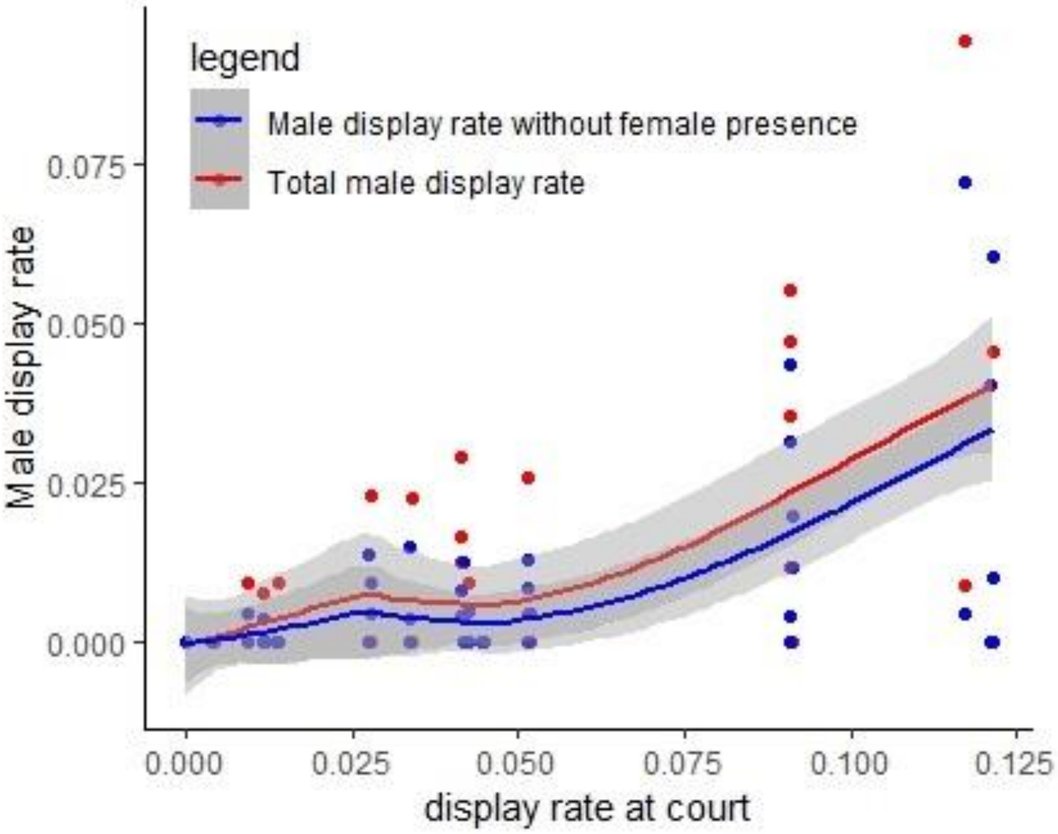


Figure S3.


legend
Male display rate without female presence
Total male display rate
Male display rate
0.000
0.025
0.050
0.075
display rate at court
0.000
0.025
0.050
0.075
0.100
0.125

CAPÍTULO 2

Display above courts of White-throated manakins: a new view about its display behavior

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Display above courts of White-throated manakins: a new view about its display behavior

Short running title: What happens above the fallen log?

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Abstract

In order to breed successfully, organisms exhibit multiple strategies to enhance mate attraction, such as elaborate physical ornamentation, behavioral courtship displays, and social interactions, leading to competition or cooperation among potential mates. Within lek mating systems, species evolve under strong sexual selection, which promotes the evolution of exaggerated sexual traits such as male courtship displays.

The White-throated manakin, *Corapipo gutturalis*, is a small Neotropical bird mating in leks where males display courtships to attract females. Their displays commonly take place on fallen logs on the forest floor, but there are descriptions of displays on higher forest stratum above the typical logs. In this study, we aimed at adding new behavioral information on the above-log displays and to compare them to log displays in their potential to attract females. For this, we conducted focal observations on seven display courts in two reproductive seasons for 193 hr. and recorded above-log displays in four of the seven observed courts. Above-log displays were always performed in groups of up to four males from multiple ages and, on only two occasions, these displays ended on the display log. We recorded the same elements previously described during above-log displays for the species, besides the side-to-side slide that had not yet been registered for the species. Above-log displays included more males than log displays. However, there was no significant difference in the frequency of females visit to above-log displays or log displays and, likewise, the number of males engaging in the above-log displays did not determine female visits either. Thus, we found no evidence that above-log displays are more effective at attracting females than those on the log display. Since above-log displays are always in the presence of multiple males, we suggest that it may represent male–male competition to define male individuals accessing the display logs.

Keywords: male-male interaction- female choice- sexual selection- lek polygyny.

Introduction

In order to increase reproductive success, animals have evolved different strategies and mechanisms to attract their reproductive partners, which defines sexual selection. As a result, individuals are constantly competing to attract the other sex for mating, a mechanism called “intrasexual selection”, while others will choose to mate with partners with good conditions, often related to their genetic quality, a mechanism called “intersexual selection” (Andersson, 1994; Darwin, 1871; Moore, 1990; Prum, 2012). Thus, both sexes play a fundamental role in sexual selection. As such, individuals invest energy to maintain ornaments, displays, weaponry, and social interactions, in order to find and compete for mates (Andersson, 1994; Morales, Alonso, Martín, Martín, & Alonso, 2003; Sardà-Palomera, Puigcerver, Vinyoles, & Rodríguez-Teijeiro, 2011).

In polygynous leks, that is, when males aggregate for the sole purpose of attracting females (Höglund & Alatalo, 1995), strong sexual selection leads to the evolution of elaborate display ornaments, vocalizations, and dances (Bostwick & Prum, 2003; Höglund & Alatalo, 1995). These displays are considered to involve high energy costs to males and, as such, they should be efficient in reaching and pleasing most females (Clark, 2012; Mappes, Alatalo, Kotiaho, & Parri, 1996). Some studies show that, within polygynous leks, females are more attracted to larger male aggregations (Alatalo, Höglund, Lundberg, & Sutherland, 1992; Bradbury, 1981; Wittenberger, 1978; Bosholn, Fecchio, Silveira, Braga, & Anciães, 2016); in other cases, females are more attracted to a high-quality male that denotes good genetic conditions (Ilmonen, Stundner, Tho, & Penn, 2009; Kempenaers, 2007). Thus, in such systems, both male aggregations and their performances are of greatest importance in attracting mates.

Lekking is thus present in most species within the Pipridae (Manakins) (Kinwan & Green, 2011), with differences among species in spatial and social organization and interactions, as well as display elements and complexity (Anciães et al., 2009; Lindsay, Houck, Giuliano, & Day, 2015; Prum, 1990, 1994). In some species, displays can be coordinated by paired males, where the alpha male is most often chosen by females, as in the genus Chiroxiphia (Cárdenas-Posada, Cadena, Blake, & Loiselle, 2018; Duval, 2007; Lukianchuk & Doucet, 2014; Trainer, McDonald, & Learn, 2002). Displays may also be solitary within courts and most often without auditory or visual contact with other males, such as in Pseudopipra pipra, Masius, and Ilicura (Anciães & Prum, 2008; Castro-Astor, Alves, & Cavalcanti, 2004). In contrast, in species of Corapipo males display mostly in solitary (Prum, 1994; Prum, 1986; Prum & Johnson, 1987; Anciães & Prum, 2008), but are also observed displaying in pairs in Corapipo altera and Corapipo heteroleuca, both of which, solo and group displays, may result in copulation, being called for that as facultative cooperation (Jones, DuVal, & Boyle, 2014). These examples show us the diversity of social associations in lekking systems.

White-throated Manakin (*Corapipo gutturalis*) is a species of Manakin that lives in the rainforest understory and is found in Venezuela, Guyana, and Brazil (Meyer de Schauensee, 1970; Snow, 2004). Like the vast majority of Manakin species, male *C. gutturalis* form leks to attract females. These leks are made up of five to eight males that perform courtships in courts. Courts are described as fallen logs in the forest floor being 30 meters apart from each other within a lek (Prum, 1986; Théry & Vehrencamp, 1995). Leks are composed by juvenile males and some adult males who do not have their own court display. These juvenile and adult males interact with older, faithful males on the court display (Prum, 1986; Théry, 1990). They exhibit marked sexual dimorphism, where males are bluish-black with a white spot on their throat and wings when open, while juvenile females and males are grayish-green, weighing an average of eight grams (Prum, 1986). This species chooses periods of the day to display using the light that reaches the display log to increase the contrast between its colors and the display log used (Anciães & Prum, 2008; Endler & Thery, 1996; Loiselle, Blake, Durães, Ryder, & Tori, 2007; Théry & Vehrencamp, 1995; Tori et al., 2008).

In this study, we add information to the displays above the logs previously described for the White-throated Manakin (Prum, 1986) and compared these displays with the typical displays on fallen logs. Specifically, we aim at understanding the purpose of displays above logs, for which we tested the hypothesis that females have different preferences between these two displays. For this, we first tested whether the number of males present on the above-log displays differs from the number of males present around the log display during the typical solitary male on log displays (M. Tolentino, unpublished data). Then, we tested whether female attraction differs between above-log displays and log displays. Lastly, we tested if the number of males present on the above-log displays varied with female visitation.

Methods

Study area

We sampled white-throated manakins at courts during display in two breeding seasons (2016 and 2017), within a continuous forest from 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) (Laurance et al., 2011). We conducted our research in the continuous forest reserve named km 41. This reserve is composed of approximately 10,000 ha of the continuous forest with a trail-grid of 1,000 ha. The area is classified as a *terra firme* forest, which is not seasonally flooded. The average annual rainfall in the area is ~2,200 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 & Mori, 1999; Laurance et al., 2010).

Data collection

During the two breeding seasons, lasting from August through January in 2016 and 2017, we mist net birds and conducted focal observations on seven display courts of the species (Figure 1a). Each court comprises perches where males aggregate to display for females, either in the forest floor, the typical log displays on fallen moss-covered logs (Figure 1b) and the above-log displays, on display perches about 5–10 m above the log display within the same display court (Figure 1c). Captures in mist nets allowed color banding birds for identification and collecting blood samples for sexing green individuals (following Ito, Sudo-Yamaji, Abe, Murase, & Tsubota, 2003).

Observations were made between 6:00 a.m. and 2 p.m. Each observation period lasted around 6 hr., and each court was sampled repeatedly three times, with an interval of at least two consecutive days between samples. We performed observations with binoculars (Nikon Monarch10 × 42 mm) behind a camouflage blind placed at about 10 m from the display log, to reduce disturbance to courts. We video recorded (Sony HD PJ 200) displays to backup and ground truth proofs of observation data. Above-log displays were rarely possible to video-record but MT observed a total of 3.5 hr. of displays at these perches, and 193 hr. of total effort at the display courts using 5-min intervals of continuous focal observations (Altmann, 1974; Bosholn & Anciães, 2018), which represents our sample unit. For each sample, we recorded the perch used by males (log-, above-log, or both), the presence and number of males, their identification when color banded, age, and quantified their displays and vocalization in number of events for each element described for the species as well as whether females were present or absent at the perch (Prum, 1986; Prum & Johnson, 1987; review in Anciães et al., 2009).

Data analysis

From the observations at each display court (illustrated in Figure 1a), we extracted for the data analysis: samples with display at the court; display perch (above logs or on logs, Figure 1b,c, respectively); number of samples with displays at each display perch; number of males present in each display perch and presence or absence of female in the display perches. First, we tested for differences in the number of males present on log- versus above-log displays with a Wilcoxon paired-sample test. We, then, run a chi-square to compare the frequency of female presence in samples during log displays to those during above-log displays. Because display perches might be non-independent, we also nested samples within courts in order to test if the frequency of female presence in samples during log displays differed from that during above-log displays occurring in perches immediately above it, that is, within the same display court, with a Wilcoxon paired-sample test. Finally, we tested if the presence of females during above-log displays was related to the number of males during these displays with a Wilcoxon test. All analyses were performed in R 3.5.2 (R Development R Core Team, 2019), and we used the ggplot2 package (Wickham, 2009) to produce figures.

Results

We conducted a total of 193 hr. of observation in the seven different courts during the two breeding seasons. We recorded above-log displays in four of the seven courts, totaling 45 samples with such displays, among 116 for all displays (at logs and above it summed). These displays were always held above the display log (Figure 1). The above-log displays were always performed by more than one male, of either age, but always with the presence of at least one male in definitive adult-like plumage and occurred in the presence or absence of females (N = 11 or 24.5% and N = 34 or 75.5%, respectively).

During the observation of the above-log displays, we recorded seven of the elements already described for the species: horizontal posture, bill pointing, chin-down, hunched posture, about-face and to and fro (examples: Figure 2a,b, Video S1), and flight between perches for to kick out expel the other individual (Figure 2c, Video S2). Additionally, we recorded side-to-side slides (Figure 2b, Video S3) on all courts with displays above.

We observed a higher frequency of log displays than above-log displays (total = 71 and 45, respectively; chi-squared = 4.99, df = 1, p = .02, N = 2,316). In only two occasions, the above-log displays ended in log displays. We found significant differences in the number of males present in displays above logs versus in log displays (x = 1.78 and 2.75 males in log displays and above-log displays, respectively, W = 2,542, p < .001, sample size = 116; Figure 3), but no significant differences in the presence of females during above logs and log displays at the seven display courts (total = 21 female visits of 71 sample in 5 log displays versus 11 of 45 sample in 4 above-log displays, chi-squared = 0.15, df = 1, p = .70, sample size = 116; Figure 4a), or when we paired female visits during log displays and above-log display at each court (x = 3.5 females in log displays versus 1.8 females in above-log displays, Wilcoxon paired-sample V = 2, p = .89, sample size = 7; Figure 4b). We also did not find association between the number of males present at above-log displays and female presence (x = 2.25 males in presence of female versus 2.34 males in absence of female, W = 191, p-value = .9107, sample size = 45, Figure 5).

Discussion

Previous studies on *C. gutturalis* behavior at leks focused their efforts mainly on ground-level displays on fallen logs, with the displays above logs only cited in their observations (Davis, 1949; Théry, 1990) and in more detailed in Prum (1986). Our observations meet those descriptions, besides adding one new element, the side-to-side slide, to the behavioral repertoire currently known for the species, as well as new information about the social context in which above-log displays are performed, including unique video footage of such displays. Based on the compilation in the review by Anciães et al. (2009), which presents 15 display elements for *C. gutturalis*, we recorded eight of the elements already described for the species during our observation of above-log displays, all of which had been also described by Prum (1986) during above-log displays of the species. The side-to-side slide had been observed mainly in species within *Ceratopipra* and *Machaeropterus* (Anciães et al., 2009; Prum, 1990). Thus, the present observation changes the current hypothesis of when this display element evolved in the family, which would then be hypothesized to have evolved earlier in the phylogeny than previously proposed Prum (1990).

We observed higher interaction between males during above-log displays than during log displays, as above-log displays were always observed with the presence of more than one male, and all males engaged in some display activity, either vocalizations or the display elements cited above. Prum (1986) did not specify whether there was ever more than one individual in the displays above logs that he observed, which were considered as preliminary (anticipated) to the log displays. In our observations, however, in only two occasions, we observed log displays on the same day as the above-log displays at a single court. This could result from either geographical variation or differences in sampling effort between studies.

Apparently, the log displays are the main mating behavior of the species, as we recorded log displays to be nearly 60% higher than the above-log displays, and copulations were always observed on logs (Prum, 1986; Théry, 1990). Most displays of this species on the fallen log are solitary, either in the presence of females or other males surrounding the log (Prum, 1986; Théry, 1990; M. Tolentino, unpublished data), unlike the above-log displays, where there are always two to four males displaying concomitantly. Several studies show that males aggregate as a strategy to attract females (Beehler & Foster, 1988; Bradbury, 1981; Hernandez, Houston, & McNamara, 1999; Lank & Smith, 1992; Sæther, 2002). We found no difference in potential female attraction between log displays and above-log displays, nor a pattern showing that displays above logs, by including multiple males, attract more females within courts. Likewise, we did not find an association between the number of males interacting during above-log displays and female visits, to the contrary of what has been observed during log displays, where solitary males are more likely to receive female visits (Foster, 1983; M. Tolentino, unpublished data). Thus, we suggest that female attraction differs between above-log displays and log displays (Figure S1).

Female visitation ends in copulation only in absence of multiple males at the display courts, a phenomenon known to prevent copulation disruption by subordinate males that is observed even in cooperative lek systems, where multi-male coalitions are reinforced by female attraction (Foster, 1977; DuVal, 2007; Trainer et al.., 2002). Although log displays in *Corapipo gutturalis* can be performed at a single log by multiple (2–4) males, each male engages in log displays only in solitary, so that multiple males display non-concomitantly at a single log. As such, log displays in *Corapipo gutturalis* are likely pre-copulatory, whereas male–male interactions might be held around (M. Tolentino, unpublished data) or above the logs as shown here, suggesting that males compete for accessing the main court (the logs), where females visit them for copulating. These findings highlight a dual role of male aggregation in the evolution of lekking, first as a source of male–male competition to define access to courts where females will copulate, likely after comparing among successive male displays at the main court. At this point, we may not uncover the specific social dynamics between above-log and log displays, that is, in the identity of males and the interplay between display perches within, and among, courts. But, considering that there are more males during above-log than log displays, we may conclude that it exerts a role in reducing the number of males that will access the logs for displaying toward females and, possibly copulate.

On an evolutionary perspective, our data on above-log displays compared to log displays in *Corapipo* and *Masius* suggests a transition from more primitive solitary displays in *Masius*, also found in *Ilicura*, toward more complex male–male coalitions among species of *Corapipo* (Anciães & Prum, 2008; Prum, 1994; Prum & Johnson, 1987). *Corapipo gutturalis* is the sister to the other species within the genus, and thus seems to present the least complex, yet group based social behavior, in comparison to the facultative cooperation reported for *C. altera*, in which males display in pairs at logs (Jones et al., 2014), just like its close relative from the Pacific-coast, *C. heteroleuca* (M. Anciães, unpublished data). Thus, our results uncover a greater behavioral diversity in the Masius-Ilicura clade than previously recognized.

Our findings elucidate the use of above-log displays by male *C. gutturalis* and shed light on its role for mate choice, through male–male competition and female choice at these perches. Although this behavior is relatively frequent (observed in about one-third of the samples with displays), they do not seem to dictate the number of males engaging the log displays, as above-log displays included multiple males and log displays were usually solo. Furthermore, the number of males engaging in above-log displays does not relate to female presence at courts, as multi-male displays above logs were also quite frequent in the absence of females. Nevertheless, the lack of difference in female visits to log and above-log displays when controlling for court ID suggests a role of above-log displays in female attraction to male comparison during these displays (both within and between courts) or through male–male competition for defining court holders (alpha males).

Finally, our study brings new field-based data that improved our understanding of the behavior and evolution of a species with complex mating systems. Additional data on the spatio-temporal dynamics of courtship displays in this species will allow more accurate conclusions about their consequences to mate acquisition and individual fitness. These data will be crucial to increase our knowledge about the effects of diverse social dynamics on the evolution of polygamous clades through sexual selection.

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Figure legends

Figure 1. Illustrative representation of display courts: (a) Fallen log and perches used in above-log displays; (b) Zoom in a typical display log, where males display mostly in solitary and where copulation takes place; (c) Zoom in a above-log display perch, (height range 5–10 m), where at least two males vocalize and display between perches

Figure 2. (a, b) Display elements observed by Prum (1986) and in this study: (a) About-face display, wing-shiver, and chin-down posture, in which males flip wings and turn 180° on the perch and fly to another perch before repeating the turn; (b), to and fro, in which males fly fast between perches before stopping to perform the display described in (a). (c) Aggressive behavior in which one male expulse another male from the display perch, who flies off to a nearby perch; and (d). Side-to-side slide, a new display element, first recorded for the species during this study, in which a male slide sideways the display perch

Figure 3. Number of males present during above-log and log displays

Figure 4. (a) Association between male displays above logs and on logs to female visits; (b) Total number of female visits (samples with female presence) to perches above logs and logs within individual courts

Figure 5. Number of males displaying above logs when females are present or absent

Supporting information

Figure S1. Number of males displaying above logs and on logs when females are present or absent. The frequency of the number of males is represented by the width of the bar.

Video S1. The video illustrates the above-log display of *Corapipo gutturalis*, with three adult males displaying different elements. Footage recorded by MT in the PDBFF Km 41 Reserve, approximately 80 Km north of Manaus, AM, Brazil.

https://drive.google.com/file/d/1JGpOzvijLpFMuXpDF-WpNUqvuiq0rWGg/view?usp=sharing

Video S2. Close-up video showing flight displays between perches in which individuals seem to expulse each other during above-log displays. Footage recorded by MT in the PDBFF Km 41 Reserve, approximately 80 Km north of Manaus, AM, Brazil.

https://drive.google.com/file/d/1za3C73nswgXMC7O2QYoIZqBQZrllVjiN/view?usp=sharing

Video S3. Close-up video of the side-to-side slide performed during above-log displays. Footage recorded by MT in the PDBFF Km 41 Reserve, approximately 80 Km north of Manaus, AM, Brazil.

https://drive.google.com/file/d/17QSQeClt2O7uHG4lXAJTFHjXSOgDnt9m/view?usp=sharing

Figure 1.

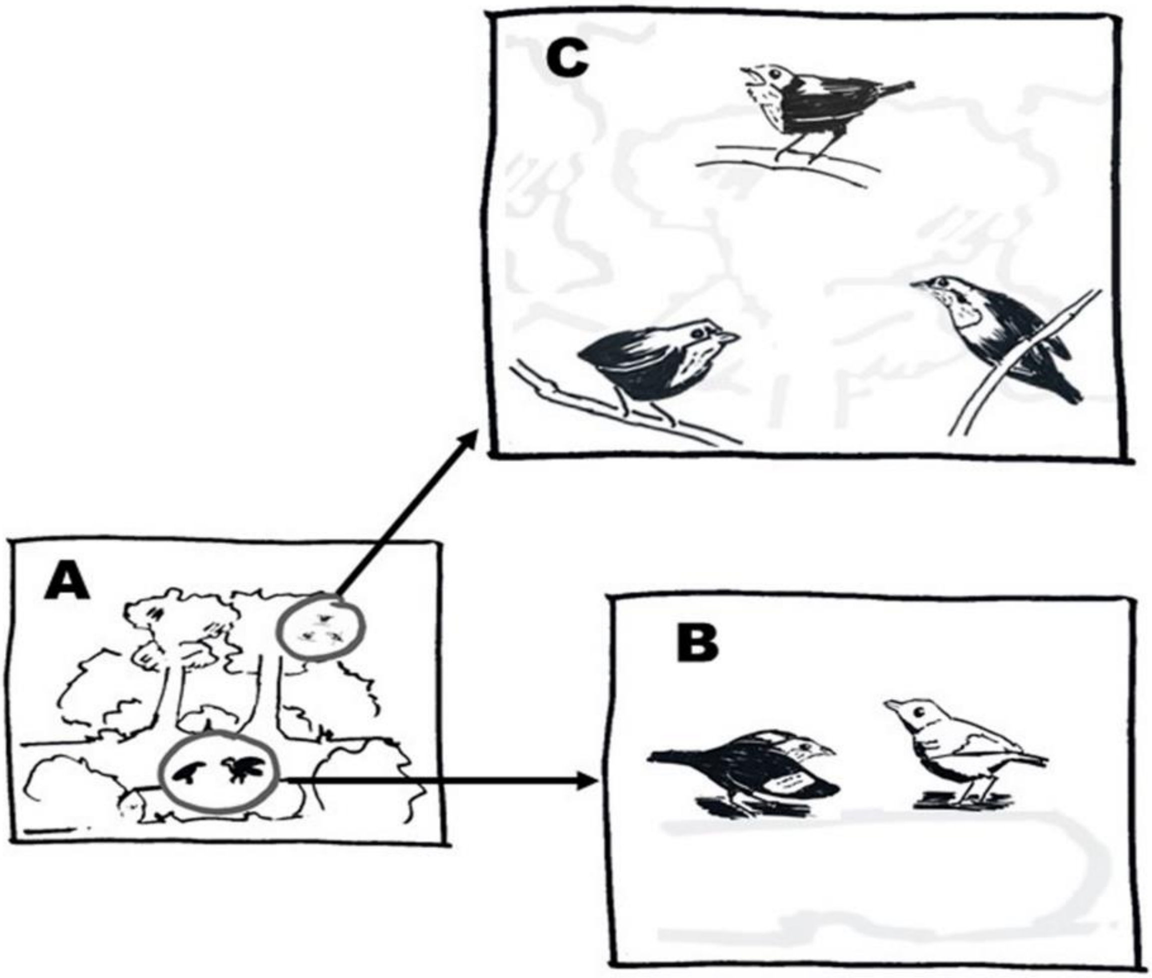


Figure 2.

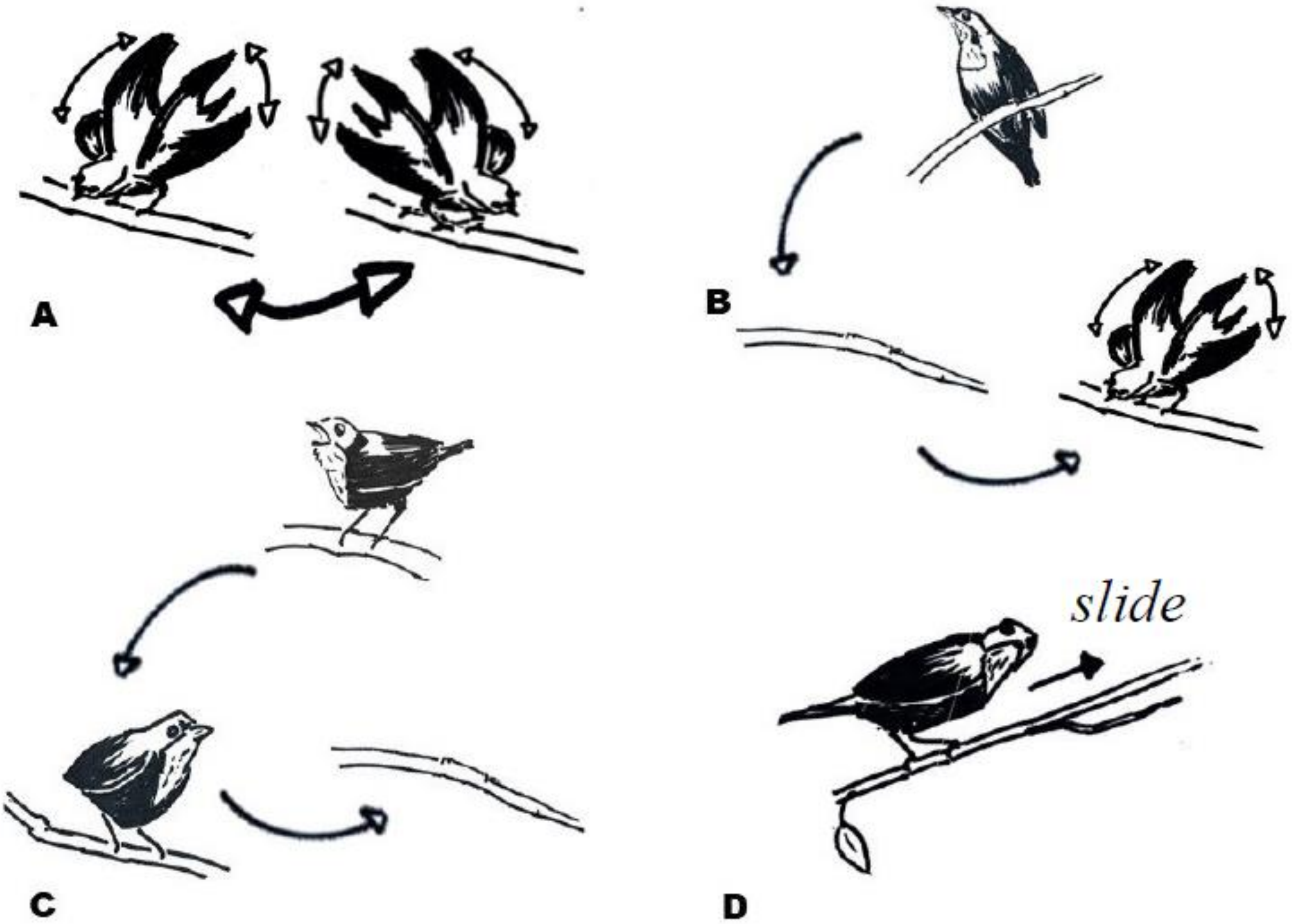


Figure 3.

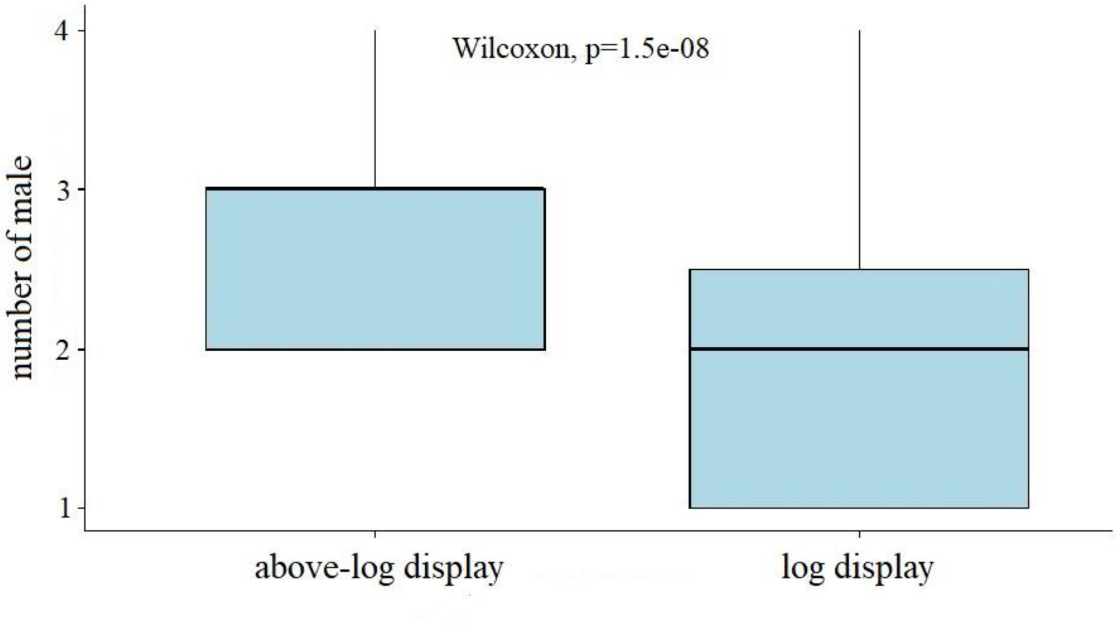

Wilcoxon, p=1.5e-08
number of male
4
3
2
1
above-log display
log display

Figure 4.

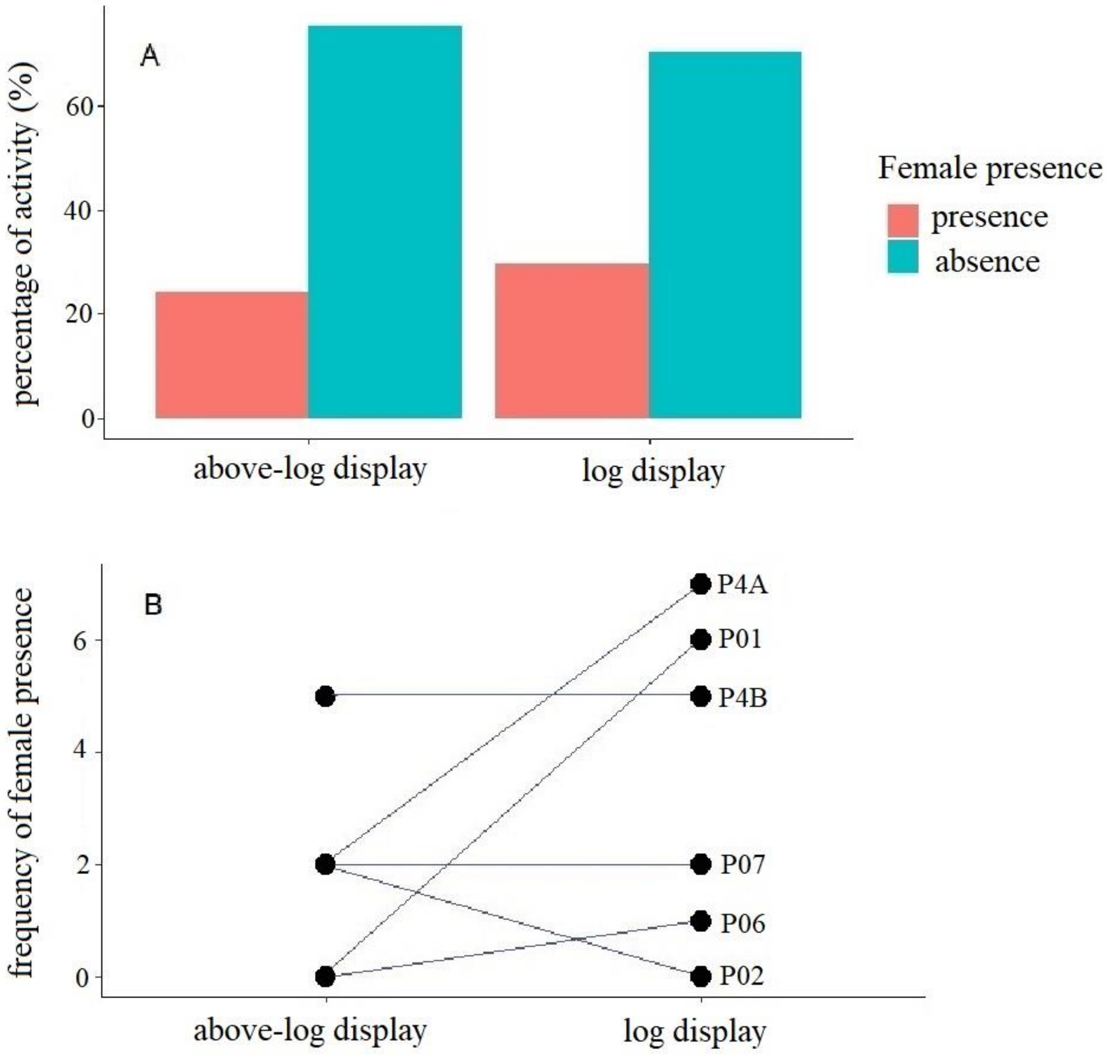

A
percentage of activity (%)
0
20
40
60
above-log display
log display
Female presence
presence
absence
B
frequency of female presence
0
2
4
6
above-log display
log display
P4A
P01
P4B
P07
P06
P02

Figure 5.

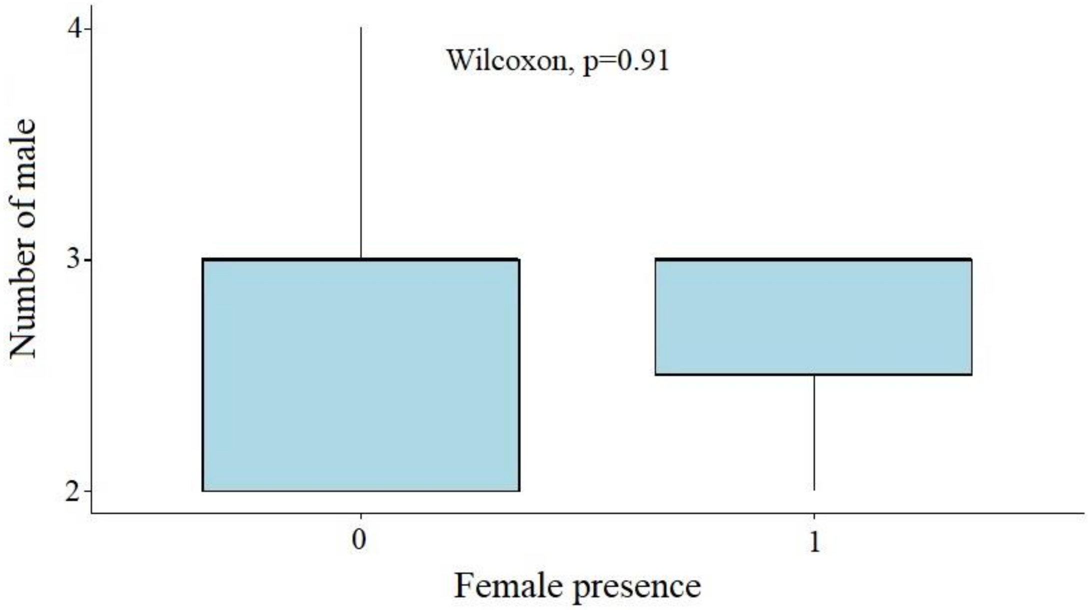
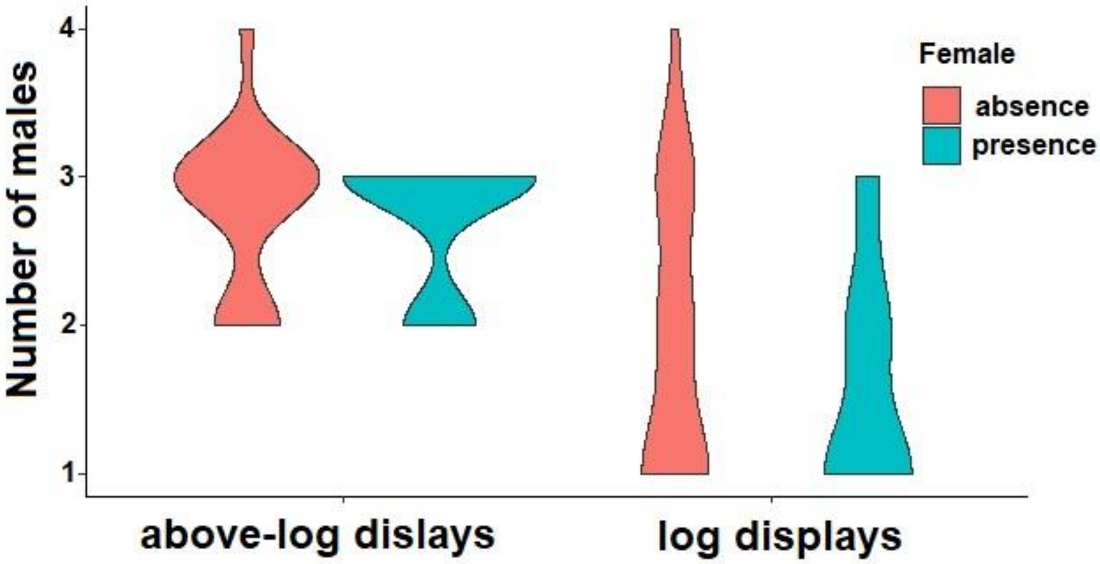


Figure S1


Number of males
4
3
2
1
above-log dislays
log displays
Female
absence
presence

Síntese

Nessa tese investigou-se como fatores sociais e espaciais determinam a agregação de machos em leques do Dançarino-de-garganta-branca, na Amazônia Central. Os resultados demostraram que, no sistema de leque em questão, temos uma associação de fatores que determinam a agregação de machos, sendo esses fatores dependentes da escala, dinâmica e interação dos indivíduos. A espécie estudada, apesar de já ter sua organização social descrita, apresentou diversas peculiaridades comportamentais, que nos leva a entender o quão diverso é esse sistema e como pode se comportar de diferentes maneiras dependendo da espécie, não sendo possível generalizar as descobertas para todo o sistema e sim procurar as peculiaridades existentes em cada espécie, como elucidado em cada capítulo.

No primeiro capítulo testei as hipóteses de *hotshot* (Beehler & Foster, 1988) e Preferência de Fêmea (Bradbury 1981), hipóteses criadas para explicar a evolução de leques, onde utilizei como proxy a agregação de machos. Os resultados mostraram que tanto machos quanto fêmeas são mais atraídos por um macho que tem um rank maior na arena. Isso corrobora a hipótese de *hotshot*. Também encontrei que fêmeas visitam mais as arenas próximas umas das outras, o que é um indicativo de preferência de fêmea. Logo, nesse sistema temos uma associação entre *hotshot* e preferência de fêmea (Figura 1). A partir desses resultados, levantei dois questionamentos para trabalhos futuros: (1) o macho mais visitado pelas fêmeas apresenta o maior sucesso reprodutivo efetivo?; e (2) considerando, se os demais machos, os que ficam próximo ao redor dos macho que recebe mais visitas, precisam competir para chegar ao topo do rank, será que existe relação entre a distância das arenas e os machos de maior rank?

No segundo capítulo, realizei descrições sobre um comportamento de exibição pouco observado anteriormente. Descrevi exibições realizadas por machos do Dançarino-de-garganta-branca em galhos acima da arena de exibição (tronco caído na floresta), entre 5-10m de altura e testei se a visita de fêmeas está relacionada com o local onde a espécie realiza as exibições (nos galhos acima da arena ou na arena). Durante as observações, realizei registros visuais e acústicos dos elementos já descritos para a espécie e adicionei um novo elemento que ainda não havia sido registrado, onde o macho em um galho acima da arena desliza para o lado. Esse elemento havia sido descrito apenas para o gênero *Pipra*, o que sugere que o aparecimento desse elemento seja diferente evolutivamente dos elementos que são descritos atualmente. Essas exibições sempre são realizadas por mais de um macho. Como resultado, observei uma diferença significativa entre o número de indivíduos que estão nas exibições acima da arena e as exibições na arena com machos ao redor do macho que se exibe, sendo que a maioria das exibições na arena são solitárias podendo ter a presença de outros machos ao redor. Apesar dessa diferença entre o número de machos, não encontrei diferenças nas visitas de fêmeas nas arenas e acima delas (Figura 2). Assim sugiro que as exibições acima da arena têm uma função mais de competição entre os machos que para a atração de fêmeas propriamente dita, mas que também tem função de atração de fêmeas já que não encontrei diferenças significativas entre as visitas no tronco e acima.

Assim as informações apresentadas nesta tese não apenas mostram novidades sobre o *Corapipo gutturalis*, como nos leva a pensar que, como visto no capítulo 1, diferentes hipóteses podem explicar a evolução de leques para uma espécie. No capítulo 2, destacamos a importância das observações de campo e que ainda existe comportamentos não observados e com funções desconhecidas. Basta, literalmente, olhar para cima e encontramos uma nova dinâmica entre os indivíduos machos que acrescenta mais um passo ao sistema, envolvendo mais tipos de exibições e interações entre os machos. Para realizações futuras e complementação desse trabalho pretendo analisar a existência de trocas de machos de diferentes idades e ranks ao longo das estações reprodutivas e entre elas, bem como, entre as arenas de exibições. Com isso, terei uma noção sobre a dinâmica dos indivíduos ao longo do tempo e do espaço.

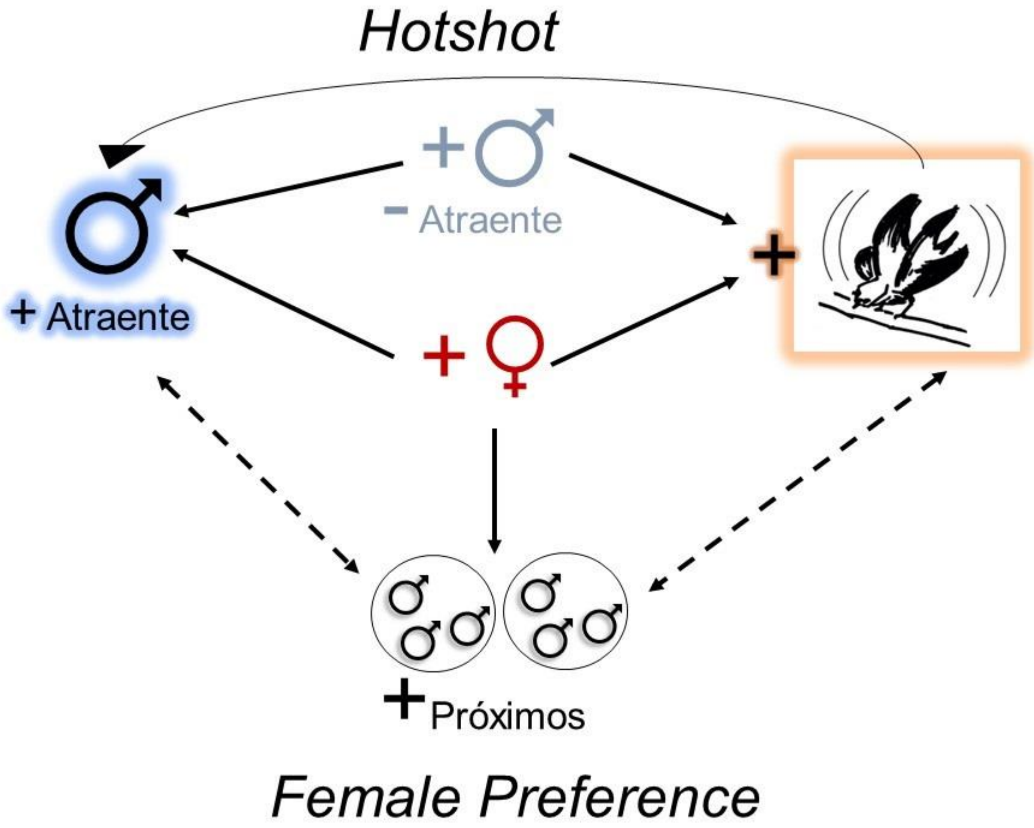


Figura 1: Uma síntese dos resultados encontrados no capítulo 1, onde com relação a hipótese de *Hotshot*: as linhas cheias apontando para o macho mais atraente significa que ele interagiu com mais machos e teve mais visitas de fêmeas, já as setas cheias voltadas mais a atividade dos arenas significa que as arenas como mais atividade também tiveram mais machos interagindo e mais visitas de fêmeas. A hipótese de *Female Preference* teve uma associação entre a proximidade das arenas e a visita de fêmeas. As linhas pontilhadas representam relações que não foram testadas nesse estudo e que fica como sugestão para estudos futuros.

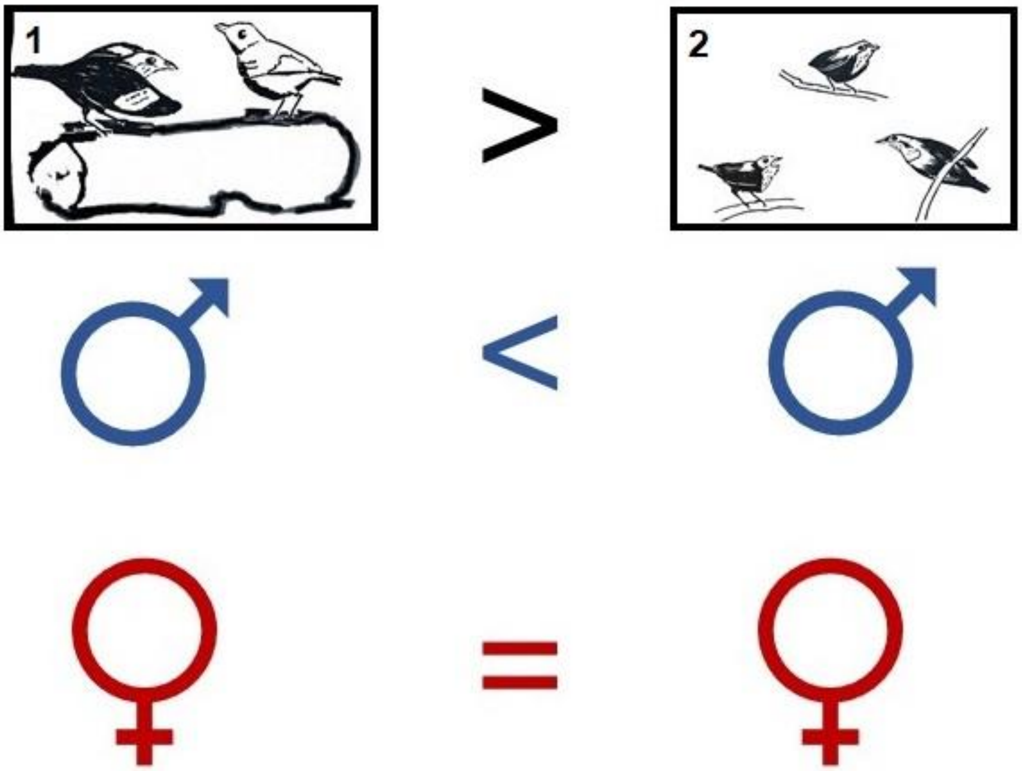


Figura 2: O capítulo 2 sintetizado na figura acima, onde em preto represento as observações das exibições: quadro 1 exibições no tronco, quadro 2 exibições acima dos troncos em galhos, o sinal de maior que representa que observei um maior número de exibições nos troncos. Em azul é representado o número de machos, onde observei mais machos participando de uma mesma exibição acima dos troncos. Em vermelho é representado a visita de fêmeas, onde as análises não mostraram diferenças significativas na visita de fêmeas nos dois locais.

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