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RESPOSTA COMPORTAMENTAL DE SAGUI-COMUM (*Callithrix jacchus*) À SIMULAÇÃO DE INTRUSOS EM UM AMBIENTE SEMIÁRIDO

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Dissertação apresentada à Coordenação do Programa de Pós-Graduação em Ecologia da Universidade Federal Rural de Pernambuco – UFRPE, como parte dos requisitos para obtenção do grau de Mestre em Ecologia.

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“What you do makes a difference, and you have to decide what kind of difference you want to make.”

Jane Goodall

Sumário

Resumo

Interações intergrupais são eventos importantes em espécies de animais com reprodução cooperativa, pois, além das interações agonísticas relacionadas à defesa de recursos, elas podem envolver interações afiliativas. Em saguis-comum, *Callithrix jacchus*, encontros entre grupos têm um papel importante na dinâmica social da espécie. Estudos observacionais sugerem múltiplas funções para esses encontros, como defesa de alimento, parceiros e oportunidades reprodutivas fora do grupo. No entanto, avaliar a contribuição desses diferentes aspectos funcionais em encontros intergrupos é uma tarefa desafiadora. Nesse sentido, estudos experimentais simulando invasores em contextos controlados são de grande utilidade. Desta forma, nosso objetivo foi entender o papel dos encontros intergrupais em saguis-comum, testando as hipóteses de defesa de território, defesa de parceiro e avaliação de oportunidades de reprodução utilizando simulações de invasores por uso de emissão de vocalizações (playbacks). O estudo foi desenvolvido com três grupos habituados vivendo em área de caatinga na Baracuhy Biological Field Station (7°31’42”S, 36°17’50”W), no município de Cabaceiras, Paraíba, Nordeste do Brasil, entre maio e dezembro de 2016. Para testar nossas hipóteses foram realizados experimentos com playbacks de coespecificos machos e fêmeas, de outros grupos, simulando a presença de intrusos nas porções nucleares e periféricas da área de vida. A intensidade da reação dos grupos (velocidade para chegar no raio de 5m do alto-falante, porcentagem de membros do grupo que chegaram ao local do alto-falante, tempo de permanência no raio do alto-falante) foi independente do sexo do intruso simulado, porém, foi maior quando o intruso foi simulado em áreas nucleares. Machos e fêmeas reprodutores se deslocaram mais rapidamente quando o invasor foi do sexo oposto, na área núcleo. Quando o invasor simulado foi do mesmo sexo, as fêmeas reprodutoras apresentaram displays agressivos (piloeração). O mesmo não foi visualizado para machos. Nossos resultados apontam que a defesa de território não é a única motivação que conduz o comportamento dos saguis-comum em resposta a intrusos, podendo também conferir oportunidades para avaliar cópulas extras, o que também resultam em motivação para defesa de parceiros, sugerindo que esses encontros podem desempenhar mais de um papel significativo na vida social desses primatas.

Palavras-chave: Callitrichidae, interações entre grupos, sistema social cooperativo, conflito sexual, oportunidade de cópula

Abstract

Intergroup interactions are important events in species of animals living in cooperative breeding societies, giving the opportunity for affiliative interaction, besides the agonistic ones related with resource defense. In common marmosets, *Callithrix jacchus*, these encounters play an important role in the social dynamics of the species. Observational studies suggest multiple functions for these encounters, such as food defense, mate defense, and reproductive opportunities outside the group. However, evaluating the contribution of these different aspects involved in intergroup interactions is a challenging task. In this sense, experimental studies simulating invaders under controlled contexts are very useful. This way, our objective was to understand the role of intergroup encounters in common marmosets, testing the hypothesis of territorial defense, mate defense, and evaluation of breeding opportunities using playbacks to simulate intruders. The study was developed with three groups living in the Caatinga, at the Baracuhy Biological Field Station (7 ° 31'42 "S, 36 ° 17'50" W), in the municipality of Cabaceiras, Paraíba, between May and December 2016. To test our hypotheses, we performed experiments with playbacks of sole males and females from the nuclear and peripheral areas of their home ranges. The strength of groups’ reaction (speed to arrive in the 5-m radius of the loudspeaker, percentage of group members that arrived at loudspeaker location, time interval in the radius of loudspeaker) was independent of the sex of the simulated intruder but was greater when the intruder was simulated in the nuclear areas. Breeding males and females moved faster towards opposite-sex intruders. When the simulated invader was of the same sex, the breeding females exhibited aggressive displays (piloerection). The same was not observed for males. Our results indicate that territorial defense is not the only motivation that drives the behavior of common marmosets in response to intruders, as these events also offer opportunities to assess extra breeding opportunities, which also result in motivation for mate defense, suggesting that such encounters may play different significant roles in the social life of these primates.

Keywords: Callitrichidae, interactions between groups, cooperative social system, sexual conflict, extra-group copulation

1. Introdução Geral

Sistemas sociais de reprodução cooperativa são comuns em aves e mamíferos (SOLOMON & FRENCH, 1997), sendo caracterizados por grupos formados por indivíduos reprodutores (dominantes), geralmente um par, e indivíduos não-reprodutores (subordinados), que colaboram na defesa territorial e no cuidado da prole (cuidado aloparental) (SOLOMON & FRENCH, 1997; KINGMA et al., 2010; LUKAS & CLUTTON-BROCK, 2012). Nesse sistema, os indivíduos dominantes podem inibir a reprodução de subordinados de duas formas: inibição hormonal, quando a fêmea dominante inibe a ovulação das fêmeas subordinadas por meio da liberação de feromônios (ABBOTT et al., 1993; LUKAS & CLUTTON-BROCK, 2012), e comportamental, realizada por indivíduos dominantes por meio de comportamentos agressivos (ABBOTT, 1986; HAMILTON, 2004). Portanto, os indivíduos subordinados apresentam reprodução tardia, a qual pode ocorrer a partir da dispersão para outros grupos em busca de parceiros reprodutivos ou a partir da herança da posição de reprodutor de seu grupo (BAKER, 1993; SOLOMON & FRENCH, 1997; LAZARO-PEREA, 2001).

Apesar dos potenciais custos reprodutivos que recaem sobre os subordinados, o sistema social cooperativo também proporciona benefícios para estes indivíduos (COCKBURN, 1998). Os benefícios vão desde o acesso a recursos compartilhados pelos membros do grupo vivendo em um território comum, até a aptidão indireta resultante da sobrevivência de indivíduos aparentados, uma vez que muitos desses grupos sociais são formados por grupos familiares (COCKBURN, 1998). Além disso, permanecendo em seus grupos, os subordinados podem vir a herdar o posto de reprodutor (TARDIF, 1997; COCKBURN, 1998).

Nesse contexto, as interações intergrupais podem ter um importante papel na dinâmica social de grupos com reprodução cooperativa, pois possibilitam interações entre indivíduos de grupos diferentes, podendo servir para diferentes finalidades, desde a defesa de recursos à avaliação de oportunidades de reprodução (SOLOMON & FRENCH, 1997; LAZARO-PEREA, 2001; YAMAMOTO et al., 2009). No cenário de defesa de recursos, todos os animais externos ao grupo podem ser percebidos como uma ameaça aos que compartilham recursos comuns em seu território, sendo observadas interações agressivas como meio de defesa do recurso (POWELL, 2000).

Interações territoriais podem acontecer tanto nas bordas das áreas de vida, como em áreas nucleares, onde há maior concentração de recursos (FALLS, 1982; GIRALDEAU &

YDENBERG, 1987; WICH, 2002; CROFOOT & GILBY, 2012). Estudos com aves (STODDARD et al., 1991), canídeos (DARDEN & DABELSTEEN, 2008) e primatas (CROFOOT & GILBY, 2012) verificaram que a intensidade de reação a intrusos é maior em áreas nucleares que em áreas periféricas, sugerindo que as regiões mais próximas ao centro dos territórios podem ser mais importantes para os seus residentes, seja por sua localização estratégica, ou por concentrar maior quantidade de recursos, como alimentos, locais de nidificação e sítios de dormir (FALLS, 1982; GIRALDEAU & YDENBERG, 1987; BROWN et al., 1993; WICH et al., 2002). Por exemplo, em um estudo realizado com macacos-prego (*Cebus capucinus*), observou-se que a chance de um animal fugir após uma disputa são maiores quando os conflitos ocorrem nas periferias da área de vida quando comparados com conflitos no núcleo do território do grupo (área de maior intensidade de uso), sugerindo que a área núcleo é percebida como prioritária para defesa (CROFOOT & GILBY, 2009).

Em relação à defesa de parceiros, a participação dos membros do grupo pode estar fortemente relacionada ao sexo do invasor, uma vez que indivíduos de mesmo sexo representam uma maior ameaça que indivíduos de sexo oposto (CHENEY & SEYFARTH, 1987; ARSENEAU et al., 2015). Por exemplo, em grupos de colobus (*Colobus guereza*), foi observado que os indivíduos machos apresentaram comportamentos mais agressivos quando o intruso dentro do seu território foi do mesmo sexo. No entanto, foi observado que as fêmeas não demonstraram o mesmo comportamento agressivo (FASHING, 2001), sugerindo que machos e fêmeas podem perceber o invasor de maneira diferente.

Interações agressivas durante encontros com membros externos aos grupos nem sempre são a regra e comportamentos afiliativos (catação, aproximação não agressiva) também podem ser observados. Cópulas extragrupais são comumente observadas em primatas (*Colobus vellerosus*; SICOTTE & MACINTOSH, 2004; *Cebus apella nigritus*, ALFARO, 2005; *Alouatta caraya*, KOWALEWSKI & GARBER, 2010; *Alouatta guariba clamitans*, LOPES & BICCA-MARQUES, 2011), bem como em outros grupos de mamíferos (CLUTTON-BROCK, 2016). Por exemplo, em simulação de intrusos com grupos de primatas gibões (*Hylobates agilis*), foi observado que machos e fêmeas reagiram mais intensamente para intrusos do sexo oposto (MITANI, 1987). Em saguis-comum (*Callithrix jacchus*), uma pequena espécie de primata neotropical de reprodução cooperativa, interações afiliativas envolvendo cópulas extragrupais são comuns, sugerindo o potencial desses encontros para a avaliação de oportunidades de procriação em grupos vizinhos (LAZARO-PEREA, 2001; ARRUDA et al., 2005; DIGBY et al., 2007; YAMAMOTO et al., 2009).

Primatas da espécie *Callithrix jacchus* formam grupos de 3 a 15 indivíduos, compostos por um casal reprodutor - geralmente dominantes -, e membros que não se reproduzem nos grupos - os subordinados -, que auxiliam no cuidado com a prole, bem como na defesa de territórios (RYLANDS & FARIA, 1993; DIGBY et al., 2007, SCHIEL & SOUTO, 2017). A espécie ocorre em todo nordeste do Brasil, em ambientes com condições bastante variáveis, de matas úmidas, como a Floresta Atlântica, a ambientes semiáridos, como a Caatinga (RYLANDS & FARIA, 1993; RYLANDS et al., 1996; BORGES et al., 2012). Esses animais se alimentam principalmente de insetos, goma e frutos carnosos, mas folhas e pequenos vertebrados também são itens comumente incorporados em sua dieta (RYLANDS & FARIA, 1993; SCHIEL et al., 2010; AMORA et al., 2013). Vivem em áreas pequenas, variando entre 0,5 a 5,2 ha (STEVENSON & RYLANDS, 1988; DIGBY et al., 2007; SCHIEL & SOUTO, 2017). Esses animais são vocalmente ativos, sendo conhecidos 17 grupos de vocalização para a espécie (BEZERRA & SOUTO, 2008). A comunicação entre grupos vizinhos ou invasores solitários pode ocorrer através de vocalizações do tipo *phee*, que são chamadas de longo alcance utizadas para se comunicar a longa distância com grupos vizinhos ou com os próprios membros do grupo (LAZARO-PEREA, 2001; BEZERRA & SOUTO, 2008).

Técnicas de playback com espécies vocalmente ativas oferecem oportunidades para simular efetivamente a presença de intrusos e examinar diretamente o comportamento respectivo de cada indivíduo no grupo (MCCOMB et al., 1994; MENNILL et al., 2002; ILLES & YUNES-JIMENEZ, 2009; CASELLI et al., 2015). Neste estudo, avaliamos o papel dos encontros intergrupos em saguis-comum através de um experimento utilizando técnica de emissão de vocalizações (playback), para simular a presença de invasores coespecíficos na área de vida dos grupos. As dinâmicas sociais em encontros intergrupos de saguis-comum foram investigadas em estudo observacional conduzido em Floresta Atlântica (LAZARO-PEREA, 2001), no qual foi sugerido o múltiplo papel desses encontros para saguis-comum: avaliação de oportunidades reprodutivas e defesa de recursos. Na Caatinga, esses animais vivem sob diferentes restrições, principalmente relacionadas à disponibilidade de recursos, como alimento e água, o que pode resultar em ajustes comportamentais, podendo assim modificar a importância desses encontros na dinâmica social desses animais, especialmente se considerarmos que a dispersão nesses ambientes pode ser ainda mais restrita devido às condições mais severas do ambiente. Além disso, para melhor compreender os diferentes aspectos envolvidos nesses contextos complexos e dinâmicos de interação entre membros com diferentes status sociais dentro de grupos de reprodução cooperativa, estudos experimentais sob condições controladas podem ser de grande importância. Técnicas experimentais, como playbacks, oferecem oportunidades para efetivamente simular a presença de intrusos e para examinar diretamente o comportamento de cada indivíduo no grupo (BEE et al., 1999; CASELLI et al., 2015; ILLES & YUNES-JIMENEZ, 2009).

2. Hipóteses

Neste trabalho testamos três hipóteses com relação ao papel das interações intergrupais em saguis-comum. Nós predizemos que as chamadas de *phee* produzidas por um intruso desconhecido devem induzir padrões distintivos de comportamento com base no sexo e no status reprodutivo dos indivíduos.

- **Hipótese da defesa de território**

  Predição: Se indivíduos fora do grupo provocam principalmente uma resposta de defesa territorial, esperamos que adultos reajam com mais intensidade a intrusos simulados independentemente do sexo simulado. Do mesmo modo, é esperada uma resposta comportamental mais robusta às emissões de playback transmitidas a partir da área núcleo das suas áreas de vida do que na períferia, uma vez que os intrusos no núcleo podem representar uma maior ameaça para os donos do território (ex: mover-se mais rapidamente, maior tempo de permanência na área de emissão do playback).

- **Hipóteses da defesa de parceiro**

  Predição: Se um intruso pode sinalizar uma oportunidade de reprodução, as chamadas de *phee* podem provocar padrões de comportamento em indivíduos que são do sexo oposto ao interlocutor simulado - como se mover para o local de emissão do playback mais rapidamente para avaliar esse indivíduo mais de perto.

- **Hipótese de avaliação de parceiro**

  Predição: Esperamos que um intruso do mesmo sexo também pode ser percebido como uma ameaça e provocar comportamentos de defesa de parceiro em indivíduos dominantes (reprodutores), incluindo um número maior de exibições agonísticas (ex: piloereção) e movendo-se mais rapidamente para o intruso simulado.

3. Objetivos

3.1. Objetivo geral

Investigar o papel das interações intergrupais em saguis-comum, *Callithrix jacchus.*

3.2. Objetivos específicos

- Determinar o tamanho da área de vida de saguis-comum na Caatinga;
- Determinar o padrão espacial de uso da área de vida e o de distribuição de recursos utilizados;
- Testar as hipóteses de defesa território, parceiro e oportunidades de reprodução para os encontros com invasores.

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Artigo: The role of extra-group encounters in a Neotropical cooperative breeding primate, common marmosets: a field playback experiment

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ABSTRACT

In cooperatively breeding species, encounters with intruders may serve multiple functions, ranging from reaffirming group territory ranges to facilitating assessments for additional breeding opportunities. While these distinctive events offer the opportunity to investigate the delicate balance of these social dimensions within animal societies, their unpredictable occurrence makes witnessing and controlling these events in the wild particularly challenging. Here we used a field playback approach to simulate conspecific territorial incursions in cooperatively breeding common marmosets, *Callithrix jacchus*, to distinguish between the three following nonmutually exclusive functions of intergroup encounters in this species of New World primate: territorial defence, mate defence and assessment of breeding opportunities. For these experiments, we systematically broadcast species-typical long-distance contact calls (‘phees’) commonly used in intergroup interactions from the core and periphery of three groups' territories using either male or female vocalizations. Consistent with a territorial defence hypothesis, a group's reaction was independent of the simulated intruder's sex and the response strength was greater when the playback stimulus was broadcast from the core area of a group's territory relative to the periphery. However, sex differences in some facets of the marmosets' responses suggest that this is not the only potential function for these encounters. Mated males and females started to move first in response to simulated intruders of the opposite sex, suggesting that these events offered opportunities to assess extrapair breeding opportunities. However, mated females also showed piloerection towards simulated female intruders, which is suggestive of mate guarding. These data provide unique experimental evidence for the theory that excursions by conspecific intruders may serve multiple functions in a cooperatively breeding vertebrate and are reflective of the known complexities of common marmoset sociobiology.

Keywords: Callitrichidae, common marmoset, cooperatively breeding, intergroup interactions, mate defense, mate-fidelity, neighbours assessment, sexual conflict, territory defense.

INTRODUCION

Despite substantial variability in the organization of social groups, ranging from large fissionefusion organizations (e.g. African elephants, Loxodonta africana: Archie, Moss, & Alberts, 2006; spotted hyaenas, Crocuta crocuta: Smith, Kolowski, Graham, Dawes, & Holekamp, 2008; spider monkeys (*Ateles paniscus chamek*): Symington, 1990; chimpanzees, Pan troglodytes: Symington, 1990) to smaller groups composed of pair-bonded individuals and their offspring (e.g. prairie vole, Microtus ochrogaster: Carter, Devries, & Getz, 1995; titi monkeys (Callicebus spp.): Bicca-Marques & Heymann, 2013; songbirds: de Kort, Eldermire, Cramer, & Vehrencamp, 2009), territoriality is a common behaviour pattern among vertebrates (Clutton-Brock, 2016; McGregor, 1993). Yet, despite the spatial segregation of social groups, encounters with neighbours and transient conspecifics are relatively common (Kinnaird, 1992; Sillero-Zubiri, Gottelli, & Macdonald, 1996; Young, Spong, & Clutton-Brock, 2007) and may be affiliative or aggressive (Kitchen & Beehner, 2007; Majolo, Ventura, & Koyama, 2005; Nichols, Cant, & Sanderson, 2015).

While many studies aim to test why and when intergroup aggression occurs (Cooper, Aureli, & Singh, 2004; Fashing, 2001; Kinnaird, 1992; Kitchen, Cheney, & Seyfarth, 2004; Korstjens, Nijssen, & Nôe, 2005), fewer data are available to address the significance of affiliative behaviours during encounters with outgroup conspecifics (Majolo et al., 2005; Nichols et al., 2015; Zhao, 1997). Potential explanations for intergroup aggression are related to food resources and mate defence (Bee & Gerhardt, 2001; Cooper et al., 2004; Fashing, 2001; Heinsohn & Packer, 1995; Kinnaird, 1992;

Kitchen et al., 2004; Matthews, 2009), while explanations of intergroup affiliative behaviours are biased towards mating and dispersal opportunity assessment (Majolo et al., 2005; Nichols et al., 2015; Taborsky, 1994; Temeles, 1994; Wiley, 1973). In fact, a single encounter between groups could serve each of these functions, given that group members do not necessarily act cohesively during these events and behaviours with distinct functional significance are displayed by different individuals simultaneously (Cant, Otali, & Mwanguhya, 2002; Fashing, 2001; Hale, Williams, & Rabenold, 2003). For instance, intergroup encounters in Tana River crested mangabey, *Cercocebus galeritus*, can involve behaviours that vary from sexually presenting towards extragroup individuals to herding of sexually receptive females of the same group, indicating the significance of these encounters for mate defence and the opportunity for extragroup copulation (Kinnaird, 1992). In more extreme cases, such as in the banded mongoose, *Mungos mungo*, affiliative behaviours such as extragroup copulations can take place even during violent encounters with resulting injuries and death (Nichols et al., 2015).

Dissecting the complexity of these encounters presents notable logistical challenges, particularly with respect to transient intruders, because of the difficulties in witnessing these events. Experimental techniques in the field, such as playbacks, offer opportunities to effectively simulate the presence of intruders and to directly examine the respective behaviour of each individual in the group (Bee, Perrill, & Owen, 1999; Caselli, Mennill, Gestich, Setz, & Bicca-Marques, 2015; Illes & Yunes-Jimenez, 2009; McComb, Packer, & Pusey, 1994; Mennill, Ratcliffe, & Boag, 2002). Here we sought to utilize field playbacks to simulate territorial incursions by conspecifics in common marmosets, *Callithrix jacchus*, in order to test the potential function significance of these pivotal social events for this Neotropical, cooperatively breeding primate.

Common marmosets offer unique opportunities to examine the relative impact of multiple social pressures on individuals' behaviour during extragroup interactions. These small primates form cohesive groups of 3-15 individuals; including two or more adults, their offspring, and even unrelated individuals (Schiel & Souto, 2017). As a result, breeding adults as well as sexually mature nonbreeding adults in the group contribute to caring for the young (Digby & Barreto, 1993; Schiel & Souto, 2017). The cooperative nature of their society extends to several facets of their social cognition (Miller, 2017; Miller et al., 2016; Schiel & Huber, 2006) and, as a result, the species has been argued to exhibit prosocial tendencies commonly associated with humans (Burkart & van Schaik, 2010; Burkart, Hrdy, & Van Schaik, 2009). However, this affiliative dimension of common marmoset society seems restricted to group members, as they commonly show aggressive displays towards potential intruders and neighbouring groups (Hubrecht, 1985; Lazaro-Perea, 2001; Stevenson & Rylands, 1988). Despite the aversion to outsiders, evidence suggests that extragroup copulations are not uncommon in this species (Digby, 1999; Lazaro-Perea, 2001). Therefore, encounters may serve multiple functions by reaffirming group identities and territory ranges while also allowing for mate defence and facilitating assessments for additional breeding opportunities, especially by nonbreeding individuals (Digby, Ferrari, & Saltzman, 2007; Lazaro-Perea, 2001). Further exploration of intergroup interaction offers the opportunity to effectively investigate the delicate balance of these social dimensions in common marmosets.

Interactions with extragroupindividuals typically take place at the periphery of a group's home range and commonly involve all group members (Lazaro-Perea, 2001). Because of the species' small body size and arboreal lifestyle, these encounters are commonly associated with vocal signals such as species-typical long-distance phee calls, which are uttered for communication between conspecifics (Bezerra & Souto, 2008; Hubrecht, 1985; Stevenson & Rylands, 1988). In fact, conspecific intruders will often announce their presence by producing phee calls (Hubrecht, 1985; Lazaro-Perea, 2001). Because this vocalization communicates critical social information about the caller, such as its individual identity, sex and group dialect (Miller, Mandel, & Wang, 2010; Miller & Thomas, 2012; Norcross, Newman, & Fitch, 1994; Zurcher & Burkart, 2017), listeners will be able to identify the caller as a territorial intruder and behave accordingly.

Given that encounters with individuals from outside the group may serve multiple distinct, but parallel roles in common marmoset sociobiology (Digby et al., 2007; Lazaro-Perea, 2001), we tested the functional importance of these distinctive social interactions in mate and territory defence as well as in the assessment of breeding opportunities. To test these nonmutually exclusive hypotheses, we performed a series of field playback experiments in which we simulated intruders by broadcasting phee calls produced by either unknown male or unknown female callers within the group's core area and at the periphery of its territory. We initially predicted that phee calls produced by an unknown intruder should elicit distinctive patterns of behaviour based on subjects' sex and mating status. More specifically, if individuals outside the group primarily elicit a territorial defence response, we expected adults to react to simulated intruders independently of the caller's sex. Likewise, a more robust behavioural response to playbacks broadcast from the core area of their home ranges than from the periphery would be expected, since intruders in the centre are believed to pose a greater threat to the territory owners (Crofoot & Gilby, 2012; Giraldeau & Ydenberg, 1987). As an intruder can signal a breeding opportunity, an intruder's phee calls could also elicit sex-specific responses, such as moving to the playback location more quickly to assess an opposite-sex intruder more closely. Likewise, a same-sex intruder could also be perceived as a threat and elicit mate-guarding behaviours in mated individuals, including a higher incidence of agonistic displays and moving more quickly towards the intruder.

METHODS

Study Site

This study was conducted in the semiarid Caatinga scrublands at Baracuhy Biological Field Station (7°31’S, 36°17’W) in the municipality of Cabaceiras, state of Paraíba, in northeastern Brazil. The study region is in one of the driest areas of Brazil. The area is characterized by a hot semiarid climate, receiving approximately 500 mm of rain per year and with temperatures reaching up to

40ºC. The rainy season lasts from February to July and the dry season from August to January. The vegetation is predominantly low, characterized by arboreal shrubs and scattered trees (see De la Fuente, Souto, Sampaio, & Schiel, 2014, for detailed information about the study site).

Subjects

Groups at the study site were composed of 4-10 individuals, and each group regularly engaged in vocal interactions with at least one neighbouring group. Natural encounters are not frequent, occurring at rates of about 0.17 per day (S. C. N. Castro & P. H. B. Ayres, personal observation). During May-December 2016, we monitored ranging patterns of three fully habituated groups that were approximately 300 m apart from each other and conducted playback experiments (Fig. 1). Given that phee calls cannot be transmitted efficiently beyond 100 m (Morrill, Thomas, Schiel, Souto, & Miller, 2013), the selected groups had no visual or acoustic contact with each other. Group 1 was composed of three adults (two males and one female) as well as two infant males at the beginning of the study. The adult female and one infant disappeared and a new female came into the group in August 2016. At the end of the study, Group 1 was composed of three adults (two males and one female) and one juvenile male. Group 2 was initially composed of five adults (four males and one female), two juvenile females and two infant females. In June 2016, one adult male and one juvenile female disappeared. At the end of the study, Group 2 was composed of four adults (three males and one female), one juvenile female and two infant females. Throughout the entire study period, Group 3 was composed of four adults (three males and one adult female) and two infants (one male and one female). We defined mated individuals as marmosets that we had observed copulating during the observational period (when we monitored space use by each group to determine territory ranges), but prior to the playback trials.

The animals were marked with coloured collars for individual recognition (see Bicca-Marques & Garber, 2004; Encarnacióm, Moya, Soini, Tapia, & Aquino, 1990) in a previous behavioural study conducted on site. The procedures involved in the capture and marking of animals complied with current Brazilian laws and adhered to the ASAB/ABS Guidelines for the use of animals in research and the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates. This study was also approved by the governmental System of Authorization and Information on Biodiversity, SISBIO (No. 46770-1) and by the Ethics Committee on Animal Use (CEUA) of the Federal Rural University of Pernambuco (131/2016).

Ranging Pattern

To identify areas of potentially higher (core) and lower (periphery) value within each group's home range, we monitored each group from dawn to dusk for at least 15 days over a 3-month period (Group 1: May-July, plus 3 days in September, totalling 18 days; Group 2: May-July; Group 3: September-November). Using a GPS receiver (Garmin eTrex Legend® HCx), we recorded each group's location every 10 min as well as the location of important resources, such as sleeping trees and important feeding sites (trees or shrubs used for fruit and gum consumption for at least two scan samples, or 20 min, in one day, or used on consecutive days). We plotted the total area used by each group using a minimum convex polygon (MCP; Hayne, 1949) with 100% of location points. To describe the intensity of range use, we estimated the utilization distributions (UDs) using the adaptive kernel method implemented with the KernelUD function of the ‘adehabitatHR’ package (Calenge, 2006) of R software version 3.2.5 (R Development Core Team., 2016) with the default method for the estimation of the smoothing parameter (the ad hoc method). A UD gives the probability of relocating each group at places within its range (Powell, 2000). We identified each group's ‘core’ areas by locating the portions within each group's territory that combined more intensely used areas and concentrated important resources (sleeping trees and important feeding sites). The ‘periphery’ consisted of the remaining portions of each group's home range outside the core areas (Fig. 1).

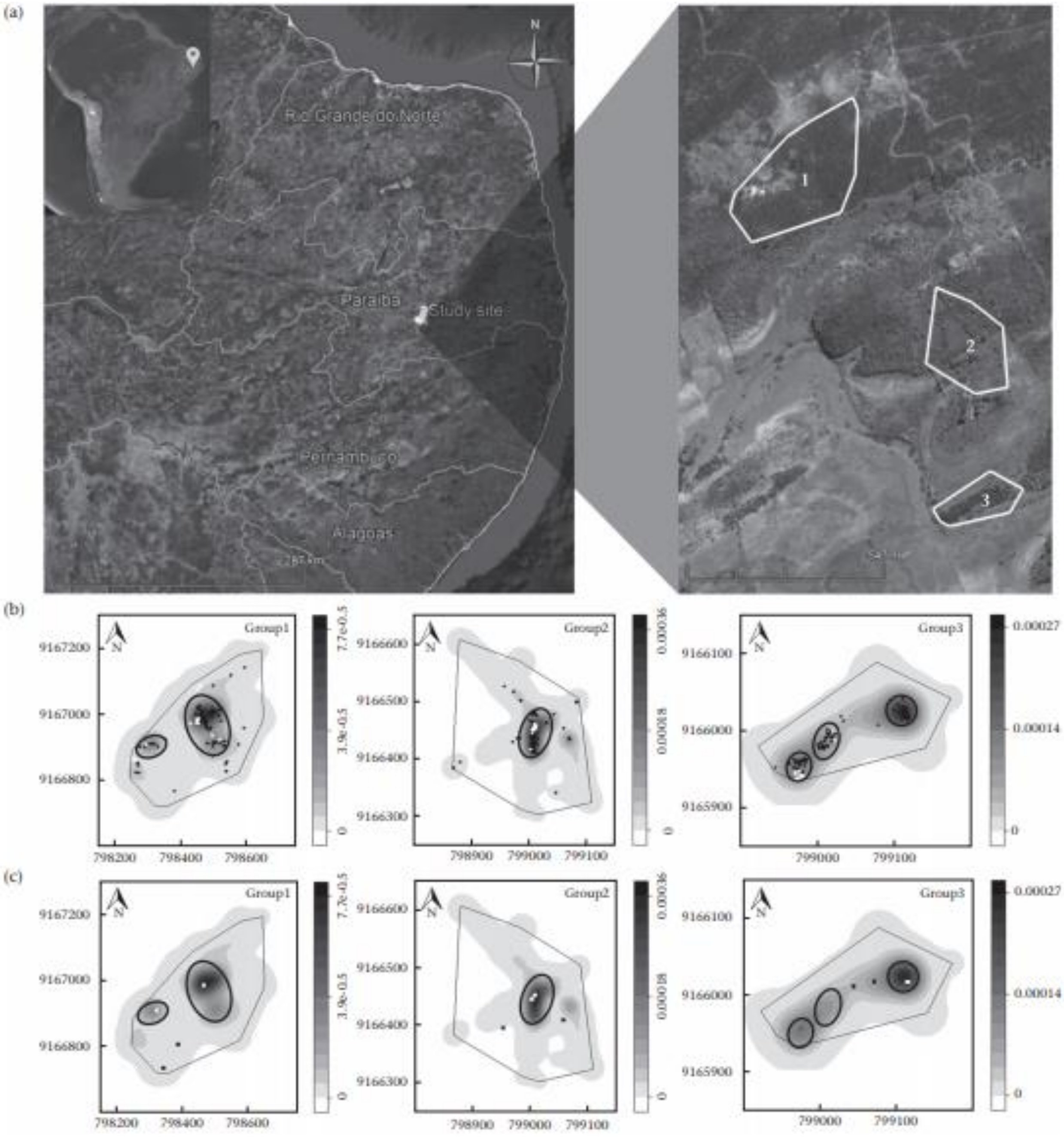

Figure 1. Spatial representations of group home ranges, significant resources and playback locations. (a) Map of the study site (left) and an expanded view (right) showing the location of each group's (Group 1, 2 and 3) range at the site. (b) Maps depict the significant resources in the territorial range for each group. Feeding trees are indicated by black dots; sleeping trees are shown with white dots. (c) Maps depict the location of the playback broadcasts within the territorial range of each group. White dots indicate playback locations in the core; black dots indicate playback locations in the periphery. (b, c) Polygons represent the total area calculated with minimum convex polygon (MCP) using 100% of location points (Group 1: 11.6 ha; Group 2: 5.26 ha; Group 3: 2.11 ha). The greyscale represents the utilization distribution (UD), estimated using the adaptive kernel method, and indicates the probability of finding the group in each location, with more frequently used areas in darker colours. Black circles highlight the location of core areas.

Stimulus Recording and Preparation for Playback Experiment

All phee calls used as test stimuli were recorded from individuals housed at the University of California San Diego (UCSD) Cortical Systems and Behavior Laboratory (La Jolla, CA, U.S.A.), so subjects in the field had no prior experience with these callers. Phee calls were recorded from six adult males and six adult females using standardized procedures (following Miller & Wang, 2006). Two individuals were placed approximately 3 m apart on opposite ends of a sound-attenuating chamber. A cloth occluder was placed equidistant from the individuals at the centre of the room. A directional microphone (Sennheiser ME66) was placed in front of each subject and all vocalizations were recorded directly to disk. Phee calls were selected as stimuli based on high signal-to-noise ratio and absence of background sounds.

To evaluate whether subjects' responses were due to conspecific stimuli (phee calls) and not to broadcast sounds per se, we also tested each group's response to recordings of stripe-backed antbirds, *Myrmorchilus strigilatus*, as a control stimulus. This species is common at our study site (BirdLife International, 2017) and its vocalizations do not seem to disturb or elicit responses from common marmosets (S. C. N. Castro & P. H. B. Ayres, personal observation). The recordings of stripe-backed antbirds were provided by the Macaulay Library of Cornell Lab of Ornithology (http://macaulaylibrary.org).

Experimental Design and Presentation

We used three different types of playback stimulus sets: male phees, female phees and control stimuli. Each stimulus set comprised a series of four exemplars broadcast with a 15 s interstimulus interval. For the phee call stimuli, the calls of only a single animal were used within a given stimulus set, but 12 different callers (6 male/6 female) were used over the course of the experiment. We broadcast these stimuli at two locations within each group's home range, in the core area and at the periphery. Each study group was presented with all playback stimulus types (male phee, female phee, control stimulus) at both locations for a total of six individual playback trials for each study group (18 trials in total across all three groups). To avoid pseudoreplication, phees produced by each UCSD common marmoset were played only once (following Wiley, 2003). In other words, the stimuli of different callers were used for each test group. We conducted only one trial per day and randomized the order of treatments assigned to each group.

We conducted playback experiments between 0600 hours and 1200 hours during September-December 2016. To simulate an invasion by conspecifics, we broadcast the stimuli from inside each group's range and within 25-30 m of the group's current location. The stimuli were presented using an Anchor MiniVox loudspeaker (Anchor, Carlsbad, CA, U.S.A.; frequency response range 100-15 000 Hz, output power: 30 W, and maximum SPL: 109 dB) connected to an iPod Nano (Apple Computer Inc., Cupertino, CA). The loudspeaker was positioned at 2 m from the forest floor to simulate realistic positioning of the animals while calling. All stimuli were normalized and the volume of broadcasting equipment was set to match the level of natural vocalizations produced by common marmosets, determined based on our field experience with natural vocalizations as well as pilot tests conducted prior to the experiment. Once established, we held this volume constant across all trials.

We began each trial when all the adults were in the sight of the observer, while foraging or resting, and only after a 30 min interval with no production of phee calls from neighbouring or focal groups. During each trial, one observer, who was hidden behind vegetation, broadcast the stimulus while another observer monitored the subjects' reactions for 30 min following the start of the trial.

Response Measures

During each playback trial, we recorded three categorical variables: (1) the identity of all individuals who reacted to the stimuli; (2) the first individual to exhibit an observable response (look towards the playback location or start to move); (3) the occurrence of agonistic displays (piloerection). Piloerection is a commonly observed agonistic behaviour in natural intergroup interactions (Hubrecht, 1985; Lazaro-Perea, 2001). Furthermore, we recorded five quantitative variables to determine the response intensity of the groups to the stimuli: (1) latency to move or to produce a vocal response after initiation of the playback stimulus; (2) percentage of monkeys in each group that started to travel towards the loudspeaker; (3) percentage of monkeys in each group that arrived at loudspeaker location; (4) the speed of travel (distance travelled/ time to arrive at loudspeaker location); (5) time spent within a 5 m radius of the loudspeaker (beginning when the first adult entered the radius and ending when the last adult moved outside of it). We calculated the percentage of individuals in each group that moved towards and reached the playback location to avoid the influence of group size on the number of individuals that travelled towards the speaker. To avoid empty cells for the analyses, we assumed that the latency to move was equal to the duration of the trial (30 min) and the remaining quantitative variables were scored as zero whenever a group did not behave accordingly (e.g. when no monkey reached the playback location).

Statistical Analysis

We used a generalized linear mixed model (GLMM) to test the predictions regarding the subjects' response strength to stimulus type (male phee, female phee, control) and location, including stimulus type and location of playbacks as the fixed effects (explanatory variables) and the identity of groups as a random effect. To determine the significance of the models, we first compared the simplest models (with only one fixed variable) to the null model (including only the intercept and random variable). When the models with only one fixed variable accounted for enough variance to reject the null hypothesis, we compared the simplest models with the complete model, including the interactions between fixed effects (stimulus type and location), to test for further improvement in the explained variance.

To determine whether the frequency of individuals' reaction type (piloerection, look or move towards speaker, reach the speaker location first) was sex dependent, we used contingency tables (2 x 2) comparing the frequency of responses based on each individual's sex and breeding status (mated male, mated female, unmated male; there were no unmated adult females in the groups) according to the conspecific stimulus types (male phee, female phee) and the location of the playback (core, periphery). The values expected by chance were calculated considering the total number of mated individuals as well as unmated males in groups during the time of the experiment.

Because groups did not exhibit any overt behaviours in response to the control stimulus, there was no variance in the monkeys' response to it. As a result, we did not include the control stimulus in our analysis and focused on the responses of animals to conspecific stimuli. All analyses were implemented in R software version 3.2.5 (R Development Core Team., 2016). To fit the generalized linear mixed models, we used the packages ‘lme4’ version 3.1-125 (Bates, Machler, Bolker, € & Walker, 2015), and to perform model comparisons, we used the ‘anova’ function (likelihood ratio test) of ‘stats’ package version 3.2.5. The significance level was set to 5% and the data are presented as means ± SD.

RESULTS

We first analysed the salience of conspecific phee calls relative to control stimuli to determine whether detection of a conspecific intruder would elicit a response beyond what would be expected of any sound in the local habitat. While playback of stripe-backed antbird calls (control stimuli; N ¼ 6 trials) elicited no response from marmosets, all playback trials in which a conspecific phee call was broadcast elicited a robust behavioural response (N ¼ 12). In response to the phee calls of simulated intruders, most group members (78.3 ± 25.3%) quickly started to move towards the position of the loudspeaker upon hearing the phee playback (latency to move: 4.2 ± 4.8 s after initiation of the playback). Only a single individual (a nonmated adult male) produced phee calls in 3 of the 12 conspecific trials (all in response to male stimuli: two broadcasts from the periphery and one from the core area). Although most members of each group started to travel towards the loudspeaker, only a small percentage of group members (31.8 ± 41.4%) actually arrived at the loudspeaker location (speed: 17.0 ± 25.9 m/min). Once arriving at the speaker location, the individuals remained within 5 m of the speaker for roughly 12.8 ± 13.7 min.

Territorial Defense Hypothesis

Group responses, based on continuous variables, provided some support for the territorial defence hypothesis. We observed that marmosets' response strength to playbacks were independent of the sex of the simulated intruder (Table 1, Fig. 2), but varied with speaker location (core versus periphery). Specifically, the rate of travel towards the playback location, the percentage of group members that arrived at playback location and the time spent within a 5 m radius of the loudspeaker were greater when playbacks were broadcast from each group's core area, relative to the periphery. The latency to initiate travel and the percentage of group members that started to move were also independent of stimulus type (Table 1).

Breeding Opportunities Assessment and Mate Defense Hypotheses

To test whether intruders might be perceived as a positive (breeding opportunity) or negative (mate defence) reproductive event, we examined sex differences in categorical responses to the playbacks. Results provide somewhat of a mixed view. The mated male and mated female were more likely to move first in response to the calls of opposite-sex intruders in the group's core area than would be expected by chance (contingency tables: mated female: $X^2{}_1$= ¼10.9, $P < 0.005$; mated male: $X^2{}_1$= ¼ 9.20, $P < 0.005$; Fig. 3).

Table 1. Result of model comparisons among null models and the models including single fixed effects (stimulus sex and loudspeaker location) as well as the comparison between the significant model with a single fixed effect and the complete model, including the interaction among predictor variables.

Dependent variable	Model	X^2	df	*P*
Latency to move (min)	Null, Model 1 (Sex)	1.73	1	0.19
	Null, Model 2 (Site)	2.83	1	0.09
	Null, Complete model (Sex*Site)	5.54	3	0.14
Time interval in the radius of loudspeaker (min)	Null, Model 1 (Sex)	0.67	1	0.41
	Null, Model 2 (Site)	9.03	1	**<0.01**
	Model 2, Complete model (Sex*Site)	2.67	2	0.26
Percentage of group members that starts to move	Null, Model 1 (Sex)	0.03	1	0.85
	Null, Model 2 (Site)	1.37	1	0.24
	Null, Complete model (Sex*Site)	1.78	3	0.62
Speed to arrive in the 5-m radius of the loudspeaker (m/min)	Null, Model 1 (Sex)	0.002	1	0.96
	Null, Model 2 (Site)	5.39	1	**<0.05**
	Model 2, Complete model (Sex*Site)	0.03	2	0.98
Percentage of group members that arrived at loudspeaker location	Null, Model 1 (Sex)	0.007	1	0.93
	Null, Model 2 (Site)	10.66	1	**<0.01**
	Model 2, Complete model (Sex*Site)	0.31	2	0.86

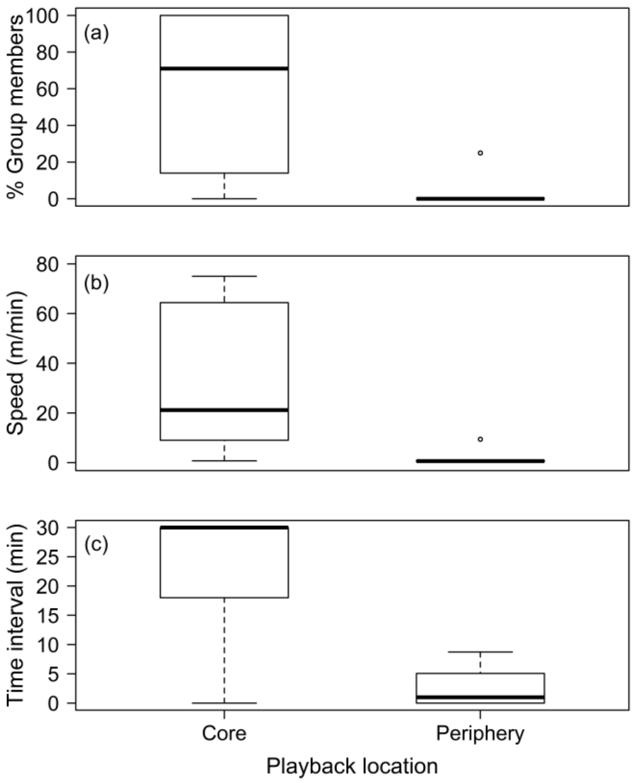

Figure 2. Comparison of groups' reaction to simulated intruders in the core and periphery of their home range. (a) Percentage of monkeys that arrived at the loudspeaker location. (b) Speed at which monkeys arrived to within a 5 m radius of the loudspeaker location. (c) Time spent within 5 m of the loudspeaker location (‘time interval’). Box plots show the median (horizontal line), the first and third quartiles (bottom and top of the box, respectively) and 1.5 times the interquartile range of the data (approximately 2 standard deviations; whiskers). Points above the bars represent outliers.

When phee calls of female intruders were presented in the core area of each group's range, mated females displayed more piloerection than expected by chance (contingency table: $X^2{}_1$= ¼7.60, $P < 0.01$; Fig. 4), providing support for the mate defence hypothesis. Piloerection responses of mated and nonmated males, however, were independent of intruder sex (contingency tables: mated male: $X^2{}_1$= ¼ 3.40, $P > 0.05$; nonmated males: $X^2{}_1$= ¼ 3.10, $P > 0.05$).

Notably, not all behaviours were consistent with these hypothesized functions. The frequency of arrival at the loudspeaker location was independent of the sex of the simulated intruder regardless of whether playbacks were broadcast from the core or the periphery (contingency tables: mated female: $X^2{}_1$= ¼1.70, $P > 0.1$; mated male: $X^2{}_1$= ¼ 3.40, $P > 0.05$; nonmated males: $X^2{}_1$= ¼ 2.09, $P > 0.05$).

DISCUSSION

Here we examined the response of wild common marmosets to simulated territorial intruders using field playbacks. These experiments were designed to test different hypotheses regarding the functional importance that extragroup encounters may play in the sociobiology of this cooperatively breeding New World primate. Overall, phee calls from unknown conspecifics broadcast within the territorial range of three groups elicited consistent and robust behavioural responses. Individuals from all groups typically responded by rapidly moving towards the loudspeaker location and producing visual or, on a few occasions, vocal displays. This response contrasted with the lack of a response to our control stimulus (calls of the local stripe-backed antbird). Different aspects of the groups' and individuals' reactions provide support for at least one aspect of all tested hypotheses, suggesting that extragroup encounters may play more than one meaningful role in the social lives of these monkeys.

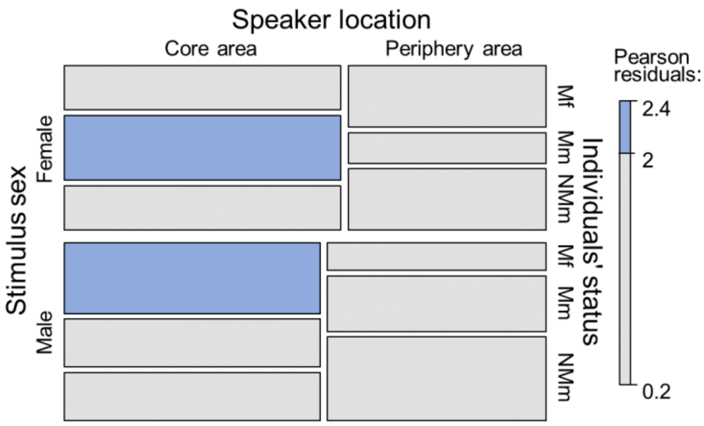

Figure 3. Mosaic plot of the status (Mf: mated female; Mm: mated male; nMm: nonmated male) of individuals that started to move towards the loudspeaker when playback of male and female stimuli were presented from core and periphery areas. The width of each cell with respect to its axis indicates the proportional contribution of each variable level to the total. The colours represent the level of the residual (Pearson) for each combination of levels, with the darker colour indicating cells in which individuals of a specific status started to travel more often than would be expected by chance.

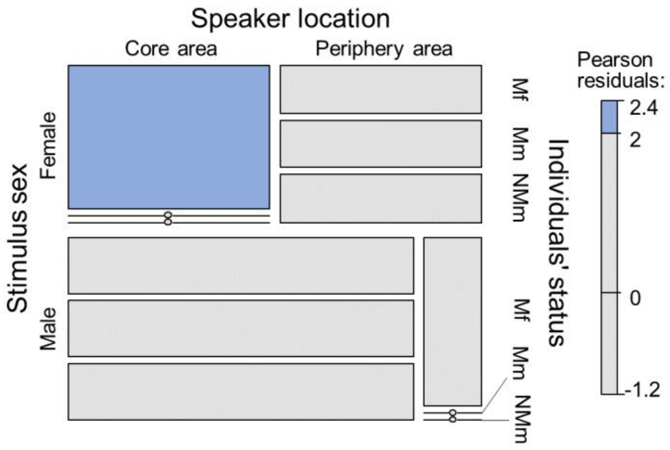

Figure 4. Mosaic plot of piloerection display responses by individuals of different status (Mf: mated female; Mm: mated male; nMm: nonmated male) to playback of male and female stimuli presented from core and periphery areas. The width of each cell with respect to its axis indicates the proportional contribution of each variable level to the total. The colours represent the level of the residual (Pearson) for each combination of levels, with the darker colour indicating cells in which there were more observations of piloerection than would be expected by chance. Circles indicate trials in which stimuli did not elicit piloerection. While all female stimuli broadcast from a group's centre elicited piloerection in mated females, it did not elicit piloerection in males.

The territorial defence hypothesis, for instance, was supported by evidence (based on continuous variables) that the groups' reaction was independent of the simulated intruder's sex and the response strength was greater when the playback stimulus was broadcast from the core area of a group's range relative to trials in which the stimulus was presented from the periphery. For instance, a greater percentage of group members reached the 5 m radius of the speaker, moved more rapidly towards the speaker and stayed longer within 5 m of the speaker when stimuli were broadcast in the core area relative to the periphery. The pattern observed suggests that common marmosets perceived intruder calls from within their core area as more significant than calls at the periphery, consistent with predictions from the territorial defence hypothesis. The relative position of the stimulus on the territory has been shown to influence the strength or nature of an individual's response in previous studies on birds, canids and primates, with increasing response strength towards the central areas of the territories (Crofoot & Gilby, 2012; Darden & Dabelsteen, 2008; Molles & Vehrencamp, 2001; Stoddard, Beecher, Horning, & Campbell, 1991) since it is presumably the most valuable area within an animal's home range (Giraldeau & Ydenberg, 1987).

The responses of common marmosets to the field playbacks, based on categorical variables, suggest that territorial defence is not the only motivation driving marmoset behaviour in response to intruders, as these events also afford opportunities to assess new individuals for potential extrapair mating. We observed that mated males and females started to move first in response to playbacks of simulated intruders of the opposite sex, lending support for this hypothesis in our data. From a female's perspective, potential benefits of extracopulation include the opportunity to increase the quality of the father (through sperm competition; Clutton-Brock, 2016) or increase the genetic variability within litters (Møller, 1992), even in callitrichids, given that twins can be sired by different males (Díaz-Muñoz, 2011). Thus, it is not surprising that female infidelity is commonly observed in some cooperative breeding birds and mammals (Leclaire, Nielsen, Sharp, & CluttonBrock, 2013; Mulder, Dunn, Cockburn, Lazenby-Cohen, & Howell, 1994; Whittingham, Dunn, & Magrath, 1997). Indeed, breeding female common marmosets have been observed engaging in extragroup copulations (Digby, 1999). Considering that neighbouring groups can be, to some extent, composed of related individuals, potentially due to migration into neighbouring groups or group division (Nievergelt, Digby, Ramakrishnan, & Woodruff, 2000), the presence of an entirely unknown male, as simulated in our study, may represent a unique opportunity to improve offspring genetic variability. Thus, the apparent motivation of mated females to move first towards simulated male intruders may be a strategy to assess the potential for additional breeding opportunities.

From the mated male's perspective, opportunities for extragroup copulation with an unknown female may represent a low-cost strategy to increase reproductive success (Clutton-Brock, 2016; Digby, 1999), which would explain why breeding males engage in extragroup copulations far more often than do breeding females (Hubrecht, 1985; Lazaro-Perea, 2001; Yamamoto et al., 2014). The presence of an unfamiliar female, as simulated here, may reduce mate-searching costs for males, thereby creating a scenario favouring polygyny (Dunbar, 1995), but also result in decreased reproductive potential of females, given the biological constraints imposed on them (Clutton-Brock, 2016). This is particularly true for social organizations inwhich females rely on male aid for infant care, such as is the case with callitrichids (Garber, 2017, pp. 1e4). Because males cannot rear multiple females' offspring, competition for a pair-bonded male may be intense among females (Ahnesjo, Kvarnemo, & Merilaita, 2001; Clutton-Brock & Vincent, 1991). Indeed, the level of competition among females in marmosets is believed to be high (Arruda et al., 2005; Garber, 1997; Yamamoto et al., 2014). Therefore, while males should demonstrate interest for female intruders, females should treat these individuals with aggression (Dunbar, 1995). This expectation is consistent with the observed increase of piloerection displays by females towards the simulated female intruders. The same agonistic behaviour was notably infrequent in male marmosets in response to simulated male intruders. However, it is important to consider that during playback trials the females were probably not in oestrus (no copulations or copulation attempts were observed and, based on the timing of infant births, mated females were probably already pregnant during the experiment). Because males are expected to be more aggressive when oestrous females are present (Cooper et al., 2004; Kitchen et al., 2004; Majolo et al., 2005), this could be an alternative explanation for the lack of male-male agonistic behaviours.

The food defence hypothesis could also explain the observed agonistic behaviour of females, given that the reproductive success of females is supposedly limited by access to food (Emlen & Oring, 1977). Thus, females are more likely to compete for these resources (Sterck, Watts, & van Schaik, 1997). However, in species in which males provide parental care, female intrasexual competition is expected to increase and, therefore, females should repel rival females to avoid a potential reduction in direct benefits from males (see Rosvall, 2011, for a review on intrasexual competition in females). Hence, considering that infant survival among callitrichids is correlated with the number of adult males in the group (Bales, Dietz, Baker, Miller, & Tardif, 2000; Garber, 1997; Koenig, 1995), the interpretation of females' behaviour as a mate defence strategy seems a more parsimonious scenario.

An alternative explanation to the observed sex-specific response of mated males and females, but the lack of a sex-specific response by nonmated males, is that extragroup encounters do not actually have a role in the assessment of breeding opportunities. The sexspecific response of mated individuals could be a mate defence strategy to reinforce their position within their partnerships and avoid being usurped (Hall, 2004). Nevertheless, under this alternative scenario we should have observed piloerection displays towards simulated intruders of the opposite sex. Since these were not observed, it suggests that the breeding opportunity assessment hypothesis is a more plausible explanation for mated individuals' behaviour. Genetic studies in cooperative species have indeed detected high rates of extragroup paternity in mammals (Goossens et al., 1998; Griffin et al., 2003) and birds (Durrant & Hughes, 2005; Whittingham et al., 1997).

The lack of a sex-specific response by nonmated males to the simulated intruders was, however, notably surprising. It is possible that helpers adopt other tactics for breeding opportunities. One strategy would be countercalling on a daily basis during intergroup vocal interactions, as observed for subordinate pied babblers (Humphries, Finch, Bell, & Ridley, 2015). This countercalling behaviour is commonly witnessed at the study site. Another strategy would be to make sporadic incursions into neighbouring groups' ranges, a behaviour that has been observed for common marmosets in the Atlantic forest (Lazaro-Perea, 2001). During these forays, nonbreeding helpers advertise their presence by producing phee calls and some engage in extragroup copulations (Hubrecht, 1985; Lazaro-Perea, 2001). Thus, these incursions may serve the dual function of providing opportunities not only for nonbreeding males to copulate, but for resident breeding males and females to mate with a genetically different individual as well. Helpers' extraterritorial forays accompanied by extragroup copulations have been observed in other cooperatively breeding species (Legge & Cockburn, 2000; Young et al., 2007), suggesting that this may be a common strategy for obtaining breeding opportunities.

Ecological constraints that are known to limit the dispersal success, such as environmental harshness and unpredictable conditions (Emlen, 1982), may have also influenced helpers' behaviour. The semiarid conditions at the study site may limit a male's propensity to leave an established group to form a new one. Although the reduced opportunity to breed in natal groups may outweigh the costs of dispersal for common marmoset females, the chances of inheriting a breeding position in natal groups are expected to be higher for males (Yamamoto et al., 2014). Thus, for nonbreeding males, an effective strategy would simply be to stay in established groups and cooperate. Cooperation in territorial defence is one way that a helper can collaborate with its natal group (Gaston, 1978; Koenig & Dickinson, 2004). A helper's cooperation in infant care and territorial defence would signal its quality to its group mates, which could result in direct benefits, either by obtaining a share of the current reproduction (Emlen, 1996), or by increasing its chances of inheriting the breeding position in its own group (Lottker, Huck, € & Heymann, 2004; Price, 1990; but see ; Tardif & Bales, 1997). In cooperatively breeding vertebrates, territorial inheritance can be an important benefit of philopatry (Buston, 2004). It is likely that our experimental design did not fully encompass all of the social pressures faced by common marmosets and the strategies they use to overcome these challenges. Additional experimental studies will be needed to more fully understand the functional significance of territorial incursions by common marmosets.

Overall, our findings based on a field playback approach are broadly consistent with previous observational studies, suggesting that the mating patterns and social organization of cooperatively breeding common marmosets are complex (Digby, 1999; LazaroPerea, 2001; Yamamoto et al., 2014). This study, however, has yielded significant insights into the complex strategies used by marmosets of different social categories for responding to conspecific territorial incursions. The complex social dynamics involved in interactions with extragroup individuals, which is more conspicuous during encounters, reveal that group members do not necessarily act cohesively due to different, and sometimes conflicting, intragroup interests. Overall, our results suggest that extragroup encounters serve multiple, nonmutually exclusive functions in a cooperatively breeding nonhuman primate species and provide powerful experimental evidence of distinct behavioural strategies that emerge based on the sex and putative breeding position of group members. The methods used in this study can be applied to other species for comparative analysis of the functional significance of intergroup aggressive and affiliative behaviours in group-living species.

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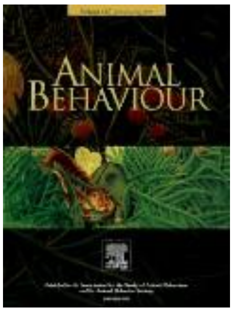
Anexos



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