Observations of infant conflict and avoidance in San Martin titi monkeys (*Plecturocebus oenanthe*)

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**Abstract**

Conflict between caregivers and infants typically centers on disagreements over the amount and frequency of care provided. Prior research has identified many variables that impact patterns of mother–infant conflict. These include wide-ranging factors such as individual temperament, reproductive status, and availability of resources. By contrast, no studies have investigated the variables that influence father–infant conflict. To better understand the nature of caregiver–infant conflict in a species with obligate biparental care, I observed two groups of San Martin titi monkeys inhabiting disturbed secondary forest fragments in the San Martín region of Peru. Using instantaneous focal sampling of infants, I recorded physical conflict between infants and caregivers and instances of infant avoidance (leaving the infant) by adult males. I summarized data as the percentage of records in which these activities occurred for each focal day and report the estimates for caregivers. I further calculated mean percentages by month of infant age to assess the relative timing of infant conflict, for each group and age/sex class, and infant avoidance by males. Percentages of conflict and avoidance were markedly higher in the larger group living in a smaller habitat than in the other group. This pattern occurred across all age/sex classes. In both groups, the greatest amount of infant conflict occurred with siblings. I discuss the substantial variation in conflict and avoidance in relation to the various socioecological conditions that may have played a role. This study provides an in-depth description and exploration of parent–offspring and sibling conflict, which has not been examined previously in this species.

**Keywords** Parent–offspring conflict · Sibling conflict · Anthropogenic habitat

**Introduction**

Parent–offspring conflict (hereafter POC) is expected to occur as parents reduce their investment in young, who often react by attempting to secure additional care (Trivers 1974; Clutton-Brock 1991). In non-human primates, disagreements between mothers and infants over maternal investment are characterized by behavioral conflict over the amount of care given. Mothers may reduce the frequency or duration of nursing and contact, reject suckling or contact attempts, or avoid infants (Trivers 1974; Wright 1990; Gomendio 1991; Maestriperi 2002). Infant avoidance is usually included as a subset of rejection, but can be more specifically defined as efforts to prevent body contact with infants by leaving an infant’s location and maintaining physical distance (Simpson et al. 1986). Rejections range from mild (leaving, breaking contact, or threatening) to more physically intense responses (pushing, slapping, hitting, or biting). Infants frequently respond to these changes with distress and may vigorously persist in trying to re-establish previous care or contact patterns (Gomendio 1991; Maestriperi 2002; Pavé et al. 2015). In species with obligate biparental care, father–infant conflict appears similar. For instance, male titi monkeys dislodge infants more frequently as infants grow (Fragaszy et al. 1982; Wright 1990).

According to the primate literature, various factors can influence mother–infant conflict. These include maternal reproductive status (*Macaca fuscata*: Collinge 1987; *Macaca mulatta*: Gomendio 1991; *Trachypithecus leucoccephalus*: Zhao et al. 2008), maternal reproductive condition (*Chlorocebus sabaeus*: Fairbanks and McGuire 1995).
the presence of newborns (Alouatta caraya: Pavé et al. 2010), the quality of parent–offspring relationships (M. fuscata: Schino et al. 2001; M. mulatta: DeVinney et al. 2003, A. caraya: Pavé et al. 2015), rates of infant distress (Collinge 1987), food availability (Chlorocebus spp.: Fairbanks and Hauser 1988), and the thermoregulatory needs of infants (M. fuscata: Schino and Troisi 1998). In contrast, only a handful of primate studies have described father–infant conflict in titi monkeys (Fragaszy et al. 1982; Wright 1990). To date, none have examined the causes of variation in such father–infant interactions.

Research that examines POC patterns is useful for identifying factors that influence struggles between parents and offspring over care and can help improve our understanding of parental investment strategies. Relatively few studies have been conducted on POC in wild primates and father–offspring conflict remains even less explored, despite the prevalence of biparental care. To address this gap in knowledge, I carried out preliminary research on POC in a primate with obligate biparental care, the Critically Endangered San Martin titi monkey (Plecturocebus oenanthe) (Veiga et al. 2013). Titi monkey groups typically consist of a single pair of breeding adults and zero to three offspring of various ages (DeLuycker 2014; Spence-Aizenberg et al. 2016). Titi monkeys give birth to singletons and the resident adult male (the putative father) is the primary infant carrier and attachment figure during the period of dependency (DeLuycker 2007; Spence-Aizenberg et al. 2016). A series of POCs occur during the transition to infant independence, consisting of physical attempts by parents to limit clinging and suckling. During this transitional period, Wright (1990) documented that fathers push infants off their back and mothers avoid, push, bite, or hit infants. Infants respond with distress and vigorous attempts to maintain contact.

Here I make the first description of POC and sibling–infant conflict in P. oenanthe. To do this, I recorded physical conflict between infants and other group members, including undispersed offspring (putative siblings). I also recorded instances when males avoided infants (termed “avoidance”), as this may constitute a form of infant rejection. I did not track avoidance by other group members since, typically, infants did not exhibit distress when the mother or other offspring left the infant. Through exploratory data analysis of two groups, I examine the timing and nature of infant conflict. I then discuss potentially important socioecological factors affecting variation, including individual study subject differences, habitat, and social dynamics. Given the small sample size, I was unable to formally test hypotheses regarding the influences of these variables. However, this study provides detailed documentation of a critical aspect of parent–offspring relationships and the results generate important questions for future research.

Methods

Study sites and groups

This study took place from July to December 2015 and from August to December 2016 in the San Martín region of Peru (Fig. 1). Study groups inhabited secondary premontane tropical forest fragments (Holdridge 1967). One group lived in a 2.15-hectare (ha) fragment near the village Calzada (UTM coordinates: 9,331,207.84 northing, 267,581.92 easting, 18 M), and the other inhabited a 4.15-ha fragment close to the village Yantaló (UTM coordinates: 9,337,614.99 northing, 273,723.07 easting, 18 M). Both sites had undergone severe habitat destruction in the form of forest clearing and selective logging and were surrounded by cultivated fields and pastures.

For each group, I identified the age and sex class of individuals based on pelage coloration, facial markings, body build, and genitalia (DeLuycker 2007). The Calzada group consisted of an adult pair, a subadult female (absent in the second field season), a subadult male, a juvenile female (classed as a subadult in second field season), and one infant born each year. The Yantaló group consisted of an adult pair, a subadult female, and one infant born each year (the first infant later disappeared). I used the terms “male–infant” and “adult–infant” conflict (vs. “father–infant” or “POC”) as paternity was unconfirmed.

Data collection

Table 1 provides definitions of the behaviors recorded. I categorized the interactions of interest as “conflict” (involving
physical aggression) and “avoidance” (leaving an infant and maintaining distance). I tracked avoidance only by males, as infants rarely exhibited distress or made attempts to follow when avoided by the mother or sibling. I collected data on conflict and avoidance during daily focal follows of infants (four total observed).

This study was carried out as part of a larger investigation on infant care activities, for which I used instantaneous sampling every 2 min (Altmann 1974). Since conflict and avoidance tended to occur quickly, these behaviors are very likely to have been underestimated. I attempted to randomly rotate infant observations between groups, but discrepancies in sampling arose due to differing birthdays. On average, I conducted follows 3 days per week in 2015 and once per week in 2016. In total, I collected 286.43 h of observation on 83 focal follow days. I observed Calzada infants over 54 days and Yantaló infants over 29 days, and recorded twice as much data in Calzada (196.93 h) as in Yantaló (89.50 h). Data characteristics for each infant are given in Table 2. Infant age was conflated with season throughout the study and I was unable to analyze this factor.

To examine conflict and avoidance, I used R Studio (R Development Core Team 2014) to calculate the respective percentage of sample points devoted to conflict and avoidance per focal follow day. I investigated daily percentages by identifying the non-zero minimum, maximum, and mean values (weighted by points sampled per day). Next, I took the mean percentage of all daily estimates (including 0.00% values) to generate monthly means (weighted by days sampled per month). The overall mean was based on individual month means. This information is summarized in Tables 3, 4, and 5. Data are available as supplementary material or in the Open Science Framework repository https://osf.io/mpyz5.

To evaluate whether home-range size could be associated with infant conflict and avoidance behaviors, I calculated home-range size following the minimum convex polygon method (Hayne 1949). I recorded GPS locations of group members with ArcGIS version 10.2.2 (ESRI 2014).

| Table 1 | Ethogram of interactions of infants with other group members for the San Martin titi monkey |
|-------------|----------------------------------------------------------------------------------------------------------------------------------|
| **Activity** | **Definition** |
| Conflict   | Aggression directed at the infant, including pulling, grabbing, hitting, or biting. |
| Avoidance  | Occurred when an adult male traveled away from an infant maintaining a distance that prevented the quick establishment of bodily contact (> 3 m). The infant then made an attempt to follow the male, but did not reach him being either unable or unwilling to travel further. The infant then emitted distress cries, high-pitched whining vocalization accompanied by grimacing, until a caregiver retrieved it. |

| Table 2 | Data characteristics by infant |
|-------------|---------------------------------------------------------------------------------|
| Infant ID | Birthdate | Days observed | Hours observed | Ages observed (month) | Season |
| Calzada 1 | 14 July 2015 | 42 | 152.60 | 0–4 | Dry–wet |
| Calzada 2 | 24 Sept. 2016 | 12 | 44.33 | 0–2 | Wet |
| Yantaló 1 | 2 Oct. 2015 | 12 | 39.90 | 0–1 | Wet |
| Yantaló 2 | 10 Aug. 2016 | 17 | 49.60 | 0–4 | Dry–wet |

| Table 3 | Minimum, maximum, and mean daily percentages (%) of conflict records |
|-------------|-----------------------------------------------------------------|
|               | Male–infant conflict | Mother–infant conflict | Sibling–infant conflict |
|               | Calzada | Yantaló | Calzada | Yantaló | Calzada | Yantaló |
| Minimum       | 0.55   | NA⁴    | 0.75   | 0.54   | 0.75   | 0.66   |
| Maximum       | 9.33   | NA⁴    | 5.34   | 0.66   | 20.31  | 3.16   |
| Mean          | 1.84 (13) | NA⁴  | 2.16 (10) | 0.60 (2) | 4.73 (31) | 1.15 (6) |

Estimates were derived from non-zero daily percentages (total sample points on which conflict occurred divided by total sample points recorded for respective days) and mean values are weighted by the number of sample days analyzed (in parentheses).

⁴No observations of conflict were available for calculation
Results

Conflict with infant

Male–infant conflict took place on 13 of the 54 observation days at Calzada (24.07% of total days) while no instances of male–infant conflict were observed in Yantaló. Mother–infant conflict occurred on ten of 54 days at Calzada (18.52%) and on two of 29 days (6.9%) in Yantaló. I observed sibling–infant conflict on 31 of 54 days (57.41%) in Calzada and on 6 of 29 days (20.69%) in Yantaló. Table 3 reports minimum, maximum, and weighted mean daily percentages of conflict considering only days during which at least one instance of conflict was recorded (i.e., non-zero values). Conflict estimates were greater at Calzada than in Yantaló for all age and sex classes. In Calzada, siblings exhibited the most conflict in all months. Male–infant conflict was greater than mother–infant conflict overall and in months 2–4, but was lower in month 1. In Yantaló, conflict for siblings exceeded maternal estimates in months 1–3 but not in month 4.

Infant avoidance by males

The Calzada male was observed avoiding infants on 38 of 54 observation days (70.37% of total days). Considering only the days when avoidance was recorded, the minimum daily percentage of avoidance was 0.71%, the maximum was 73.17%, and the weighted mean was 11.24%. In Yantaló, avoidance took place on three of 29 days (10.34%). When avoidance was observed, the minimum daily value was 1.09%, the maximum 1.32%, and the weighted mean 1.16%. Table 5 reports weighted monthly means of infant avoidance (including 0.00% values). Avoidance means were higher in Calzada than in Yantaló each month and the overall mean was 62 times greater in Calzada.

Home-range size

The Calzada group occupied a home range of 0.76 ha (Fig. 2a) and the Yantaló group inhabited a home range of 2.18 ha (Fig. 2b).

Discussion

According to my observations of San Martin titi monkeys, there was substantial variation in behavior between the two groups. In Calzada, POC and avoidance began at younger ages and was sampled at higher percentages than in Yantaló for all classes. Mother–infant and male–infant conflict peaked in month 3 in Calzada, while mother–infant conflict peaked in month 4 at Yantaló. Notably, I never observed...
male–infant conflict in Yantaló. Below I discuss my results in the context of prior studies and the socioecological factors that may have led to the striking behavioral differences. As I monitored only two groups, it was not possible to definitively conclude which variables may have affected activity patterns.

The onset and intensity of adult–infant conflict in both study groups appear outlying relative to the current literature on titi monkeys. According to prior research, adults began to reject infant clinging at months 4–5 in both captive (Fragaszy et al. 1982) and wild groups (Wright 1984, 1990). Compared to these previous studies, adult–infant conflict began earlier in Calzada (month 1), was observed later by the Yantaló mother (month 3), and was never observed by the Yantaló male. Infant carrying ended by month 5 in both wild *P. oenanthe* (DeLuycyker 2007) and other captive and wild titi monkey species (Fragaszy et al. 1982; Wright 1984, 1990). Given the similar timing of infant independence, it is unclear why adult–infant conflicts began at younger ages in Calzada compared with findings from other titi monkey species, or why overt male–infant conflicts were unobserved in Yantaló.

There are multiple socioecological conditions that may have influenced titi monkey behavior, such as habitat quality and seasonality. In the current study, I compared site habitat using fragment and home-range size. The Calzada group was composed of six individuals (including the infant) inhabiting a 2.15-ha fragment with a home range of 0.76 ha. The Yantaló group consisted of four individuals (including the infant) living in 4.15-ha fragment with a home range of 2.18 ha. Similarly, DeLuycyker (2007) documented a home range of 3 ha for a group of four *P. oenanthe* occupying an anthropogenic forest fragment in the nearby city of Moyobamba (12 km from Calzada and 6.9 km from Yantaló). It is unknown what the typical home-range size is for this species in continuous forest, however study site fragments lacked connectivity to other forested areas, which may have limited home-range areas. The documented home ranges for *P. oenanthe* are much smaller than those observed for eight of the ten other *Plecturocebus* species for which home range has been recorded (5–30 ha) (Wright 1985; Rowe and Myers 2016). However, home-range size has been shown to be smaller for titi monkeys occupying secondary forest compared with those in primary forest. For example, *Plecturocebus toppini* (previously *Callicebus brunneus*) living in secondary forest occupied home ranges of 2–3.2 ha (Lawrence 2007), while those in primary forest inhabited 6–18 ha (Wright 1985). High rates of deforestation persist in the San Martín region, where the average forest fragment size is 6.43 ha (Shane et al. 2013).

The differences between study groups in fragment and home-range sizes may reflect variation in food quality and access (Chapman et al. 2006), however I did not examine this possibility. Additionally, prior research has challenged the use of home-range size as an indicator of resource availability or quality (Bortolamiol et al. 2014). Food abundance has been shown to vary seasonally for this species, which may have influenced caregiver–infant interactions in this study (DeLuycyker 2007). Since season was conflated with infant age, I was unable to investigate this factor. Further research is required to assess whether ecological conditions differed significantly between sites, as possibly suggested by measurements of habitat. If resources were more severely limited in Calzada compared with Yantaló (based on fragment and home range size), then adults may have been unable to reliably provide care while also meeting personal survival needs, triggering earlier, more frequent conflicts in this group. This has
been observed in Chlorocebus spp. (Hauser and Fairbanks 1988). Additional data on habitat and season factors is needed to clarify the role of ecological conditions in POC.

Additionally, variation in tolerance of infants or caregiver style may have affected conflict and avoidance. This has been shown in research on C. sabaeus, which found stable individual differences in maternal style (protectiveness and rejection) across infant age and identity (Fairbanks 1996). Further, prior parental experiences may have affected the overall form of caregiving by adults (reviewed in Fairbanks 1996). For instance, in Yantaló, one infant disappeared before the start of the study and one infant disappeared between field seasons. This may have influenced parents to be more protective and less rejecting of infants.

Finally, the elevated percentages of sibling–infant conflict relative to those of adults in both groups is unsurprising as titi monkey siblings are known to exhibit distress and intolerance when infants cling to them (Fragaszy et al. 1982). Since males are the primary infant caregivers, conflict values for mothers and siblings in each group may have been related to instances of male–infant conflict. Specifically, increased levels of male–infant conflict and avoidance in Calzada may have redirected infant clinging attempts to other group members, thereby elevating conflict estimates for the mother and siblings. This behavioral sequence has been documented in captive titi monkeys (Fragaszy et al. 1982).

As a final caveat, it is possible that the higher rate of sampling at Calzada compared with Yantaló produced the discrepancy in outcomes. However, I consistently documented the divergent interaction patterns in two sets of infants over two field seasons with roughly equivalent rates of sampling in the second season. Therefore I do not expect that sampling bias played a significant role in the results. Despite the limitations of my data, the findings provide an in-depth representation of conflict with, and avoidance of, infants by titi monkey caregivers that can be used to shape future research on POC and parental investment.

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Compliance with ethical standards

Conflict of interest The author declares there are no conflicts of interest related to this work.

Ethical approval This research followed the IPS Code of Best Practices for Field Primatology and adhered to all legalities in Peru (Permit #: N°0208-2012-AG-DGFFS-DGEFFS, N°329-2016-SERFOR-DGGSPFFS).

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