

A Saki Saga: Dynamic and Disruptive Relationships among *Pithecia aequatorialis* in Ecuador

Amy M. Porter^a Mark N. Grote^a Lynne A. Isbell^{a, b}
Eduardo Fernandez-Duque^{c, f} Anthony Di Fiore^{d, e}

^aDepartment of Anthropology, and ^bAnimal Behavior Graduate Group, University of California, Davis, Calif., ^cDepartment of Anthropology, Yale University, New Haven, Conn., ^dDepartment of Anthropology, University of Austin at Texas, Austin, Tex., and ^eCenter for the Study of Human Origins, Department of Anthropology, New York University, New York, N.Y., USA; ^fCentro de Ecología Aplicada del Litoral, Conicet, Argentina

Key Words

Saki monkey · Variable grouping pattern · Male immigration · Log-odds ratio

Abstract

Saki monkeys live in socially monogamous groups and in groups containing more than one same-sex adult. As part of a 10-year study of equatorial sakis (*Pithecia aequatorialis*) in Ecuador, we documented the immigration of a second adult male into a group containing a resident male-female pair that had associated with one another for seven years and the resident female's two daughters. In the first month after immigration, the resident male spent more time closer to and grooming his putative adult daughter than the resident female, and the two males were seen performing a cooperative territorial display. After two months, the resident male interacted more with the resident female than with his putative adult daughter, while that daughter interacted more with the immigrant male and copulated with him. After three months, the males left the group together and associated with an unfamiliar female, leaving the resident females and a neonate behind. The resident male then paired with a new female, while the immigrant male joined another group, again as a second male. Compared to other socially monogamous primates, sakis appear to have a more variable social system whereby additional males can join established groups and form relationships with putatively unrelated males.

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Introduction

During the last two decades, increasing numbers of behavioral and genetic studies have revealed that many socially monogamous animals can exhibit considerable variation and flexibility in both their grouping and mating patterns [Davies, 1992; Fuentes, 1999; Kyle et al., 2007; Lappan, 2007; Savini et al., 2009; Thompson and Norconk, 2011]. This variability and flexibility has been seen both between and within species, suggesting that some socially monogamous taxa may express multiple mating strategies.

Although researchers have long known that extra-pair copulations are a common mating strategy among many socially monogamous animals [Griffith et al., 2002; Morino, 2009; Huck et al., 2014], the formation of relatively stable groups with more than one adult of each sex in putatively pair-living species is only now being more thoroughly investigated. Among primates, early accounts of groups with multiple same-sex adults were first documented in gibbons [*Hylobates* spp.: Fuentes, 2000], but they were frequently interpreted either as rare exceptions or as unstable groups going through transitions in composition [Srikosamatara and Brockleman, 1987; Bleisch and Chen, 1991]. Since then, however, white-handed gibbons (*H. lar*), Cao-vit gibbons (*Nomascus nasutus*) and siamangs (*Symphalangus syndactylus*) have all been documented to sometimes form groups with multiple adults that can be quite stable over several years [Lappan, 2007; Reichard, 2009; Fan et al., 2015].

The formation of groups with multiple same-sex adults is somewhat unexpected in primates that are considered monogamous. Many pair-living primates show strong and sometimes lethal intrasexual aggression by both males and females toward extra-group competitors [e.g. neighbors or solitary individuals: Palombit, 1993; Fernandez-Duque and Huck, 2013]. Indeed, one hypothesis suggests that monogamy evolved when females were highly intolerant of each other due to feeding competition, and their spatial distribution consequently constrained males to guard only one female from other male competitors [Emlen and Oring, 1977; Lukas and Clutton-Brock, 2013]. If strong intrasexual aggression is typical for some socially monogamous primates, under what conditions might pairs tolerate additional adults?

Extra-group males may be able to immigrate into an established group by providing a service to the resident male, such as assistance with parental care, mate defense or territorial defense [Davies, 1992; Savini et al., 2009; Thompson, 2015]. Joint mate and/or territorial defense may be especially important if floaters (i.e. solitary individuals without territories of their own) are prevalent in the area [Port and Johnstone, 2013; Thompson, 2015]. Indeed, a study of Azara's owl monkeys (*Aotus azarai*) revealed that encounters with floaters can lead to high turnover rates among pair-mates [Fernandez-Duque and Huck, 2013]. Offspring of neighbors that are ready to disperse can present the same threat as floaters. Studies of white-handed gibbons have shown that young immigrant males, often from neighboring groups, frequently force themselves into groups with established pairs, leading to the resident male becoming a beta male [Savini et al., 2009]. If secondary males can help groups persist and increase male tenure length, as has been documented in birds [Davies, 1992; Seddon et al., 2003], ungulates [Acrese, 1999] and primates [Brockelman et al., 1998; Bradley et al., 2005; Snyder-Mackler et al., 2012], resident

males may tolerate additional males. Secondary males, in turn, may decide to stay in a group if they gain mating opportunities, whether these are shared with little-to-no resistance [white-faced sakis, *Pithecia pithecia*: Thompson, 2013] or are contested [dunnocks, *Prunella modularis*: Davies, 1992]. Immigrant supernumerary males may also stay if their prospects of reproducing are greater by queuing [Kokko and Johnstone, 1999] than by trying to take over another group. Alternatively, successful immigration may be the result of a resident's inability to keep out persistent intruders [Davies, 1992].

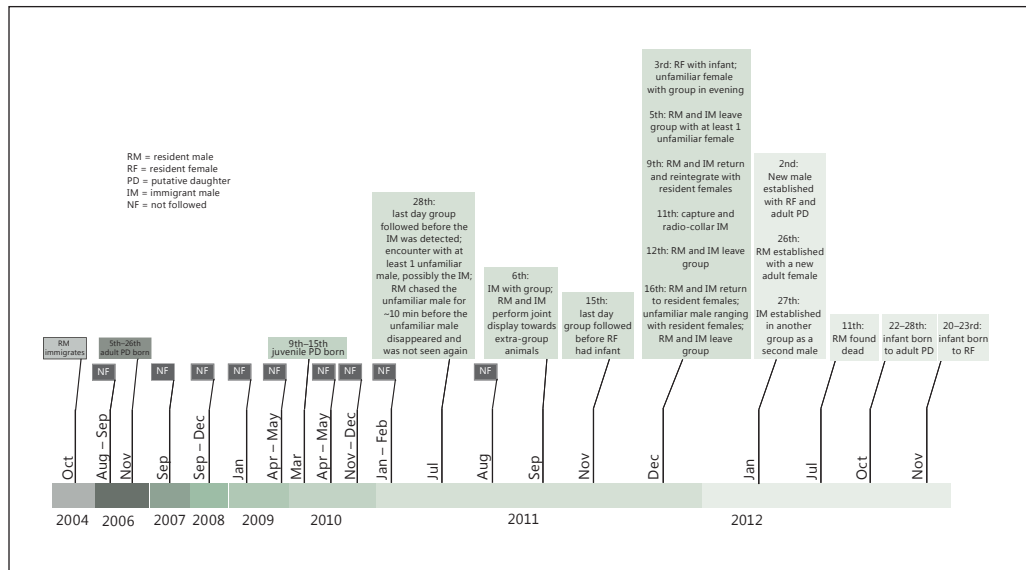
Saki monkeys are an example of a putative socially monogamous primate that exhibits variable grouping and mating patterns, occurring in both male-female pairs and in small groups with multiple adults of one or both sexes [Thompson and Norconk, 2011]. These authors have suggested that a variable social organization in white-faced sakis could be driven by the benefits of male cooperation in territorial defense. These animals show a strong male bias in territorial behavior, with males more frequently engaging in displays (e.g. branch-shaking and vocalizing) and chases than females [Thompson et al., 2012]. Females occasionally scent-mark and vocalize during encounters, but they have not been observed to engage in direct interactions, and they tend to remain behind the male(s) during intergroup encounters [Norconk, 2006; Thompson et al., 2012]. Similar observations have been made in equatorial sakis (*P. aequatorialis*) [Porter et al., unpubl. data].

In this study, we describe the immigration of an adult male equatorial saki into an established group consisting of a resident adult male, a resident adult female who was pregnant and her 5-year-old and 1.5-year-old daughters (both putative daughters of the resident male). At the time of immigration, the resident male and female had been an established pair for seven years. Until now, immigration in sakis has only been described for animals moving into groups lacking same-sex residents [Di Fiore et al., 2007]. To gain insights into the process of group formation and possible functions of multiple males in saki groups, we evaluated the hypotheses described above by testing the following predictions:

(1) If mate-guarding is an important component of saki mating strategies, then, in the face of a new immigrant, the resident male should be highly attentive toward the resident female. This should be reflected by the resident maintaining proximity (<1 m) or contact with her and/or preventing proximity or contact between her and the immigrant male by increased rates of aggression.

(2) Alternatively, if the resident male benefits from a service provided by an immigrant male (e.g. mate and/or territorial defense), then the resident should be tolerant toward the immigrant, and this should be reflected in little to no aggression being directed towards the immigrant. The immigrant male, in turn, is expected to actively participate in territorial displays.

To test these predictions, we examined spatial and social relationships between the adult animals before and after the arrival of the immigrant male. In addition, we describe a joint territorial display performed by the resident and immigrant males and three events in which the two males left the territory together and associated with at least one unfamiliar female, while the resident females and a neonate remained behind.



Color version available online

Fig. 1. Timeline of key events in the history of the study group, indicating the months when animals were not followed.

Methods

Study Site and Subjects

This study was conducted at the Tiputini Biodiversity Station (76°08' W, 0°38' S), located in the Yasuní National Park and Biosphere Reserve in eastern Ecuador. The study site covers approximately 650 ha of primary tropical rainforest, including both várzea (periodically flooded) and terra firme (unflooded) forest.

The study group has been regularly monitored since November 2003 as part of a larger research project on the comparative socioecology of Neotropical primates, Proyecto Primates. The results presented here cover the period from June 2009 to December 2012. Figure 1 chronicles key events in the history of the group dating back to 2004 (when the resident male first entered the group) and shows intermittent gaps when the animals were not followed.

When this study began, the group consisted of a resident adult male ('resident male'), a resident adult female ('resident female') and the resident female's two daughters. It is likely that the resident male was the father of both younger females because he was the only adult male observed interacting with the resident female throughout his tenure with the group until the arrival of the immigrant male (fig. 1). However, until paternity analyses confirm this, we refer to the younger females as the 'putative adult daughter' and the 'putative juvenile daughter' of the resident male. We classified the older putative daughter as an adult based on the literature on ontogeny and life history traits from both wild and captive populations of sakis [Savage et al., 1995; Norconk, 2006; Van Belle et al., 2015]. In addition, at the time the immigrant male joined the group, the putative adult daughter was almost five years old and, later in the study, at the age of 5.5 years she gave birth to an infant. Two days before the males left the group, the resident female was first seen carrying a new infant. Based on a study of captive white-faced sakis [Savage et al., 1995], we assume a gestation period of approximately 146 days. Thus, it is likely that the resident female was pregnant before the arrival of the immigrant male. However, the potential remains that she conceived on the earliest possible date that the immigrant male was with the group (fig. 1).

It seems unlikely that the immigrant male was the resident male's son or another close relative. Throughout the resident male's tenure with the resident female, the resident female never gave birth to a male infant. Additionally, from the physical examination conducted when we captured the immigrant male, we estimated that he was a relatively young adult based on the wear and staining of his teeth. If he were the resident male's son, it would have been most likely from an extra-group mating, but to this date, we have never seen extra-group mating in this population. We cannot yet rule out the possibility of the resident and immigrant males being brothers; however, the subsequent establishment of the immigrant male in yet another social group makes it unlikely that kinship facilitated his immigration.

All of the animals in the group, except the putative juvenile daughter, were captured and fitted with radio-collars and identification tags. The resident male, resident female and putative adult daughter were captured prior to the immigrant male's arrival. The capture procedures followed those used for owl monkeys [Fernandez-Duque and Rotundo, 2003] and titi monkeys [Di Fiore and Schwindt, 2004].

Data Collection

Between June 2009 and December 2011, we conducted 794 continuous 20-min focal samples of individual animals during 817 h of observation. We obtained similar numbers of focal samples per individual per month. Because sakis are cryptic and often out of view, the animals were sampled opportunistically based on visibility (i.e. they had to be in view at the beginning of the focal sample). Focal samples of the same individual were always separated by at least 20 min. During focal sampling, we conducted instantaneous point sampling every 2 min, recording the focal animal's nearest neighbor (NN, or neighbors, if multiple animals were equidistant from the focal individual). NN data were recorded as 'unknown' whenever the focal animal was out of view. We collected a total of 1,643 instantaneous point samples, in which the NN was identified and was a single animal of interest. We also recorded all observed occurrences of the following behaviors: approaches (an animal moves from outside 0.5 m to within 0.5 m of another individual and stays within that distance for at least 3 s), leaves (an animal moves from within 0.5 m of another individual to outside of that distance), grooming, vocalizing, scent-marking, copulating, fights, chases, displays and intergroup encounters. These data were collected using a dictaphone (Olympus WS-311M) and were then transcribed and entered into a Microsoft Access database.

Daily travel maps were generated using a datalogging GPS unit (Garmin GPSMAP 60CSx) and then plotted in the statistical programming software, R v2.15.2 [R Core Development Team, 2012]. These data were used to identify the location and borders of the group's territory as well as movements outside of it.

Data Analysis

We used NN, approach and grooming data to examine the spatial relationships and social dynamics between the adult individuals before, during and after the immigration. We did not include the putative juvenile daughter in the analysis because we were primarily interested in how the two males partitioned their time between the two females of reproductive age.

We used longitudinal data to establish baseline rates of behavior prior to the immigration. Data from June 2009–July 2011 served as these baseline data. We used time-course graphs fitted with nonparametric smooth functions to display trends in behavioral interactions across the study period.

NN and Approach Interactions

NN and approach data for each individual were analyzed using log-odds ratios to infer an animal's affiliation with one potential partner relative to another. The log-odds ratio that the NN of a focal individual is animal A, relative to animal B, is calculated as:

$$LOR_{A/B} = \log \left(\frac{\text{number of instantaneous point samples animal A is NN} + 0.5}{\text{number of instantaneous point samples animal B is NN} + 0.5} \right).$$

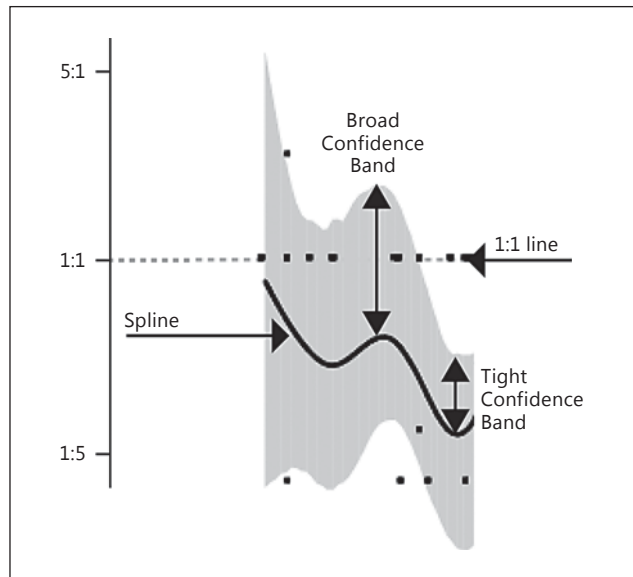


Fig. 2. Components of the time-course graphs. Observations falling on the 1:1 line represent focal samples in which the focal animal had an equal tendency to interact with one animal relative to another. The spline is a smooth curve revealing time-dependent changes in behavioral interactions. The confidence bands (i.e. shaded regions) characterize uncertainty in these time trends. A log-odds ratio distinct from the 1:1 line, surrounded by a tight confidence band, supports an inference of differential affiliation. Thus, important time trends in affiliation can be discerned by noting where the confidence bands include (i.e. a broad confidence band) or exclude the 1:1 line.

The addition of 0.5 in both the numerator and denominator is a standard boundary correction to avoid ratios involving the number zero; this correction introduces no bias toward either of the two possible neighbors [Agresti, 1990]. Log-odds ratios for approach interactions were defined analogously, using the numbers of approaches occurring in a focal sample. For both NN and approach data, we first calculated a log-odds ratio for each focal sample, which treats the focal sample as the basic unit of observation. For the NN data, the log-odds ratios were based on the number of instantaneous point samples in a focal sample that a given animal, and only that animal, was the NN. For a focal sample to be included in the NN analysis, there had to be at least one positive identification of a known NN. Similarly, at least one approach had to have occurred during a focal sample for it to be included in the approach analysis.

For the resident and immigrant males, we always calculated log-odds ratios relative to the resident female (i.e. the resident female was always the animal in the denominator). For the resident female and the putative adult daughter, the ratios were always calculated relative to the resident male (i.e. the resident male was always the animal in the denominator). Positive and negative trends in log-odds ratios describe changes in affiliative tendencies over time. These are displayed schematically in figure 2, with each data point corresponding to one log-odds ratio. Log-odds ratios from focal samples close together in time may be correlated, as time series observations typically are. In order to accommodate this correlation, and because these log-odds ratios may be highly variable (noisy), we fit cubic splines to the time-course graphs (fig. 2). We use the splines to dampen noise and reveal changes in affiliative behaviors over time, captured by trends in the log-odds ratios. Periods when the spline falls on the 1:1 line (i.e. log-odds ratio = 0) indicate

an equal tendency for the focal animal to interact with either of the two potential partners being compared. Areas where the spline rises above the 1:1 line indicate that the focal animal's interactions are biased toward the animal in the numerator while those below the 1:1 line indicate that these interactions are biased toward the animal in the denominator. For each graph, the y-axis is labeled, so that, for example, 5:1 marks the level at which the focal animal is five times as likely to interact with one animal relative to the other.

We quantified the uncertainty in time-course trends by obtaining 95% confidence bands (represented by the shading around the spline) using 1,000 basic nonparametric bootstraps. The bootstraps resample log-odds ratios with replacement, within each month of observation (i.e. a stratified bootstrap with months as strata). This approach respects the approximate balance of focal sample numbers obtained for each individual during each month of observation. We detected periods during which an animal showed a statistically supported bias toward one partner relative to another by noting where confidence bands exclude the 1:1 line. The text 'Tight Confidence Band' in figure 2 marks a period in which the focal animal displayed more affiliation toward the partner in the denominator of the log-odds ratio; the exclusion of the 1:1 line from the confidence band here indicates high certainty about this bias toward a particular partner. In contrast, the 'Broad Confidence Band' marks a period in which the 1:1 line is included, indicating low certainty about the bias. We use the terms 'tight' and 'broad' loosely, in order to describe two distinct signal-to-noise conditions relevant to our narrative. Tight confidence bands surrounding the 1:1 line would suggest that the focal animal had no bias in affiliation toward either partner and that the relationship was statistically supported.

Our threshold for claiming a trend in the bias for one partner relative to the other was determined by a consistent pattern over periods of several weeks (each month generally includes several weeks of observations). We believe the trends, although not statistically supported in all cases, reveal a bias in affiliation when similar trends (some of which are statistically supported) are seen across multiple behaviors and when similar trends are seen in the focal samples of their preferred partner.

Grooming

We collected time-stamped grooming bouts from June 2010 until December 2012. We defined a grooming bout as a continuous period of one animal grooming another. The bout ended if the focal animal changed from active groomer to receiver, or if the grooming was suspended for 30 s. If the focal animal was already involved in a grooming bout at the beginning of the focal sample or if it continued grooming beyond the end of the focal sample, we recorded the bout as 'censored' to prevent artificially shortening the long bouts. We used survival analysis methods [Cox and Oakes, 1984] to estimate how long censored bouts would have been if observed to completion, and used these estimates in the graphs when necessary (i.e. we performed conditional mean imputation). An exponential distribution was a good fit for bout lengths [based on the test described in section 3.7: Cox and Oakes, 1984], and this provided the conditional means. For grooming data, we produced a log-odds ratio for each focal sample similar to that used for NN and approach interactions, as follows:

$$LOR_{A/B} = \log \left(\frac{\text{total time in minutes grooming (as actor) animal A} + 1/60}{\text{total time in minutes grooming (as actor) animal B} + 1/60} \right).$$

One second (1/60) was added to both the numerator and denominator as a boundary correction. The same procedure was used for grooming bouts when the focal animal was the recipient of grooming. For a focal sample to be included in the grooming analysis, at least one grooming bout had to have occurred in the sample. The figures depict the grooming ratios on a log scale, similar to the log-odds of count observations for the NN and approach interactions. Because the grooming data are sparse, the same stratified bootstrap procedure that we used to obtain confidence bands for NN and approach graphs was not feasible. Instead, the confidence bands for the grooming graphs were obtained by a rough approximation, which tends to produce wider bands (<http://www.uni-muenster.de/ZIV.BennoSueselbeck/s-html/helpfiles/smooth.spline.html>). All statistical analyses were conducted in R [R Core Development Team, 2012].

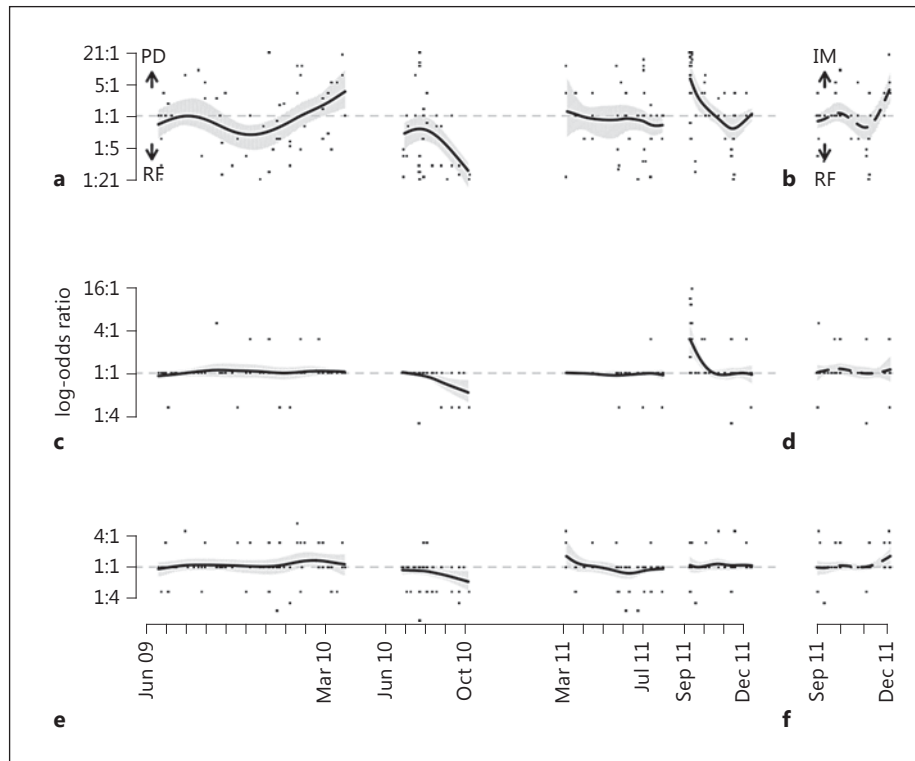


Fig. 3. Time-course graphs with the log-odds ratios for the resident male's NN (**a, b**), approach interactions (**c, d**) and approach received interactions (**e, f**). For each behavior, the log-odds ratios with a solid spline (**a, c, e**) compare the putative adult daughter (PD) to the resident female (RF); observations above the 1:1 line indicate a greater tendency for the resident male to interact with the PD, while those below indicate a greater tendency for him to interact with the RF. The log-odds ratios with a dashed spline (**b, d, f**) compare his associations with the immigrant male (IM) versus the RF.

Research was in full agreement with Ecuadorian legislation and was approved by the IA-CUC at the University of California, Davis (protocol No. 16117). All capture and collaring protocols were approved by the University Animal Welfare Committee at New York University (protocol No. 04-1217).

Results

Signs of Integration

When we first detected the immigrant male (fig. 1), he was ranging relatively close (<25 m) to the group and he foraged and slept with them. In addition, on the first day that we observed him with the group, he performed a territorial display with the resident male. The group encountered at least one unfamiliar male saki and an-

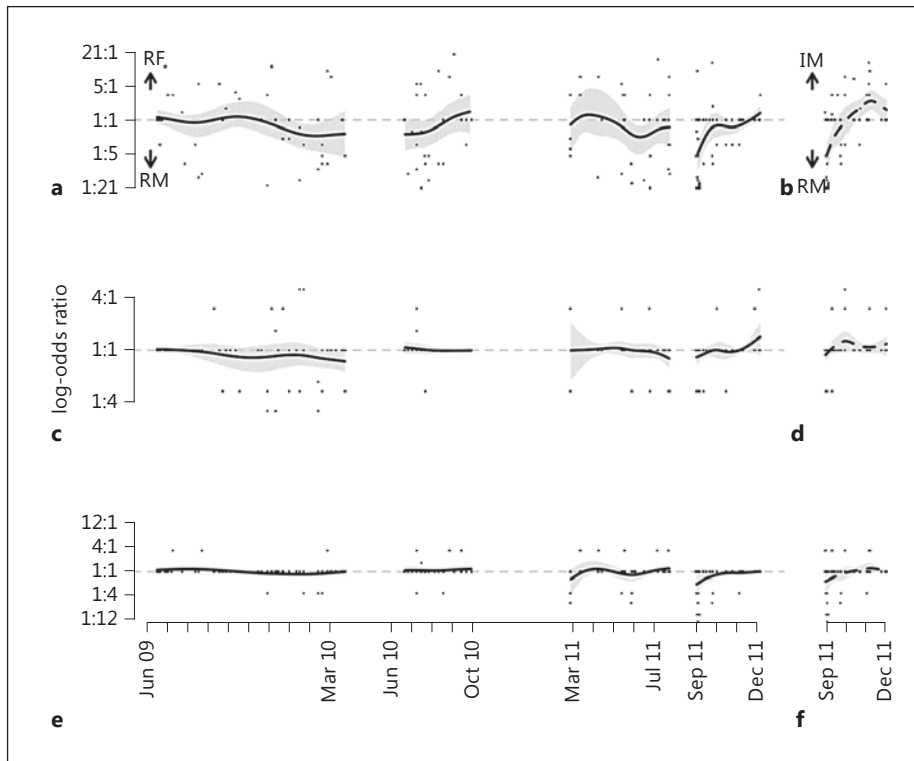


Fig. 4. Time-course graphs with the log-odds ratios for the putative adult daughter's NN (**a, b**), approach interactions (**c, d**) and approach received interactions (**e, f**). For each behavior, the log-odds ratios with a solid spline (**a, c, e**) compare the resident female (RF) to the resident male (RM); observations above the 1:1 line indicate a greater tendency for the putative adult daughter to interact with the RF, while those below indicate a greater tendency for her to interact with the RM. The log-odds ratios with a dashed spline (**b, d, f**) compare her associations with the immigrant male (IM) versus the RM.

other individual of undetermined sex. As these animals approached, the resident and immigrant males sat 3 m apart in the same tree and both vocalized while orienting toward them. After the other animals moved away, the resident and immigrant males continued vocalizing for 45 min.

Social Dynamics between Animals

September 2011

During the first two weeks that we observed the immigrant male with the group, the resident male displayed more mate-guarding behaviors toward his putative adult daughter than toward the resident female. His putative adult daughter was his NN more often than the resident female (fig. 3a), whereas the resident female and immigrant male were equally his NN (fig. 3b). The resident male also approached his putative adult daughter more than he did the resident female (fig. 3c) whereas he ap-

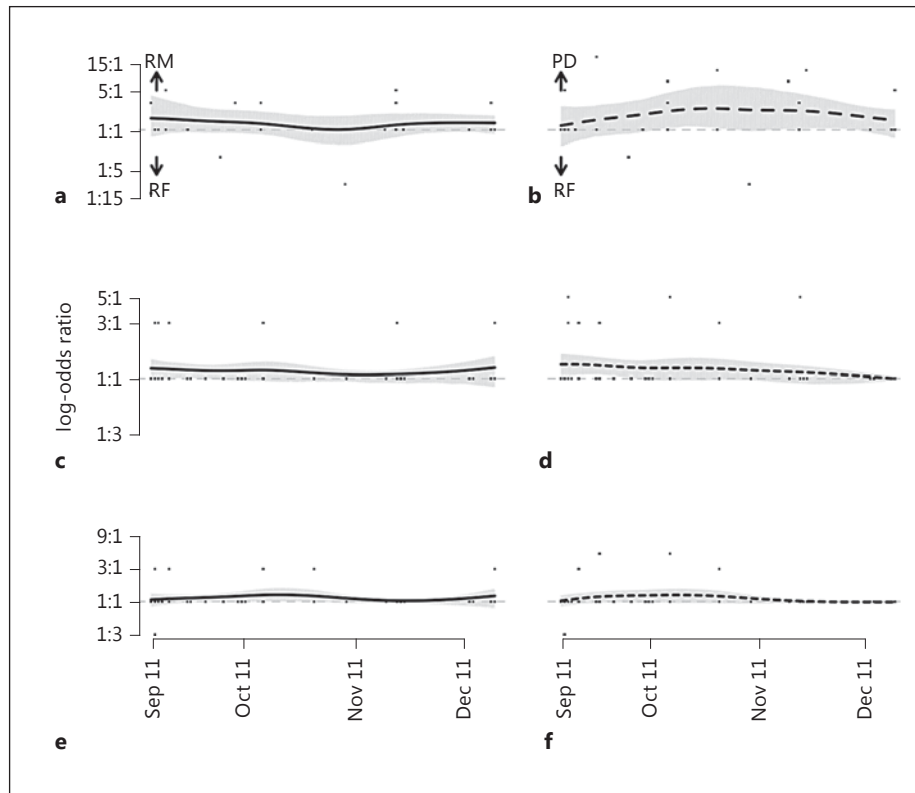


Fig. 5. Time-course graphs with the log-odds ratios for the immigrant male's NN (**a, b**), approach interactions (**c, d**) and approach received interactions (**e, f**). For each behavior, the log-odds ratios with a solid spline (**a, c, e**) compare the resident male (RM) to the resident female (RF); observations above the 1:1 line indicate a greater tendency for the immigrant male to interact with the RM, while those below indicate a greater tendency for him to interact with the RF. The log-odds ratios with a dashed spline (**b, d, f**) compare his associations with the putative adult daughter (PD) versus the RF.

proached the resident female and immigrant male equally (fig. 3d). All three animals approached him equally (fig. 3e, f).

Similarly, the putative adult daughter had the resident male as her NN more often than she did either the resident female or the immigrant male (fig. 4a, b). She approached the resident male slightly more often than the resident female, but she approached both males equally (fig. 4c, d). She was, however, approached by the resident male more often than by either the resident female or the immigrant male (fig. 4e, f).

In addition to maintaining close proximity with his putative adult daughter, the resident male also tried to keep the immigrant male away from her. Every time the immigrant male approached the putative adult daughter ($n = 20$), the resident male growled and, on 15 occasions, this growling escalated to short bouts of chasing and aggressive interactions (e.g. grappling or biting). In contrast, the resident male inter-

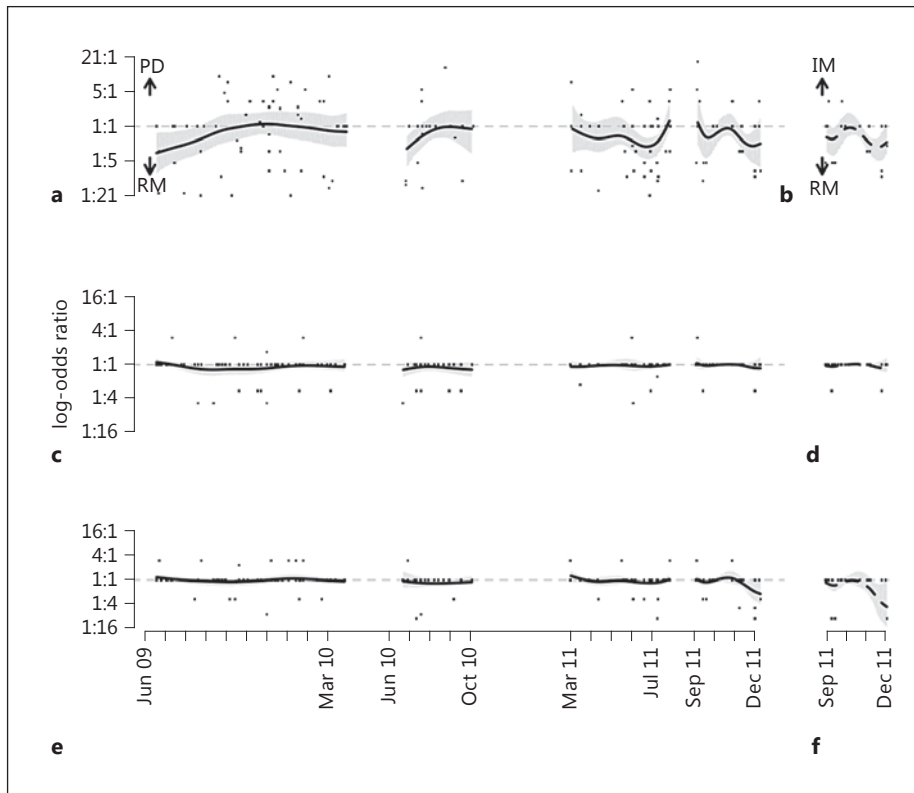


Fig. 6. Time-course graphs with the log-odds ratios for the resident female's NN (**a, b**), approach interactions (**c, d**) and approach received interactions (**e, f**). For each behavior, the log-odds ratios with a solid spline (**a, c, e**) compare the putative adult daughter to the resident male (RM); observations above the 1:1 line indicate a greater tendency for the resident female to interact with the PD, while those below indicate a greater tendency for her to interact with the RM. The log-odds ratios with a dashed spline (**b, d, f**) compare her associations with the immigrant male (IM) versus the RM.

rupted only one of 10 interactions between the immigrant male and the resident female. In this one interaction, he immediately moved between the immigrant male and the resident female when the immigrant male inspected the resident female's urine and anogenital region; the resident male then inspected her anogenital region himself. The resident female and immigrant male left the tree together, but were not followed by the resident male.

Despite the resident male's guarding of his putative adult daughter, the immigrant male consistently approached them. Both the resident male and the putative adult daughter were his NN more often than the resident female (fig. 5a, b), and the immigrant male approached both of them more often than he approached the resident female (fig. 5c, d). He was also approached by them slightly more often than by the resident female (fig. 5e, f).

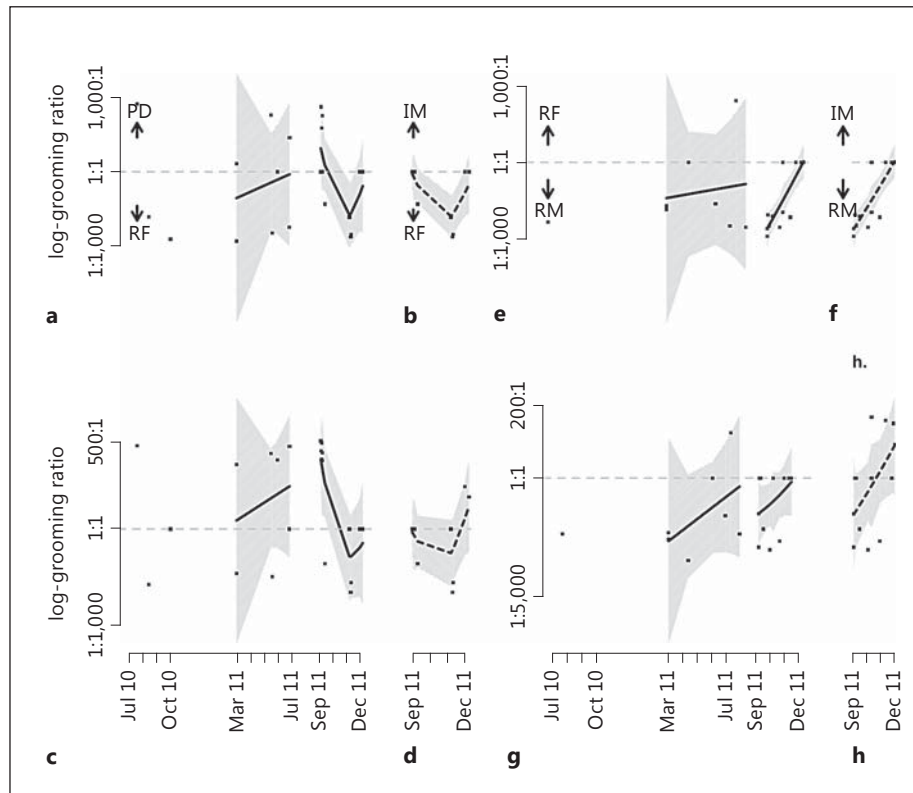


Fig. 7. Time-course graphs with the log-grooming ratios for the resident male's grooming interactions (**a, b**) and grooming received interactions (**c, d**) and for the putative adult daughter's grooming interactions (**e, f**) and grooming received interactions (**g, h**). For the resident male, the log-grooming ratios with a solid spline (**a, c**) compare the putative adult daughter (PD) to the resident female (RF); observations above the 1:1 line indicate a greater tendency for the resident male to groom with the PD, while those below indicate a greater tendency for him to groom with the RF. The log-grooming ratios with a dashed spline (**b, d**) compare the resident male's interactions with the immigrant male (IM) versus the RF. For the putative adult daughter, the log-grooming ratios with a solid spline (**e, g**) compare the RF to the RM; observations above the 1:1 line indicate a greater tendency for the putative adult daughter to groom with the RF, while those below indicate a greater tendency for her to groom with the RM. The log-grooming ratios with a dashed spline (**f, h**) compare her interactions with the IM versus the RM.

The resident female did not clearly interact with one animal more than another (fig. 6a–f). Although the resident male was her NN more often than the immigrant male (fig. 6b), she approached all three animals equally (fig. 6c, d).

Grooming relationships also revealed a close affiliation between the resident male and his putative adult daughter. The resident male spent more time grooming with his putative adult daughter than he did with either the resident female or the immigrant male (there had not yet been any grooming interactions with the immigrant male; fig. 7a–d). Similarly, the putative adult daughter spent more time grooming

with the resident male than with either the resident female or the immigrant male (fig. 7e–h). Furthermore, on five out of nine evenings, the resident male and his putative adult daughter engaged in long grooming bouts in their sleeping tree while the resident female and immigrant male were out of view.

We were not able to analyze the grooming bouts in the immigrant male's or the resident female's focal samples because there were too few observations. However, we did observe three cases of the immigrant male grooming and being groomed by the putative adult daughter, but no bouts of the immigrant male grooming or being groomed by the resident female.

October to November 2011

By October, new patterns of behavioral interactions began to emerge. Despite occasional bouts of the resident male chasing the immigrant male ($n = 7$), they began grooming each other and spending extended periods of time resting near each other. The resident male became less attentive toward his putative adult daughter and began spending more time with the resident female. By November, the resident female was the resident male's NN more often than either his putative adult daughter or the immigrant male (fig. 3a, b), and the resident male spent more time grooming with the resident female than he did with either the putative adult daughter or immigrant male (fig. 7a–d).

During this time period, the putative adult daughter began interacting more with the immigrant male. The immigrant male was her NN more often than was the resident male (fig. 4b) and, although she approached and was approached by both males almost equally (fig. 4d, f), the immigrant male groomed her more often than did the resident male (fig. 7h). She also played with the immigrant male, shared sleeping trees with him and, by mid-November, copulated with him at least three times.

December 2011

On 3 December 2011, 18 days after the group was last followed, the resident female was observed carrying a new infant, the putative adult daughter was seen with a split lip, and an unfamiliar female was noticed with the group as the animals settled into their sleeping area. The resident and immigrant males settled in an area approximately 50 m from the resident female, her daughters and her neonate, but we were unsure where the unfamiliar female settled. The next morning, the animals moved constantly and quickly, making detailed observations impossible. The following morning, the resident and immigrant males left the group together, along with at least one unfamiliar female, leaving the resident females and neonate behind. For the next four days, the two males traveled together with at least one unfamiliar female. They ranged within the group's territory (yet separate from the resident females), but also traveled approximately 500 m north, beyond its boundaries (fig. 8). During this time, we caught glimpses of the two males grooming each other and feeding in the same trees. They also became separated at times, and occasionally made a low-frequency, raspy growl that we had not heard before.

After four days, the two males returned together to the group's territory and re-joined the resident females and neonate. They all remained together for the next three days. On the afternoon of the third day, we captured and radio-collared the immigrant male and released him that evening with the group. The next morning, the

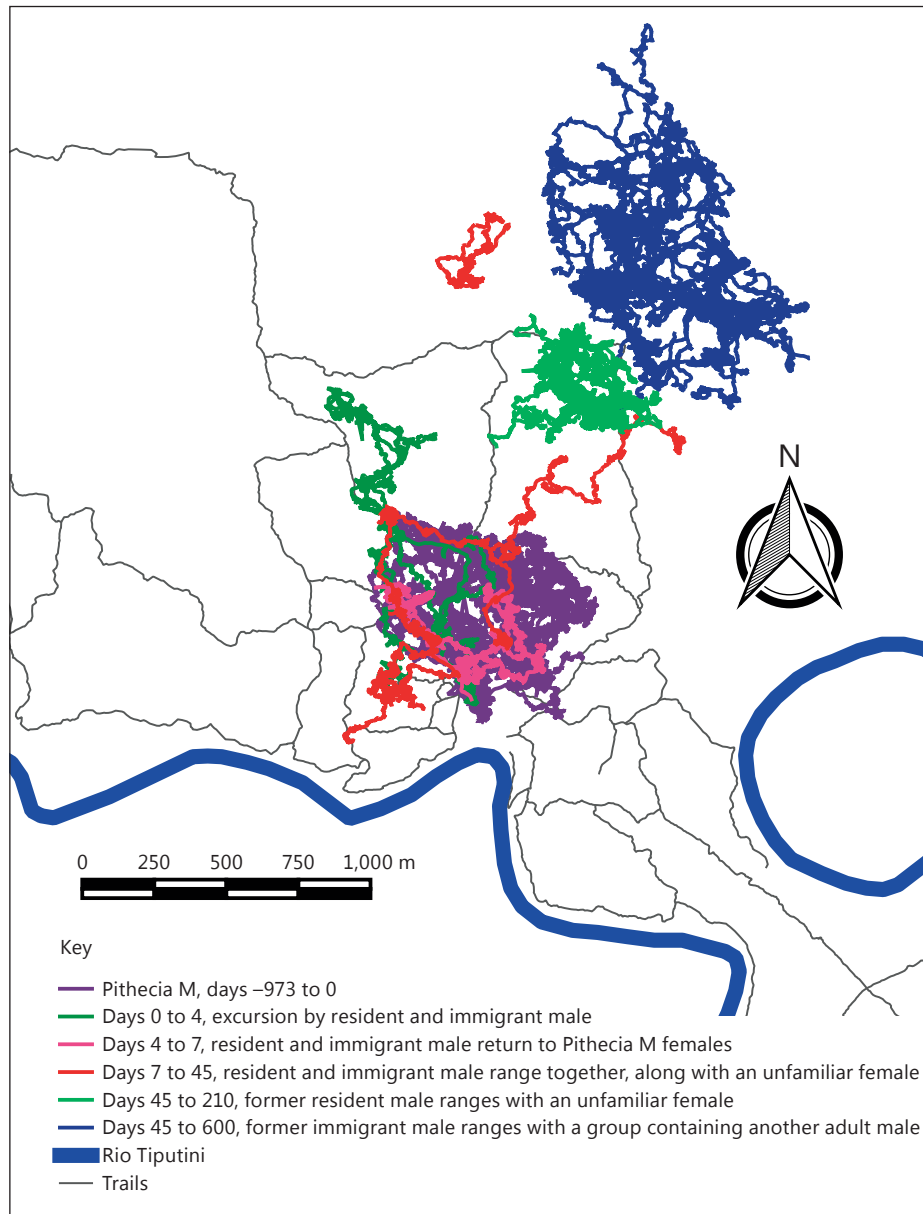


Fig. 8. Map of the Tiputini trail system indicating the saki home territory and the animals' movements outside of that territory. Purple lines represent the home territory based on 973 days of ranging data *before* the arrival of the immigrant male. Day 0 represents the last day the two males were with the group before they left together for the first time.

resident and immigrant males left the group together again (fig. 8). After four days, they once again returned to the territory, but by this time there was an unfamiliar male associating with the resident females. The resident male began making vocalizations that, on other occasions, were given during intergroup interactions. He vocalized while orienting toward the resident females and the unfamiliar male, who were approximately 25 m away (but mostly out of view of the observers). The immigrant male sat in the same tree with the resident male, but it was unclear if he also vocalized. At least one animal that was not the immigrant male responded vocally to the calls of the resident male. After approximately 20 min of calling, we lost contact with the animals in heavy rain. We recontacted the original resident and immigrant males 1 h later in the same area, but we did not see the resident females or the new, unfamiliar male again that day. We then followed the resident and immigrant males, and, 3 h later, they left the group's territory.

Over the next 40 days, the resident and immigrant males continued to travel together, along with at least one unfamiliar female. They ranged to the north/northeast of the group's territory, and traveled up to 1,100 m from the edge of that territory (fig. 8). We were not able to document the two males separating, but after approximately 40 days the resident male settled in a new territory with a single adult female and remained there until his death in July 2012. This territory was approximately 400 m from its edge to the nearest edge of his former territory (fig. 8). The immigrant male moved into a territory adjacent to where the resident male settled and joined another group containing one adult male, one adult female and two young females. This territory was approximately 700 m from its edge to the nearest edge of the main study group's territory (fig. 8). The immigrant male associated with these animals for approximately 20 months before leaving the group, again, on his own. The resident female and her daughters remained in their territory with a new male that became established in the group within one month of the resident and immigrant males' final departure [Porter et al., unpubl. data].

Discussion

In our study, we documented equatorial sakis temporarily forming groups with multiple adults, as well as a resident male abandoning a well-established territory, his pair-mate of seven years and a newborn infant, in order to travel with a putatively unrelated male and an unfamiliar female to other areas of the forest. These observations, coupled with reports of white-faced sakis, suggest that saki social groups can be quite variable in composition and that sakis may employ multiple mating strategies.

Potential Functions of Saki Groups with Multiple Males

Neither of our hypotheses was fully supported by the observations we made during and after the immigration of a new male. The first hypothesis, i.e. that mate-guarding is an important male mating strategy, was tested by examining whether the resident male maintained proximity (<1 m) or contact with the resident female following the entrance of a new immigrant, and whether he aggressively prevented proximity or contact between the resident female and the immigrant male. We found that the resident male did not guard the resident female and rarely aggressively discour-

aged the immigrant male from approaching her, which would suggest that mate-guarding is not an important component of male mating strategies. However, the resident female was pregnant at the time that the immigrant male joined the group, which might have reduced the need for mate-guarding. Although it is not possible to determine if the males were aware that the resident female was pregnant, there is evidence that male white-faced sakis can distinguish olfactorily between noncycling and cycling/ovulating females [Thompson et al., 2011]. This may help explain why the immigrant male did not actively pursue the resident female.

Curiously, the resident male did guard his putative adult daughter during the first two weeks following our first observations of the immigrant male in the group. We cannot yet explain this behavior. Guarding is expected more from males who are unrelated to females than from male relatives. Although we cannot yet confirm genetically that the resident male is her father, his long tenure in the group suggests a father-daughter relationship. In addition, we never observed the resident male copulating or attempting to copulate with this female. Eventually, the resident male's guarding behavior subsided and the immigrant male copulated several times with the resident male's putative adult daughter without interference. Future studies focusing on mate-guarding behavior may shed more light on the conditions under which mate-guarding behavior occurs in sakis.

We also evaluated the hypothesis that the immigrant male provided a service (e.g. mate and/or territorial defense) to the resident male by examining whether the resident was tolerant of the immigrant and whether the immigrant actively participated in territorial displays. There appears to be more support for this hypothesis. Although the resident male was initially aggressive toward the immigrant, eventually the two males formed an affiliative relationship, and they subsequently left the group and traveled together outside the group's home territory; this suggests a high degree of tolerance. In addition, though our observation of the males jointly performing a territorial display is anecdotal, it offers some support for the idea that secondary males may provide assistance to resident animals. As female equatorial sakis do not appear to engage in active territorial defense [Porter et al., pers. obs.], allowing additional males into the group may be particularly valuable for a resident male, especially if there are numerous floaters in the environment. We saw at least one unfamiliar female around our study group when the males first left and observed an unfamiliar male associating with the resident females within four days of the males' second departure from the group's territory. Furthermore, several unknown males were seen in proximity to this study group following the death of the original resident male in 2004 and the immigration of the resident male in this study [Di Fiore et al., 2007].

On the other hand, if extra males are indeed beneficial for more effectively defending resources, females or infants against outside individuals [Thompson, 2015], it is unclear why the males would have jointly abandoned a well-established territory, two reproductive-age females and a newborn infant, without being challenged. Although the males ranged partially outside of the group's territory, they also ranged within it and they returned to this territory and to the resident females twice. However, neither male attempted to reclaim the territory from the new male when they returned the second time. Instead, the resident male settled on a new territory with a different female and the immigrant male joined a different group, again as a secondary male.

Compared to the relationship among titi monkey pair-mates, equatorial saki pair-mates appear to be much less affiliative (i.e. they groom one another less often, do not cooperate in conspicuous territorial displays such as vocal duets and frequently sleep in separate trees [Fernandez-Duque et al., 2013; Spence-Aizenberg et al., 2015]). Such social dynamics, coupled with the absence of direct paternal care, may allow sakis to be more variable in their mating strategies than titi monkeys and other socially monogamous primates.

Although sakis have been reported to occasionally occur in groups with multiple adults [summary: Norconk and Setz, 2013], it is only in the last 10 years that multiyear behavioral studies have begun to describe the social relationships among the animals living in these groups [Thompson and Norconk, 2011, 2013; Thompson, 2013]. These accounts have referred exclusively to white-faced sakis, however. By documenting the process of group formation, unusual expressions of mate-guarding and male-male social behavior in equatorial sakis, this study adds to our knowledge of saki social dynamics and confirms that this taxon can be quite variable in its grouping patterns. Their flexibility makes them an ideal model taxon for investigating the environmental and social influences on mating and parenting strategies and, ultimately, on the evolution of variable grouping patterns.

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