Pair-Mate Relationships and Parenting in Equatorial Saki Monkeys (*Pithecia aequatorialis*) and Red Titi Monkeys (*Callicebus discolor*) of Ecuador

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**ABSTRACT**

Socially-monogamous primates are often described as displaying a suite of behavioral characteristics that includes a prolonged and essentially exclusive mating relationship between mates, joint participation of mates in territory defense, and extensive male involvement in offspring care. Amongst the pitheciins, titi monkeys (*Callicebus* spp.) and saki monkeys (*Pithecia* spp.) frequently live in socially-monogamous groups. We present here comparative data collected over four years on the social interactions of Neotropical adult male and female titi monkeys (*Callicebus discolor*, *n* = 2 groups) and saki monkeys (*Pithecia aequatorialis*, *n* = 1 group comprising 2 different male-female pairs) in the Yasuní National Park and Biosphere Reserve in Ecuador.

Our data suggest that these two pitheciins do not both fit the mold of “classic” social monogamy. Despite their similar grouping patterns, the two species differ markedly in the quality of the social relationships between pairmates. Saki pairmates are less affiliative and engage less in behaviors thought to be instrumental to the development and maintenance of pair bonds (e.g., grooming, coordinated vocal displays) than titi pairmates. There are also dramatic differences in the extent to which males invest directly in offspring. While titi males invest heavily in infants, saki males provide little direct paternal care. Male sakis may be providing indirect investment, but they certainly do not seem to mitigate the energetic costs of infant care for their partners to the same extent as titi males do. Thus, male sakis apparently remain in socially-monogamous relationships for reasons disassociated from paternal care. Our results
suggest that different ecological and/or social factors may underlie the expression of social monogamy in these two pitheciins.
INTRODUCTION

Socially-monogamous primates are often described as displaying a suite of behavioral characteristics that includes a high degree of affiliation and social tolerance among pairmates (Kleiman 1977; Fuentes 2002; Reichard 2003). Traditional conceptions of pair bonding also imply that the affiliation is mutual, with both individuals being responsible for maintaining their close spatial association (Anzenberger 1988; Palombit 1996; Fernandez-Duque et al. 2000).

Among the pitheciins, titis (Callicebus spp.), conform to this “classic” pattern of social monogamy. They are always encountered in small groups of two to five individuals, the nucleus of which is an adult male and an adult female (Kinzey 1981; Wright 1985; Robinson et al. 1987; Defler 2004; Carrillo et al. 2007; Norconk 2007). In wild groups, pairmates typically stay within a few meters of each other during feeding, traveling and resting periods, and show coordinated activities (Mason 1966; Robinson 1979; Robinson 1981; Kinzey and Wright 1982; Wright 1985; Mendoza and Mason 1986; Price and Piedade 2001). Based on the high degree of intimacy, coordination, and interdependence between pairmates, the existence of a strong and specific mutual attachment or “bond” is regularly inferred (Mason 1975; Anzenberger 1988; Fernandez-Duque et al. 1997). The existence of a pairbond has been unequivocally demonstrated in captivity, where pairmates show clear behavioral and physiological signs of distress following separation (Mendoza and Mason 1986).

Our understanding of pairmate relationships in sakis (Pithecia spp.) is far less clear than in titis. Sakis have also been reported to live in small social groups that include a single breeding pair and up to several young. Although there have also been studies reporting larger groups (Norconk 2007), most of those groups were found in island habitats that limit the dispersal possibilities of individuals (Setz and Gaspar 1997; Vié et al. 2001; Norconk 2006), or during censuses of non-habituated individuals that limit the possibility of precise group identification (Lehman et al. 2001). Thus, there is little demographic evidence suggesting routine deviation from social monogamy in Pithecia. Additionally, our knowledge of saki social behavior is likewise limited, since there have only been a handful of studies focused on identified and habituated individuals (Setz and Gaspar 1997; Norconk 2006; Di Fiore et al. 2007).

Coordinated displays and joint participation in territory defense are also thought to reflect the existence of a pair bond between the male and the female of a socially monogamous group (Robinson 1979; Robinson 1981; Mitani 1984; Raemaekers and Raemaekers 1985). Titis use ranges with relatively little overlap, and routinely perform behaviors at the borders of those ranges that include duetting and joint visual displays (Mason 1968; Robinson 1981; Wright 1985; Price and Piedade 2001). The two adults perform these behaviors in a highly coordinated fashion, sitting or standing side-by-side while calling or displaying. For sakis, on the other hand, the specific contributions of male and female pairmates to inter-group interactions or territory defense remain unexamined. The limited data available on use of space by sakis in non-island habitats indicate that their ranges may be somewhat exclusive and defended (Vié et al. 2001; Norconk et al. 2003). Preliminary playback experiments in Pithecia aequatorialis suggest that the male may respond more to a potential intruder than the female (Di Fiore & Fernandez-Duque, unpublished data, 2006).
Finally, extensive male involvement in infant care is also commonly associated with social monogamy (Kleiman 1981; Kleiman and Malcolm 1981; Palombit 1999; Maestripieri 2002). Among the pitheciins, the involvement of the titi male in infant care is one of the most unique aspects of the social organization of the genus (Wright 1984; Mendoza and Mason 1986; Hoffman et al. 1995; Norconk 2007). The male carries the infant most of the time and also plays, grooms, and shares food with the infant. Although studies of infant care in free-ranging habituated groups have been somewhat limited (Kinzey and Becker 1983; Wright 1984; Tirado-Herrera and Heymann 2000; Tirado-Herrera and Heymann 2004), there have been several detailed studies of parental behavior and infant development in captive groups (Fragaszy et al. 1982; Mendoza and Mason 1986; Hoffman et al. 1995). These studies suggest that, in titis, the infant may be primarily attached to the putative father rather than the mother (Mendoza and Mason 1986; Hoffman et al. 1995). In all of the other pitheciin genera, by contrast, direct paternal care is relatively absent. Male sakis do not routinely transport infants, although they may play and interact socially with older young (Norconk 2007).

The extent to which strong pair bonds characterize sakis like they do in titis has not been investigated. Nor have there been evaluations of paternal care in sakis that consider the services that males may provide to females and their offspring, such as anti-predator vigilance or territory defense. In the following paragraphs, we give a descriptive overview of the patterns of pairmate relationships and paternal care seen in Equatorial saki monkeys (P. aequatorialis) and red titi monkeys (Callicebus discolor), based on comparative data collected from two groups of titis and one group of sakis in western Amazonia.

METHODS

Area of study

Since 2003, we have been studying three species of monogamous primates (owl monkeys: Aotus vociferans; titi monkeys: Callicebus discolor; saki monkeys: Pithecia aequatorialis) at the Tiputini Biodiversity Station (76° 08’ W, 0° 38’ S), located in the Yasuní National Park and Biosphere Reserve in Ecuador (Carrillo et al. 2007; Di Fiore et al. 2007; Fernandez-Duque et al. in press). The study site, on the left bank of the Río Tiputini, covers approximately 650 hectares of primary tropical rainforest that can be accessed by an extensive trail system (Figure 1). Rainfall in the region typically totals more than 3000 mm per year (Di Fiore and Rodman 2001).

Groups of Study

The saki group has been monitored continuously since November 2003. During that month, we darted and captured the adult male and fitted him with a radio collar following procedures we have also used to capture owl monkeys (Aotus azarai) in Argentina (Fernandez-Duque and Rotundo 2003), as well as owl monkeys (Aotus vociferans), titi monkeys (Callicebus discolor), capuchins (Cebus albifrons), squirrel monkeys (Saimiri), spider monkeys (Ateles belzebuth), and woolly monkeys (Lagothrix lagotricha) in Ecuador (Di Fiore & Fernandez-Duque, unpublished data, 2007).
At the time of darting, the group consisted of an adult male, an adult female, and a male juvenile of approximately six months of age. The original adult male was replaced by a new adult male in October 2004 (Di Fiore et al. 2007); the dependent juvenile dispersed in October 2007, when he was approximately 4.5 years of age; and two infants were born to the adult female in March 2005 and November 2006. The first infant disappeared in February 2006 when it was approximately 11 months old and the second one is in the group as of December 2007.

Regarding the titis, we report data collected from one fully-habituated group studied since November 2003 and a second group added to the study in October 2006. The first group consisted initially of two animals, an adult male and an adult female. During these years, the female gave birth to two offspring. The first one was born in January 2004 and disappeared in November 2006 when it was almost three years of age. The second one, born in January 2005, disappeared in February 2006 when it was 13 months old. The original adult female disappeared in March 2007, and she was replaced by a new adult female shortly thereafter. A new infant was born to the new female in December 2007. The second group consisted of an adult male-female pair when it was added to the study. Two infants were born in this group, one in November 2006 and the other in November 2007.

Data collection

We collected behavioral data during 20-minute focal samples of all group members. Each day we sampled animals opportunistically based on visibility, but following the rule that successive focal samples of the same individual had to be separated by at least 20 minutes. Across days, we maintained an approximate balance in the number of focal samples collected per individual. During each focal sample, we recorded one of six basic behavioral states (‘resting’, ‘foraging’, ‘moving’, ‘social’, ‘other’, and ‘out of view’) for the focal animal, and the identity of its nearest neighbor (or neighbors, if multiple group members were equidistant from the focal individual) as instantaneous sampling points every two minutes. Additionally, between the instantaneous sampling points, we continuously recorded all occurrences of select behaviors relevant to parental care and male-female relationships (e.g., grooming, food sharing, play, vigilance, nursing, rejection, infant transfers, and approach/leave interactions). Finally, we recorded ad libitum any conspicuous but rare events (e.g., intergroup encounters, fights among group members) that occurred too infrequently for our sampling protocol to yield an adequate assessment of their rate.

Data analysis

Between July 2004 and March 2007 we collected approximately 530 hours of focal data on the saki group (63 h while the original adult male was in the group and the remainder with his replacement). We also collected approximately 330 hours on two groups of titis; 320 h with the primary study group and 11 h with the second one.

To characterize the social behavior of individual titis and sakis, we first calculated, for each focal sample, the proportion of instantaneous sampling points that focal individuals spent with each other group member as its nearest neighbor, the proportion of sampling points they spent giving and receiving grooming, and their rates of participation in food sharing, play, vigilance, nursing, rejection, and infant transfers.
We calculated rates as the number of occurrences of the behavior of interest per focal sample. We then computed a mean across focal samples for each individual.

To examine which individuals were more responsible for maintaining the observed spatial patterns, we calculated Hinde’s indices for each pair of individuals within a group. The index ($I$) is calculated as the proportion of “approaches” ($AP$) between two individuals (A and B) that one of them is responsible for, minus the proportion of departures (“leaves”, $LV$) that the same individual is responsible for, multiplied by 100.

$$I_{AB} = \left( \frac{\# AP \text{ } A \Rightarrow B}{\# AP \text{ } A \Rightarrow B + \# AP \text{ } B \Rightarrow A} \right) - \left( \frac{\# LV \text{ } A \Rightarrow B}{\# LV \text{ } A \Rightarrow B + \# LV \text{ } B \Rightarrow A} \right) \times 100$$

Thus, the index ranges from 100 (if individual A is responsible for all approaches to B and no departures from B) to -100 (if A never approaches B and consistently leaves B). A value of zero would indicate that those two individuals approach and leave one another at similar rates.

Because our data were not normally distributed, we used only nonparametric statistical tests, treating each focal sample as an independent observation.

**RESULTS**

Species difference in pair mate relationships

Titis and sakis differed in the spatial relationships between mates. Both male and female titis had their partner as the nearest neighbor more frequently than the sakis did (Figure 2).

**- INSERT FIGURE 2 ABOUT HERE -**

Titi pairmates also spent more time in social contact (i.e., resting in contact and tail twining) than did saki pairmates (Figure 3a). Despite the difference in time spent in contact, the amount of grooming seen among pairmates, at least following the replacement of the original resident male saki, was similar in the two species (Figure 3b). Titi pairmates also approached each other more frequently than did saki pairmates (Figure 4).

**- INSERT FIGURES 3 AND 4 ABOUT HERE -**

Both species showed sex differences in the relative contributions to proximity maintenance. Males were more responsible than females for maintaining proximity, as reflected in Hinde’s indices of 25 and 24 for male titis and sakis respectively. In general, males of both species approached their partners more than females approached males, while females were more often responsible for breaking proximity from their partners (Table 1).

There were other aspects of saki and titi social behavior that may reflect additional differences in the nature of the bond between mates. The two titi pairs regularly performed coordinated duets, in good agreement with previous findings (Mason 1966; Kinzey and Robinson 1983). On the other hand, no coordinated vocalizations were observed between saki pairmates. Moreover, preliminary playback experiments to the study group showed that the male responded more strongly to playbacks of territorial
vocalizations than the female, by vocalizing and approaching the speaker (Di Fiore and Fernandez-Duque, unpublished data, 2006).

Species differences in parenting

Differences in social behavior between titis and sakis were most pronounced with regard to patterns of infant care. The male titis were heavily involved in infant care. They started carrying the infants the first week after birth, and during the first four months of life they carried them substantially more than the mothers did. Even when not carrying the infant, the adult male titi monkey was more often the nearest neighbor of infants than was the adult female. In fact, over the first four months of life, one titi infant whom we focused on collecting parental carrying data spent between 80 and 100% of its time either in contact with or closest to its putative father rather than its mother (Figure 5).

- INSERT FIGURE 5 ABOUT HERE -

Male sakis, by contrast, were never observed carrying infants. However, when the saki infant was already independent, there were interactions between him and the male that plausibly be interpreted as indirect male care. For example, on several occasions (n = 7), we noted bouts of babysitting by the male, with the offspring staying next to the stationary male while the female moved off to forage. In most of these cases, the offspring tried to climb onto the male, but was often rebuffed by cuffs or biting. Additionally, when the infant was approximately seven months of age, we observed the male sharing food with him, although this was not a common behavior.

The differences between titis and sakis in patterns of care were also manifest later in the life of the offspring. For example, there were clear differences in the spatial arrangements of adults and their weaned offspring. Saki juveniles had their mother as a nearest neighbor more frequently than they had the resident adult male, whereas the titi juveniles had the resident adult male as their nearest neighbor more frequently than they had their mother (Figure 6). In both species, the juveniles were more responsible than the adults for maintaining proximity, although the pattern was less skewed in the titis than the sakis (mean juvenile-to-adult Hinde Index, 20 versus 44, respectively).

DISCUSSION

Our data show that although both titis and sakis live in socially monogamous groups, there are important differences between the species in the nature of the relationship between males and females, as well as in the nature of the parent-offspring interactions. In this preliminary examination, those differences were reflected in: 1- the spatial relationships among group members, 2- the differences in sex-specific contributions to the maintenance of spatial proximity, and 3- the differences in the amount of direct care provided by males.

The spatial associations among group members were very different in the titi and saki groups. Titi pairmates stayed in close proximity to each other most of the time, whereas the saki male and female tended to be further apart. Still, it is important to note that the incoming saki male spent substantially more time with the female as his nearest neighbor than did the initial resident male (Di Fiore et al. 2007), suggesting that a close
spatial association may be important in saki monkeys during the process of pair formation.

It is usually expected that the characteristic low level of physical dimorphism observed in socially monogamous primates (Kay et al. 1988; Plavcan 1993; Smith and Jungers 1997) will occur together with a similar reduction in behavioral dimorphism. In other words, males and females in a monogamous relationship will make similar contributions to the maintenance of their social arrangement. For example, pair mates may contribute similarly to the spatial cohesion of the social group, to the defense of the territory, or to the care of the infants. Sakis and titis differ in size and in the extent of physical dimorphism between the sexes. Titi monkeys are small, weighing on the order of 900 to 1200 grams and show little sexual dimorphism (Smith and Jungers 1997; Norconk 2007). Sakis, by contrast, are much larger (on the order of two to three kilograms), and more sexually dimorphic (Norconk 2007). Our data show that, despite differences in the extent of sexual dimorphism, males showed more interest in females than females did in males in both species. This was reflected in both the rate of approaches and in Hinde’s index, which summarizes both the “approach” and “leave” sides of proximity maintenance. A similar pattern of sex differences in behavior was found when captive pairs were tested while responding to potential intruders (Fernandez-Duque et al. 1997; Fernandez-Duque et al. 2000). Preliminary playback experiments and adlibitum observations suggest that saki males may be more likely than females to respond to the presence of an intruder. And, although it has been reported that titi pairmates regularly approach the territory border together and display in a coordinated fashion (Mason 1966; Robinson 1981), our own experience indicates that there may be important sex differences in the responses to intruders. During playback experiments and group territorial encounters males more frequently led the group towards the sound source, while displaying, standing on hind legs and chasing intruders (Di Fiore & Fernandez-Duque unpublished data). Finally, it was very clear that the two genera differed in the contribution of the two sexes to infant care.

In agreement with previous reports, the male titi was the main carrier of the infant from the first week of life (Mendoza and Mason 1986; Norconk 2007). This is a most remarkable aspect of the behavioral biology of titis, only seen elsewhere in primates among owl monkeys (Wright 1984; Rotundo et al. 2005) and callitrichines (Digby et al. 2007). Given that paternal care is prevalent in those small-bodied taxa, but absent in the relatively larger sakis, it seems reasonable to suggest that social monogamy is maintained because the care provided by the male contributes to reducing the metabolic costs to the female of raising relatively large offspring.

Socially-monogamous primates have historically been described as having a relatively prolonged and essentially relationship that included exclusive mating between them. This assumption, however, has appropriately been questioned (Palombit 1994), and reports of extra-pair copulations among socially monogamous primates keep accumulating (Mason 1966; Palombit 1994; Reichard 1995; Fietz et al. 2000; Oka and Takenaka 2001). Pairmate turnover has been documented in all three socially monogamous genera we are investigating (Di Fiore et al. 2007; Rodman and Bossuyt 2007; Fernandez-Duque et al. 2008). In the future, on-going genetic analyses of group structure will help us elucidate the temporal stability of these socially monogamous
groups, as well as the relative importance of paternal care in favoring the evolution of monogamy.

In conclusion, social monogamy is not a unitary phenomenon in primates; it can exist without males and females being strongly pair bonded, and it can exist in the absence of paternal care (Di Fiore and Fernandez-Duque 2007). Thus, in searching for explanations for social monogamy and paternal care in primates, we should expect that there may be different mechanisms at play for different taxa.

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REFERENCES


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Table 1. Rates of approaches and leaves among titi and saki pairmates (± S.E.)

<table>
<thead>
<tr>
<th></th>
<th>Male AP Female</th>
<th>Female AP Male</th>
<th>Male LV Female</th>
<th>Female LV Male</th>
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<tbody>
<tr>
<td>Titis</td>
<td>0.18 ± 0.002</td>
<td>0.11 ± 0.001</td>
<td>0.14 ± 0.001</td>
<td>0.28 ± 0.003</td>
</tr>
<tr>
<td>Sakis</td>
<td>0.08 ± 0.001</td>
<td>0.04 ± 0.001</td>
<td>0.08 ± 0.001</td>
<td>0.12 ± 0.001</td>
</tr>
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AP = Approach, LV = Leave

Rates calculated as number of occurrences of approaches or leaves per 20-min focal sample averaged across samples
Figure 1. Location of the study site in the Yasuni National Park and Biosphere Reserve in the Ecuadorian Amazon.
Figure 2. Differences between species in the nearest neighbor relationships among pair mates of titi and saki groups. Bars show the mean proportion of sampling points per focal sample (± S.E.) when the focal animal’s pair mate was the nearest neighbor.
Figure 3a

Mean Percentage of Sampling Points

Focal Animal

Titi Female  Titi Male  Saki Female  Saki Male 1  Saki Female  Saki Male 2
Figure 3b

Figure 3. Differences between species in the time spent (a) in social contact and (b) grooming among pair mates of titi and saki groups. Bars reflect the mean proportion of sampling points per focal sample (± S.E.) when the focal animal’s pair mate was in social contact or grooming/being groomed by the focal animal.
Figure 4. Differences between species and between the sexes in the rates of approach among pair mates of titi and saki groups. Bars reflect mean number of approaches to partner plus approaches received from partner per focal sample (± S.E.). AP refers to approach.
Figure 5. Patterns of carrying and nearest neighbor relationships between one titi monkey infant, its mother and the putative father during the first four months after birth. Bars reflect the mean proportion of sampling points per focal sample when the infant was being carried by the mother, the putative father or moving independently with the mother or putative father as its nearest neighbor.
Figure 6. Species differences in the nearest neighbor relationships between juveniles and their parents. Bars reflect the mean proportion of sampling points per focal sample (± S.E.) when the mother and the putative father were the nearest neighbor of the juvenile. Stars indicate statistically significant differences (Wilcoxon tests for two related samples, p < 0.001).