



The role of extragroup encounters in a Neotropical, cooperative breeding primate, the common marmoset: a field playback experiment

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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.

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Despite substantial variability in the organization of social groups, ranging from large fission–fusion 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,

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Nijssen, & Nöe, 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 galerritus*, 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 extragroup individuals 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 40 °C. 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

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