NOT SO PEACEFUL: AGGRESSIVE ENCOUNTERS BETWEEN BENI TITI MONKEY *(PLECTU-ROCEBUS MODESTUS)* GROUPS IN BOLIVIA

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Abstract

We report observations of intergroup interactions from a free ranging group of the endemic and threatened Beni titi monkey (*Plecturocebus modestus*). Our observations over the course of one study year suggest that competition for food resources is the main reason for most observed intergroup encounters (n = 64), including aggressive interactions (n = 28). Additionally, threats to group integrity, such as potential loss of members, might promote very aggressive encounters, including three fights observed between adults of neighbouring groups. We provide new information on the intraspecific relationships for these endemic primates related to their use of space and food resources.

Key Words: *Plecturocebus modestus*, intergroup interactions, use of space, Beni, Bolivia.

Resumen

Damos a conocer información sobre las interacciones de un grupo libre de mono lucachi cenizo o tití del Beni (*Plecturocebus modestus*) con otros grupos vecinos. Nuestras observaciones realizadas durante un año sugieren que la competición por recurso alimenticio es la razón principal para la mayoría de los encuentres entre grupos (n = 64), incluyendo interacciones agresivas (n = 28). Adicionalmente, amenazas a la integridad de grupo, como es la potencial pérdida de integrantes, podrían promover encuentros muy agresivos tales como tres peleas observadas entre adultos de grupos vecinos. Proveemos nueva información sobre las relaciones intraespecíficas de estos primates endémicos, vinculadas a su uso del espacio y de recursos alimenticios.

Palabras Clave: *Plecturocebus modestus*, interacciones intergrupales, uso del espacio, Beni, Bolivia.

Introduction

In social species, such as primates, interactions between conspecific groups vary in frequency and type depending on the degree of territoriality in the species (Cheney, 1987). Species living in small groups tend to have small spatial requirements, promoting marked territorial behavior as groups try to maintain exclusive access to areas, as observed in distinct Neotropical primate species (Peres, 1989). Apart from the relationship between the frequency of intergroup encounters and group density, intergroup encounters can occur due to: a) competition for access to limited defendable resources, and b) the need to assess dispersal and mating possibilities in surrounding groups (Sicotte and Macintosh, 2004).

Territorial defense helps a group to ensure food availability in its home range (Peres, 1989). Nevertheless, this task represents an energetic investment in which trade-offs are more favorable for species with small home ranges, capable of patrolling most of their territory (Sigiura et al., 2000). Intergroup encounters related to social processes such as mating and infant defense usually involve aggression between individuals (Thompson et al., 2012). However, the cost-benefit balance conditions the type of interaction between groups, which can vary from relatively neutral interactions such as territorial vocalizations, to aggressive encounters (Sugiura et al., 2000; Thompson et al., 2012). Information about the degree of aggression during encounters can help us gain a better understanding of how social ecology and intraspecific competition condition how populations use or share resources.

Titi monkeys (*Callicebus, Cheracebus, Plecturocebus*; Byrne et al., 2016) are a group of Neotropical primates, characterized by their emission of territorial calls which regulate intergroup spacing and help to avoid direct interactions or aggression between groups (Kinzey, 1981; Bicca-Marquez and Heymann, 2013). Nevertheless, some aggressive encounters between conspecific groups of titi monkeys have been reported, although it is not clear whether they correspond to resource or mate defense (Robinson, 1979; 1981; Price and Piedade, 2001). In general, titi monkey home ranges are small (usually less than 30 ha) which, together with their territorial and monogamous mating system, suggests food resource competition might be the most likely cause for territorial defense (Peres, 1989; Bicca-Marques and Heymann, 2013). Ecological data is not available for many titi monkey species, highlighting the need for research on this diverse primate subfamily (Bicca-Marques and Heymann, 2013).

The Beni titi monkey, *Plecturocebus modestus*, is an Endangered Bolivian endemic found in naturally fragmented forest habitats (Martinez and Wallace, 2010, 2016a; Wallace et al., 2013). To gather natural history knowledge not previously available for this species, we conducted a behavioral study, and here we report on intergroup interactions from one focal group, including the frequency and type of interactions (distant, direct, and aggressive), their relative location, as well as details of three fight events with individuals from neighboring groups. In this way, we provide valuable information for a better understanding of the mechanisms underlying intergroup relationships in Callicebinae.

Methods

We conducted our study at San Miguel cattle ranch in the southwestern portion of Beni Department, Bolivia (13°57'5.49"S, 66°50'5.07"W), in the Llanos de Moxos ecosystem where forest patches are immersed in a grassland matrix (Hanagarth, 1993). Two groups of *P. modestus* were observed, but only the Maramacho group (adult pair, one juvenile, and one infant) had three direct neighboring groups with whom it interacted (Chontal, Sujo, and Mangal). This group was located in the southeastern edge of a large 65 ha forest patch, so neighboring groups were to the northwest of the focal group (Fig. 1). We present information on this focal group, observed from July 2010 to June 2011 (dry and wet seasons) for 10 days per month for an average of 10 hours per day.
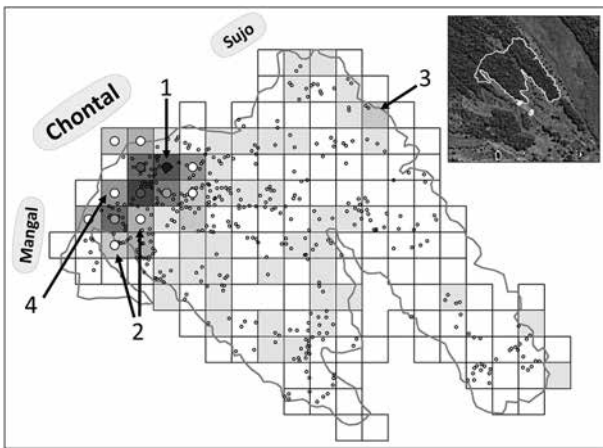

Figure 1. Map showing intergroup interactions in the area occupied by our focal group Maramacho and neighboring groups (group names in gray circles show relative location) in relation to the amount of food plants (smallest marks). Grid cells (25 × 25 m) show the places occupied by our focal group during the study with shading corresponding to the relative amount of intergroup interactions (darker shading indicates higher amount of records). Circles indicate cells with aggressive interactions Maramacho - Chontal (more records in darker circles). Numbers indicate cells with occurrence of: 1) first fight observation, 2) fights when adults fell from trees, 3 and 4) encounters with Sujo and Mangal groups, respectively. The inset photo is a reference image showing the area occupied by our focal group in relation to forest coverage.

We sampled the occurrence of intergroup interactions by means of *ad libitum* behavioral sampling (Altmann, 1974). An 'effective interaction' between groups was considered when a vocal or visual stimulus from a group promoted an immediate response in another group (vocal, movement, or other). We differentiated effective interactions based on the degree of contact between individuals of distinct groups. 'Indirect interactions' consisted of the exchange of territorial calls or displacements between individuals of distinct groups with no visual contact due to distance or visual barriers, such as dense vegetation. As territorial calls can be heard from more than 500 m, indirect interactions can involve both direct neighboring or more distant groups. 'Direct interactions' were considered when individuals of distinct groups interacted with visual contact, distinguishing 'aggressions' as chasing-retreat displays and 'fights' involving aggressive physical contact.

We registered the location of our focal group during each interaction event by means of compass bearing and distance to reference points. As part of our behavioral study, we registered the locations of plants consumed by the focal group during the entire study. This spatial information was mapped using a 25 × 25 m grid overlapped on the forest patch occupied by the focal group. Additionally, from all occurrence sampling of group displacements and feeding events (Altmann, 1974), we calculated the total amount of time and the feeding time spent by monkeys per grid cell.

Based on observation hours, we calculated the frequency of the distinct intergroup interactions observed. For aggressions and fights, we determined the winning group based on the behavioral context. With the frequencies and locations of the interactions, we estimated the number of intergroup interactions per cell grid. We assessed the relationship between interactions and feeding behavior reflected through feeding time and the number of plants per grid cell (SPSS v.24, significance level 0.05).

Results

We registered 227 effective intergroup interactions between our Maramacho focal group and surrounding groups from 574 cases when stimuli for interactions were detected (from 1,236 hours of observation). Most of these effective interactions (76.65 %) occurred between our focal group and the Chontal group (Table 1), while interactions with other direct neighboring groups were less frequent (9.69 % and 1.76 % for the Sujo and Mangal groups, respectively). The remaining interactions (11.69 %) were territorial call exchanges between our focal group and other more distant groups in distinct forest patches. This trend was similar for indirect interactions between groups (Table 1).

Table 1. Number of each type of intergroup interaction between our Maramacho focal group and neighboring groups. Direct neighboring groups marked in bold.

Group	All stimuli	Effective interactions	Indirect interactions	Direct interactions	Aggression	Fight
Chontal	**259**	**174**	**112**	**62**	**27**	**3**
Sujo	**64**	**22**	**21**	**1**	**1**	**0**
Pozero	104	21	21	0	0	0
Corral	39	4	4	0	0	0
Mangal	**12**	**4**	**3**	**1**	**0**	**0**
Tapao	72	1	1	0	0	0
Far OSO	14	1	1	0	0	0
Oeste	7	0	0	0	0	0
Guayabochi	1	0	0	0	0	0
Far NNO	1	0	0	0	0	0
Far NNE	1	0	0	0	0	0
	574	227	163	64	28	3

Direct interactions (with visual contact between groups) occurred almost exclusively between our focal group and its neighbor Chontal (n = 62), with only one direct interaction with each of the Sujo and Mangal groups (Table 1, Fig. 1). Direct interactions took place in the northwestern part of the area occupied by our focal group, that corresponds to 9.74 % of the group home range (0.94 of 9.63 ha, Fig. 1). From these interactions, we observed 27 cases of aggressive chase-retreat encounters between our focal group and Chontal, with the loser group leaving the 'conflict' site. The Chontal group won the majority of these encounters (14 vs. 11). There was only one aggressive encounter observed between the Maramacho and Sujo groups, which was won by Maramacho (Table 1).

We observed three fights (aggressive body contact) between individuals of the Maramacho and Chontal groups. In the first case (05/17/2010 at 12:00 h), both adults of our focal group confronted the adult male of Chontal group after he caused the retreat of the juvenile and infant of our focal group, apparently in an accidental way as the groups had not interacted previously in the day. During the encounter, the Maramacho adult female hit the side of the body of the Chontal male with her hand, and immediately the Maramacho adult male approached, pilo-erecting his body fur. There was not any direct contact between males as the Chontal adult male then ran away towards his territory, and this encounter was considered as a win for the Maramacho group.

The other two fights were separated by almost exactly one year and occurred in nearby locations (Fig. 1). In the first one (06/16/2010), groups met unexpectedly when moving during the morning (08:28 h). Just after visual contact, the adult males of each group charged each other until they made contact holding each other by the shoulders, apparently trying to bite each other's arms. As a result of the

struggle, both individuals lost equilibrium and fell to the ground from a height of around 7 m. A few seconds later, both monkeys climbed trees and returned to their respective groups. No further interactions occurred and there was not a clear winner.

The second case (06/10/2011) occurred in the late afternoon (17:12 h), after groups were in close proximity for almost an hour. The Maramacho infant was moving far from the adults and was chased by the Chontal adult male, instigating the fight. Similar to the previous case, the Maramacho male charged the other male and repeated a similar fight display with the same result of both individuals falling from a similar height. Again, the males retreated to their respective groups with no clear winner of this encounter.

Most interactions between the Maramacho and Chontal groups occurred during the wet season, but aggressive encounters, including the intergroup fights, took place mainly in the dry season (Table 2; from 619 and 617 hours of observation in wet and dry seasons, respectively). Interactions with the Sujo neighbor group occurred mainly in the wet season, but the opposite happened for the Mangal group.

The locations of intergroup interactions between Maramacho and Chontal groups had relatively high plant food source densities (mean of 6.8 plants per grid cell, range: 0-16, n = 15; Fig. 1). We found that aggressive interactions mainly took place in cells with a high amount of plant food sources (Spearman correlation: $rs_{(52)} = 0.282$, $p = 0.039$). Monkeys also spent more time in these cells ($rS_{(174)} = 0.798$, $p < 0.001$), and invested more time on feeding ($rs_{(174)} = 0.826$, $p < 0.001$). Nevertheless, fight events occurred in cells that did not necessarily have the highest plant food source densities (5-9 plants per cell). The only direct and aggressive encounter between the Maramacho and Sujo groups occurred in a grid cell with just two food plants.

Table 2. Seasonal variation in the number of interactions between our focal Maramacho group and its three direct neighboring groups.

Group	Season	Effective interactions	Indirect interactions	Direct interactions	Aggression	Fight
Chontal	Dry	77	48	29	15	3
	Wet	97	64	33	12	0
Sujo	Dry	4	4	0	0	0
	Wet	18	17	1	1	0
Mangal	Dry	4	3	1	0	0
	Wet	0	0	0	0	0

Discussion

Titi monkeys are well known as monogamous and territorial species (Kinzey, 1981; Bicca-Marquez and Heymann, 2013). Some studies have revealed low degrees of territoriality related to large home ranges, consisting exclusively of territorial calls (*Cheracebus torquatus*, Kinzey and Robinson, 1983; *Callicebus personatus*, Price and Piedade, 2001). More direct intergroup interactions occur in species needing to defend smaller home ranges (*Cheracebus lugens*, Robinson, 1979, 1981). Compared to other titi monkey species, the home range of *Plecturocebus modestus* (9.69 ha) is relatively small (Martinez and Wallace, 2016a). Thus, our observations of direct intergroup interactions suggest our focal group needed to defend a relatively small territory from conspecific intruders.

Determining the underlying causes of the observed interactions can help to understand intraspecific competition in Beni titi monkeys, who already face spatial restrictions in the fragmented forests they inhabit (Cheney, 1987; Martinez and Wallace, 2010; Wallace et al., 2013). In the three observed fight events, male participation suggests mate and infant defense in order to ensure reproductive success (Thompson et al., 2012). This type of aggression is usually initiated by incursions of males looking for reproductive opportunities; this can include solitary males, or males who have left their original group temporarily, as observed in white-thighed colobus (*Colobus vellerosus:* Sicotte and Macintosh, 2004). Before two of the three fights reported here, the infant of our focal group was chased by the Chontal adult male. This shows that infant defense may have driven the most aggressive encounters observed between the Maramacho and Chontal groups.

As well as reproductive opportunities, the need to ensure access to food resources can promote active territorial defense and can be distinguished according to which group members are involved (Sigiura et al., 2000; Sicotte and Macintosh, 2004). Female active defense of food resources is expected to ensure reproductive success, but similar defense can be carried out also by males as an indirect way to ensure permanence of female(s) in a group (Thompson et al., 2012). In our study, a great majority of the direct interactions involved both male and female adults of the

focal group during chase-retreat events, which suggests the interest of both adults to maintain food resources for their benefit. Nevertheless, it could also be linked to the monogamous social organization of titi monkeys, with the adult pair sharing most activities, including territorial defense (Kinzey, 1981).

As food resources are not homogenously distributed, areas with higher amounts of food should be defended more vigorously, as was observed in grey-cheeked mangabeys (*Lophocebus albigena*) and redtail monkeys (*Cercopithecus ascanius*; Brown, 2013). Our spatial data of intergroup interactions clearly show that the areas with most direct Maramacho-Chontal interactions offered a higher number of plant food sources as compared to other zones. Moreover, we found that our focal group spent most of the time in grid cells with a high amount of food plant sources. This may also explain the relative lack of interactions with other neighboring groups that occurred in areas of low food availability.

In addition, even though forest fragmentation in the range of *P. modestus* is mainly the result of natural processes (Hanagarth, 1993), this landscape configuration results in high food resource densities towards the center of forest patches due to edge effects (Rogan and Lacher, 2018). Our focal group, that inhabits a marginal zone of the forest patch, moved frequently to the central part of the patch to look for food. This demonstrates how these primates assessed the cost-benefits of obtaining food over the risks of aggressive intraspecific interactions, which might be more relevant for groups living in the marginal areas of forest patches. Increased levels of forest fragmentation amplify edge effects and could reduce the size of feeding sites for *P. modestus*, which might increase aggressive encounters between groups and could even affect the abundance of this threatened primate species (Rogan and Lacher, 2018).

Reduced availability of food resources during lean periods can promote their vigorous defense, but species with small home ranges are more sensitive to intergroup encounters and may need to defend their food resources against invaders even during periods of food abundance, as observed in Tana River crested mangabeys (*Cercocebus galeritus*; Kinnaird, 1992). Our data shows the latter trend, with more interactions between the focal Maramacho group and its

neighbors during the wet season, with aggressive encounters occurring mainly in the dry period when the youngest individual of our focal group showed independence from adults. This suggests that the most frequent motivation for intergroup interactions for our focal *P. modestus* group might be food resource defense against individuals of other groups.

Based on our results, there seem to be two main triggers for the distinct intergroup interactions observed between our focal group of *P. modestus* and its neighbors. Food resources are vigorously defended, but not with so high intensity as occurs with mate or infant defense, as observed in moustached tamarins (*Saguinus mystax*: Garber et al., 1993) and Japanese macaques (*Macaca fuscata*: Saito et al., 1998), showing that long-term reproductive success has higher priority than short-term disputes over food. Our observations suggest that territorial calls and chase-retreat events might be a sufficient response for food resource defense, whereas infant defense is in response to high risks to reproductive success, making fight encounters worthwhile.

Aggressive interactions between groups can result in reduced access to areas with resources by the losing group (Gordon, 1996), which could affect group permanence in the long term, as was reported for baboons (*Papio cynocephalus*) unable to exploit food resources in a conflict area (Mackhan et al., 2012). Although the neighboring Chontal group won more of the intergroup encounters against our focal group, the difference was not great (14 vs. 11), and we observed our focal group using food resources in the conflict area during the entire study. Home range overlaps of up to 16.6 % was reported in groups of *Cheracebus lugens*, whose home ranges varied between 3 and 4 ha (Robinson, 1979). In our case, the overlap corresponds to around 10 % of the home range of our focal group, which was more than twice the previous size (9.63 ha). Additionally, a study on territorial calls of *Plecturocebus modestus* suggested that these primates do not face intense spatial competition (Martinez and Wallace, 2016b). Thus, both groups could be sharing the conflict area with confrontations occurring only occasionally during close encounters.

On the other hand, fights can have lethal results, as reported for white-faced capuchins (*Cebus capucinus*; Gros-Louis et al., 2003) and white-bearded gibbons (*Hylobates albibarbis*; Cheyne et al., 2010). The fights we observed did not seem so dangerous, especially as titi monkeys do not have large canines to produce serious damage (Hershkovitz, 1990; Kobayashi, 1995) and because these events lasted for just a few seconds. Nevertheless, falling from a height of 7 m represents a serious risk of broken bones, or immediate or subsequent death. Considering the monogamous social organization of titi monkeys (Kinzey, 1981; Bicca-Marques and Heymann, 2013), this would represent a serious risk for group survival, as adult individuals guide access to food and guard against predation risk.

This is the first study about intergroup relationships of *Plecturocebus modestus*, providing valuable knowledge to better understand how these endemic Bolivian primates use and defend food resources and retain group integrity. Although our data come from just one focal group, they represent a good starting point for further detailed research on intraspecific relationships in this threatened primate within the naturally fragmented forests of southwestern Beni Department, Bolivia.

Acknowledgements

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