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RESEARCH ARTICLE

Playback Responses of Socially Monogamous Black-Fronted Titi Monkeys to Simulated Solitary and Paired Intruders

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Many birds and primates use loud vocalizations to mediate agonistic interactions with conspecifics, either as solos by males or females, or as coordinated duets. The extensive variation in duet complexity, the contribution of each sex, and the context in which duets are produced suggest that duets may serve several functions, including territory and mate defense. Titi monkeys (*Callicebus* spp.) are believed to defend their home range via solo loud calls or coordinated duets. Yet there are remarkably few experimental studies assessing the function of these calls. Observations of interactions between wild established groups and solitary individuals are rare and, therefore, controlled experiments are required to simulate such situations and evaluate the mate and joint territorial defense hypotheses. We conducted playback experiments with three free-ranging groups of habituated black-fronted titi monkeys (*Callicebus nigrifrons*) to test these hypotheses. We found that titi monkeys responded to the three conspecific playback treatments (duets, female solos, and male solos) and did not respond to the heterospecific control treatment. The monkeys did not show sex-specific responses to solos ($N = 12$ trials). Partners started to duet together in 79% of their responses to playback-simulated rivals ($N = 14$ calls in response to playback). Males started to approach the loudspeaker before females regardless of the type of stimulus. The strength of the response of mated pairs to all three conspecific treatments was similar. Overall, our results are consistent with the idea that black-fronted titi monkeys use their loud calls in intergroup communication as a mechanism of joint territorial defense. Am. J. Primatol. 77:1135–1142, 2015.

Key words: loud calls; long calls; mate defense; territory defense; primates

INTRODUCTION

Many birds and primates use loud vocalizations to mediate agonistic interactions with conspecific competitors [Hall, 2004; Serpell, 1981; Wich & Nunn, 2002], either as solos by males or females, or as coordinated duets and choruses by two or more individuals [Bradley & Mennill, 2009; Geissmann, 2002; Grafe & Bitz, 2004; Langmore, 1998; Wich & Nunn, 2002; Wilson et al., 2001]. The extensive variation in the complexity of these vocalizations, the contribution of each sex to coordinated vocal emissions, and the context in which animals produce them suggest that they play many roles. The idea that calls function as a means of mate and joint territorial defense has received considerable support across diverse taxa [Douglas & Mennill, 2010; Bradbury & Vehrencamp, 2011; Hall, 2004; Wich & Nunn, 2002].

From a mate defense perspective, an individual participates in coordinated vocal emissions to advertise its partner's or its own mated status [Hall, 2004;

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Rogers et al., 2007]. In this context, the contribution of individuals to a coordinated duet can be directed to same-sex outsiders to prevent rivals from copulating with or usurping their mates [Grafe & Bitz, 2004; Levin, 1996; Seddon et al., 2002], or it may be directed toward opposite-sex individuals as a strategy to reinforce their mated position within the partnership [Appleby et al., 1999; Hall, 2004]. From a joint territorial defense perspective, individuals participate in coordinated vocal emissions to increase the effectiveness of demonstrations of resource holding potential and to advertise a stronger willingness to defend the shared resource than lone callers [Hall, 2004; Robinson, 1981]. In this cooperative context, partners coordinate their calls when facing intruders of any sex, paired or not [Dahlin & Wright, 2012; Hall, 2004; Hall & Peters, 2008].

The emission of coordinated loud calls is a conspicuous behavior of the Neotropical titi monkeys (*Callicebus* spp.). These small (*ca.* 1 kg) primates live in family groups composed of an adult breeding pair and one to three offspring [Kinzey, 1997]. Although loud calling is a widespread titi monkey behavior, this behavior has been investigated in detail in only three of the 32 species [*C. ornatus*, formerly *C. moloch*: Robinson, 1979a,1981; Mason, 1968; *C. torquatus*: Kinzey & Robinson, 1983; *C. nigrifrons*: Caselli et al., 2014]. The shy behavior of these primates, which hinders careful and continuous observation in the field [Bicca-Marques & Heymann, 2013; Pinto et al., 2013], is probably the cause of the scarcity of studies on the function of titi monkey loud calls. The few studies conducted so far suggest that coordinated loud calls serve to defend territories or mates [Kinzey & Robinson, 1983; Mason, 1968; Robinson, 1979a, 1981].

A recent observational study of the calling behavior of black-fronted titi monkeys (*C. nigrifrons*) suggests that the joint territorial defense hypothesis may best explain the coordinated emission of loud calls in this species [Caselli et al., 2014]. However, because either paired adult initiates duets, the possibility that mated individuals call to attract extra-pair mates (and that their partners join in forming duets to repel competitors) cannot be ruled out, suggesting that duets may also play a role in mate defense [Levin, 1996; Sonnenschein & Reyer, 1983]. Opportunities for witnessing interactions between established groups and solitary individuals are rare. Therefore, playback experiments simulating such interactions are key to test the mate and joint territorial defense hypotheses.

In this study, we tested the mate and joint territorial defense hypotheses by presenting four types of acoustic stimuli (duets, male solos, female solos, and a control sound) to established titi monkey pairs. If duets play a role in mate defense, we predict that responses should be sex specific. Specifically, we predict that (i) the type of stimulus (same-sex or opposite-sex solo) should determine the sex of the mated individual who starts calling and (ii) the sex of the individual who initiates an approach to the loudspeaker should depend on the type of solo (same-sex or opposite-sex). Further, we predict that (iii) playbacks simulating a solo rival will evoke more intense responses than duet stimuli because a paired individual is less sexually threatening or attractive to mated individuals than an unpaired one. On the other hand, if duets play a role in joint territorial defense, we predict that responses should not be sex-specific. Specifically, we predict that (iv) mated individuals will start vocal emissions together regardless of the type of stimulus (solos or duets); and (v) there will be no relationship between the type of stimulus and which sex initiates an approach to the loudspeaker. Additionally, we predict that (vi) duet stimuli will evoke (a) more intense responses than solos because a mated pair is more threatening than a solitary individual or (b) responses of equivalent strength to solo stimuli because any intruder may be perceived as a potential competitor for shared resources.

METHODS

Study Site and Subjects

We conducted this playback experiment with three habituated family groups of black-fronted titi monkeys living under similar conditions at three Atlantic forest remnants (approximately 54 km apart from each other) in the state of São Paulo, southeastern Brazil. Group 1 (a mated pair and three young individuals) was studied at Serra do Japi Municipal Ecological Reserve (23°14′3.38″S, 46°56′8.81″W), municipality of Jundiaí; group 2 (a mated pair and one young) was studied at Ribeirão Cachoeira (22° 49′48.43″S, 46°55′26.06″W), municipality of Campinas; and group 3 (a mated pair and two young) was studied at the municipality of Nazaré Paulista (23° 11′30.95″S, 46°21′34.42″W).

All study sites are characterized by semideciduous secondary forest and a temperate humid climate. At Serra do Japi, a 350-km^2 forest remnant, the focal group had at least four neighboring groups, whereas the focal groups of Ribeirão Cachoeira (2.45-km^2) and Nazaré Paulista (0.5-km^2) had at least two neighboring groups. All groups were known to show site fidelity and to interact vocally and agonistically with neighboring groups [Caselli et al., 2014; Nagy-Reis, 2012; Knogge C., *pers. comm.*].

Although *Callicebus* monkeys are sexually monomorphic, males are slightly larger than females [Robinson et al., 1987] and adults (>30 months) are larger than subadults (18–30 months) and juveniles [6–18 months; de Luna et al., 2010; Valeggia et al., 1999]. Therefore, we were able to distinguish adult males and females and their offspring based on body size (particularly when animals were close to each other, which was the case during playback experiments). Marks on the face and tail also helped in the identification of some individuals.

We observed the animals in the wild and did not capture or handle any individual. This research adhered to Brazil's legal requirements and the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

Stimulus Recording and Preparation

We recorded the vocalizations used as stimuli in WAV format using a Sennheiser ME-67 directional microphone and a Marantz PMD-671 digital recorder at a 48 kHz sampling rate and 16-bit resolution. We recorded duets and solos emitted by free-ranging habituated groups (groups 1 and 2) and three captive groups held at the Bauru Zoo (Bauru, São Paulo State), the Guarulhos Zoo (Guarulhos, São Paulo State) and the Center of Environmental Development of Companhia Brasileira de Metalurgia e Mineração (Araxá, Minas Gerais State). Recordings of captive monkeys were primarily necessary to obtain solos, which are rare and difficult to record in the wild. All captive study subjects that we recorded were wild born and were able to perform the species' typical song when stimulated by playback.

To record all stimuli played in this experiment (duets and solos) we exposed captive and wild monkeys to playbacks of duets emitted by groups 1 and 2 and then recorded their response calls. From these recordings, we selected a 30 sec portion with a high signal-to-noise ratio of each recording, filtered it to remove background noise below 100 Hz and normalized the stimulus to a standard amplitude of −1 dB. This normalization aimed at standardizing call amplitude with respect to peak amplitude because recording distances could vary across subjects. Whenever necessary, we removed the solo beginning of duet recordings to simulate duets in which mates started calling together.

To evaluate whether study subjects responded to the specific playback of conspecifics rather than to any sound broadcast by the loudspeaker, we selected recordings of the display call of the male dusky-legged guan (*Penelope obscura*) as a control stimulus. Guan loud calls are appropriate control stimuli because this species is common at our three study sites and wild titi monkeys appear not to react to them [Caselli CB *pers. obs.*]. We obtained guan recordings from the "Fonoteca Neotropical Jacques Vielliard" collection (http://proj.lis.ic.unicamp.br/fnjv/). These recordings were subjected to the same treatment described above for titi monkey calls.

Playback Experimental Design

Playbacks consisted of four treatments: (i) duets, (ii) male solos, (iii) female solos, and (iv) guan calls (control stimuli). Each study group received all four treatments, resulting in a total of 12 trials. Each study group received a single presentation of each stimulus and each stimulus was played only once to avoid pseudoreplication [Wiley, 2003], except for the female solos because we had only two high-quality recordings of this vocalization. Consequently, one female solo was played to two groups. We conducted only one trial/day, randomizing the order in which each treatment was assigned to each group to avoid habituation or interference between trials. We also randomized the stimulus exemplar assigned to each pair, always avoiding the use of a pair's own vocalizations on itself.

No sex-specific duet contributions have been detected in titi monkeys, either in our study species (according to our observations on black-fronted titi monkey spectrograms) or in studies with other titi monkeys [*C. ornatus*, Robinson, 1979b; *C. cupreus*, Müller & Anzenberger, 2002]. Nevertheless, male and female duet contributions may differ in the acoustic characteristics of elements (syllables) that are assembled to compose the song parts of duets' long sequences, such as the loudness, the tonal quality, the dominant frequency, or duration [Robinson, 1979b]. We assumed that titi monkeys are able to identify the caller's sex based on these acoustic properties. For instance, Australian magpie-larks (*Grallina cyanoleuca*) distinguish between male and female solos [Hall, 2000] despite the absence of clear sex-specific mate contributions to duets.

Playback Presentation

We conducted playback experiments in August and September 2012 between 7:00 and 11:00 am, when titi monkeys are normally vocally active. We began each trial when the mated pair was resting in sight and no calls from neighboring groups were heard during at least the previous 30 min. We broadcast the stimuli using a T-120B CSR loudspeaker (audio output: 40 W; frequency response: 25 Hz–15 kHz) connected to a Marantz PMD-671 portable digital recorder from places inside each group's home range at distances of 40–60 m from the tree in which the monkeys were resting. We held the volume of the loudspeaker at a constant level across trials. This level matched the volume of vocalizations produced by monkeys based on our field experience. During each trial one observer played the stimulus while another monitored and recorded the reactions of the study subjects during the 30 min following the start of the playback.

Response Measures

We recorded the identity of the animal that first moved and counter-called in response to each stimulus. We also generated spectrograms of the recordings of mates' responses to playbacks to confirm whether an animal started calling before the other. Response intensity to stimuli was assessed by the following vocal and physical variables: latency to move from their position at the start of playback, latency to counter-call, number of response calls, mean call duration, speed of arrival to within 10 m of the loudspeaker (distance travelled/time to arrive within 10 m of the loudspeaker), identity of the individual who initiated the movement toward the loudspeaker, and type of call emitted (male or female solo, duet started by male or female, or duet started concurrently). When more than one vocalization emission event occurred in response to playback (this was true in 5 out of 12 trials), we recorded the type of the first.

If a group did not react to a stimulus, we assumed that latency to move and to counter-call was 30 min (i.e., the duration of the trial), whereas the remaining quantitative variables were scored as zero. We adopted this criterion to avoid empty cells in the analyses. We chose to record the reaction of animals during the 30 min after the beginning of playbacks because previous behavioral observations on group 1 indicated that it never took more than 29 min to counter-call a neighbors' vocalization [Caselli et al., 2014].

Data Analysis

We used an extended form of the Fisher's exact test (from 2×2 tables to general $n \times m$ tables), known as the Freeman–Halton test [Freeman & Halton, 1951], to test our four predictions regarding response sex-specificity (predictions 1–2 and 4–5). With this test we evaluated whether the motivation of females, males, or pairs to start calling or moving is dependent on the simulated intruder.

To test the two remaining predictions on the strength of responses to different types of stimulus (predictions 3 and 6), we first used a principal component analysis (PCA) based on correlation matrices to combine our five quantitative response variables (latency to move, latency to counter-call, number of response calls, mean call duration and speed to arrive within 10 m of the loudspeaker) into a single composite response variable. We adopted this procedure, following McGregor's [1992] recommendation, because our response variables were significantly correlated with each other (Spearman's rank correlation coefficient ranging from 0.61 to 0.89, all $P < 0.05$). We then chose the first unrotated principal component factor (PC1), which accounted for 63% of the variance (Eigenvalue = 3.14), to test whether a group's responses differed among the four stimuli. We then extracted the PC1's coefficient of each variable [as in McGregor, 1992; Burt et al., 2001] to calculate the response score for each trial as follows: $(0.49 \times \text{number of calls}) + (0.51 \times \text{mean call duration}) + (0.20 \times \text{displacement velocity}) - (0.48 \times \text{latency to move}) - (0.48 \times \text{latency to counter-calling})$. Higher values indicate stronger reactions for this combined response score. We compared the score values among stimuli using a generalized linear mixed model (GLMM), including stimulus as the fixed effect (the explanatory variable) and the identity of groups as a random effect. No groups responded to the control stimulus (i.e., there was no variance in the monkeys' response to it). Therefore, we did not include the control stimulus in our analysis, focusing on the responses of animals to conspecific stimuli.

The distance between the loudspeaker and the animals at the playback start varied from 40 to 60 m. We used a Spearman rank correlation between the response score and the loudspeaker distance from groups to test whether distance modulates the response.

All analyses were implemented in R software version 3.1.2 [R Development Core Team, 2014] using the packages "Stats" and "nlme" version 3.1-118 [Pinheiro et al., 2014].

RESULTS

Playbacks of control stimuli (dusky-legged guans) did not elicit responses from titi monkeys (Fig. 1). Monkeys looked toward the location of the loudspeaker upon hearing the control stimuli, and usually stopped looking before the broadcast sound ended. In contrast, upon hearing playbacks of conspecific vocalizations, titi monkeys quickly adopted a posture of vigilance (head-up and staring in the direction of the loudspeaker), then approached (in 8 of 9 trials) and/or counter-called (in 8 of 9 trials; Fig. 1). Monkeys typically began moving toward the loudspeaker less than 2 min after the playback stimulus began, sometimes moving during the broadcast (mean latency to move = 1.5 min; range:

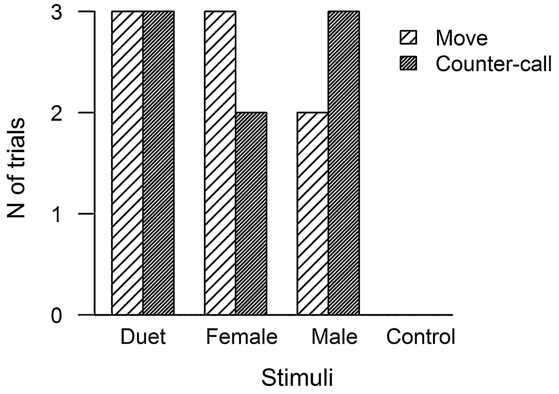

Fig. 1. Number of trials in which groups of black-fronted titi monkeys responded to playback (i.e., moved towards the loudspeaker or produced calls in response to the playback) for each of our four types of stimuli (duet, female solo, male solo, control; number of trials per stimulus type = 3; total number of trials = 12).

<1–6 min), and they usually began counter-calling less than 10 min after the start of the playback (mean latency to counter-call = 8 min; range: <1–30 min).

The responses of mated pairs to conspecific playback treatments did not vary with the type of stimulus (Fisher's exact test: sex starting to move: $P = 0.23$; sex starting to counter-call: $P = 1.00$). Mated pairs always counter-called by producing duets, never solos. Partners started calling together in 79% of these duets (N calls in response to playback = 14; Fig. 2). In the remaining three cases, the female started counter-calling first on two occasions (once in response to duet playback and once in response to female solo playback), and the male started counter-calling on the third occasion (in response to duet playback). Offspring joined their parents, thereby creating a group chorus, in 56% of the conspecific trials ($N = 9$). Although the adult male of each group started moving first in most conspecific stimulus trials (5 out of 9 responses; Fig. 2), all group members followed him closely. Males and females alternated the leading position on their path towards the loudspeaker. Therefore, the response of mated individuals was not sex specific, lending no support to the first two predictions of the mate defense hypothesis. However, this result is compatible with the joint territorial defense hypothesis.

Response scores varied from −29.0 (no reaction to the control stimulus) to 42.9 (mean ± SD response scores to: duets = 24.5 ± 17.9; male solos = 15.5 ± 13.5; female solos = 14.3 ± 28.8). The groups' reactions did not differ among conspecific stimuli (GLMM: $F_{(2,4)} = 0.27$; $P = 0.778$). Responses also were not influenced by distance to the playback speaker (Spearman rank correlation: $R = -0.32$, $N = 12$, $P = 0.40$). Therefore, there was no support for the last mate defense prediction that solos evoke more intense responses than duets (prediction 3). On the other hand, the last prediction of the joint territorial defense hypothesis, that duets evoke similar responses to solos (prediction 6.b), was supported.

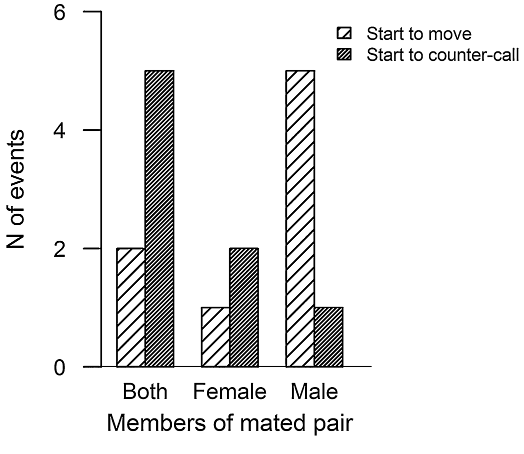

Fig. 2. Black-fronted titi monkeys' responses to conspecific playback (i.e., cases where monkeys started to move toward the playback or counter-call in response to conspecific stimuli) distinguished by the sex of the responding animals (number of trials with calls produced in response to playback stimuli = 8).

DISCUSSION

Black-fronted titi monkeys reacted to all conspecific playback treatments, but not the control. Individuals did not show sex-specific responses to the playback of conspecific solos. Males and females consistently produced duets, never solos, in response to playbacks, and they often began calling simultaneously. Although adult males tended to initiate movement toward the playback, all group members acted as a unit, moving and approaching the loudspeaker together. The mates' coordinated response is compatible with the joint territorial defense hypothesis [Hall, 2004; Hall & Peters, 2008] rather than the mate defense hypothesis; the latter hypothesis predicts sex-specific uncoordinated responses by each member of the mated pair [Hall, 2004], which we did not observe. Additional support to the joint territorial defense hypothesis comes from the similar responses to all conspecific stimuli. That is, all intruders (single individuals or paired) were apparently treated similarly as potential competitors [Benedict, 2010; Dahlin & Wright, 2012].

The importance of coordinated vocalizations in resource defense is also implied by the behavior of young individuals that joined their parents to produce a group chorus in many occasions, as previously observed during intergroup encounters [Caselli et al., 2014]. If vocalizations simulate the intrusion of potential food competitors within a group's home range, the threat is shared by all resident individuals and a unified response might be expected. Chorusing behavior has received little attention in studies on the function of loud calls in titi monkeys [Robinson, 1979a,b, 1981] and other socially monogamous primates [Cowlishaw, 1992; Heimoff, 1986; Mitani, 1985, 1987; Müller & Anzenberger, 2002; Wich & Nunn, 2002]. It is likely that choruses play a function similar to duets in the collaborative maintenance of territories, as proposed for other species [Bradley & Mennill, 2009; Fan et al., 2009; Geissmann & Mütschler, 2006; Wilson et al., 2001].

In this study, we explicitly addressed two forms of mate defense: mate guarding by either males or females via the defense of (i) their own positions [Levin, 1996] or (ii) their mates' positions within the partnership [Appleby et al., 1999; Hall, 2000]. We did not test the two other forms of mate defense, namely (iii) commitment signaling, in which an individual prevents its partner from deserting [Hall, 2000, 2004; Seddon et al., 2002] and (iv) paternity guarding, by which males prevent their fertile females from having extra-pair copulations [Sonnenschein & Reyer 1983].

Our results do not provide support for the first three forms of mate defense; individuals did not show sex-specific responses and solos did not prove to be more threatening than duets to any sex (see Hall, 2004, for a review of hypotheses for duet functions). Because paternity guarding can only account for the mate defense function of duets when females are fertile [Hall, 2004], we cannot reject this fourth form of mate defense with our results, since our experiments took place outside of the period when females are likely to be fertile [March–April; Caselli et al., 2014]. However, we found in a previous observational study that black-fronted titi monkeys emit coordinated loud calls throughout the year and did not call more often when females are supposed to be fertile [Caselli et al., 2014], rejecting the mate defense hypothesis via paternity guarding. Therefore, unlike Robinson's [1981] observations on ornate titi monkeys, we found no support for any form of mate defense in black-fronted titi monkeys.

It is possible that the responses of black-fronted titi monkeys (current study) and ornate titi monkeys [Robinson, 1981] were modulated by population characteristics. Ornate titi monkeys were studied in a high-density population [57 individuals/km^2; Bicca-Marques & Heymann, 2013; Robinson et al., 1987] in which study groups occupied contiguous home ranges [Robinson, 1979a] that were two to eight times smaller than those used by black-fronted titi monkeys at Serra do Japi [8–28 ha; CB Caselli *pers. obs.*]. Although we do not have quantitative data on population density at our study sites, we estimate density at *ca.* 20 individuals/km^2 based on group and home range sizes.

Living in a denser population may increase resource competition [Maher & Lott, 2000], but also the likelihood of encountering conspecific groups or solitary individuals, thereby enhancing opportunities for extra-pair copulation [Mason, 1966]. In addition, it is possible that dispersing titi monkeys inhabiting high-density habitats will be less likely to find vacant areas to establish a new group. These dispersing individuals, unable to settle their own home ranges, would have no option but to attempt extra-pair copulations with established individuals. However, the availability of vacant areas will also depend on resource availability. This means that at a given density, groups may need larger home ranges in low-quality areas than in high-quality ones. Therefore, the availability of vacant areas may be greater in the latter. Living in larger home ranges, on the other hand, may impose a different kind of risk to titi monkeys, such as having their food usurped by unnoticed intruders rather than the risk of encountering with strangers. So, a collaborative group action for defending shared resources might be expected in this context. These different scenarios would explain why ornate titi monkeys were involved in mate defense, whereas we found no evidence of that in black-fronted titi monkeys.

Given that our study forests showed a low range of population density, and our sample size included no replicates at each site, our rejection of the mate defense hypothesis for explaining the calling behavior of black-fronted titi monkeys remains to be confirmed. Furthermore, our support of to the territorial defense hypothesis does not rule out the possibility that duets also play a role in mate defense. Although these hypotheses generate non-overlapping predictions, they are not mutually exclusive [Grafe & Bitz, 2004; Hall, 2004]. The defense of a territory against all kinds of intruders also promotes mate defense as a welcome side effect to both mates [Fashing, 2001; Robinson, 1981].

McGregor [2000] argues that the lack of difference in the subjects' responses to stimuli might indicate that they do not perceive a difference among them. In our case, the use of a single speaker to broadcast playbacks could have interfered in the ability of study subjects to differentiate solo versus duet stimuli. However, like Mitani [1985, 1987] and Douglas and Mennill [2010], we believe that we appropriately simulated solos and duets with the single speaker. Although male and female titi monkeys may perform both parts of a duet call, they often alternate song parts while singing [Müller & Anzenberger, 2002; Robinson 1979b]. Careful examination of spectrograms of black-fronted titi monkey recordings indicates that males and females also alternate song parts [CB Caselli, *pers. obs.*]. Therefore, different song parts are usually emitted simultaneously in a duet, but not in a solo, potentially signaling to listeners the number of callers. Additionally, titi monkey mates routinely perform duets in very close proximity [Caselli et al., 2014], a situation that may be simulated by use of a single speaker.

We cannot rule out the possibility that the lack of response differences among stimuli resulted from the level of sensitivity of our response variables [McGregor, 2000]. Our response variables may have failed to detect conflicts of interest between mates during their collaborative behaviors. For instance, singers of some bird species select songs that best resemble the songs sung by rivals [song match; Burt et al., 2001; Vehrencamp, 2001] as a likely mechanism of showing its motivation or likelihood to attack [Bradbury & Vehrencamp, 2011]. Within the apparent joint performance of duets, males and females may target their aggression at same-sex competitors by using their contributions to match the song types of same-sex rivals, as observed for plain wrens, *Thryothorus modestus zeledoni* [Marshall-Ball & Slater, 2004]. As far as we know, this line of inquiry remains to be investigated in primate communication systems.

In summary, our observations of black-fronted titi monkeys responding to playback simulations of mated pairs and single males and females provide support for the joint territorial defense as the major function of long calls in this species. Future experimental studies on the role played by duets and solos within this highly speciose and widespread New World monkey genus [van Roosmalen et al., 2002] shall evaluate the influence of population density, the occurrence of subtle differences in the response to playbacks (e.g., structural differences) and song matching for testing whether the motivation for duetting differs between mates.

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