RESEARCH ARTICLE

Within-Group Social Bonds in White-Faced Saki Monkeys (*Pithecia pithecia*) Display Male–Female Pair Preference

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White-faced saki monkeys (*Pithecia pithecia*) lack most of the behavioral and physical traits typical of primate monogamy [Fuentes, 1999]. In order to determine if social bonds in this species reflect patterns displayed by pair-bonded groups or larger multimale–multifemale groups, we draw on 17 months of data collected on wild white-faced sakis at Brownsberg Nature Park, Suriname. We analyzed within-group social bonds for three habituated groups (one two-adult and two multiadult groups) by measuring grooming, proximity, and approach/leave patterns between adult and subadult group members. We found that both two-adult and multiadult groups showed significantly stronger social bonds between a single male–female dyad within each group (deemed ''primary dyads''). In all three groups, primary dyads were composed of the oldest adult male and a breeding female. These pairs had significantly higher levels of grooming than other within-group dyads and were also in close proximity (<1 m) more often than nonprimary dyads. Grooming in primary dyads was nonreciprocal, and consistently biased toward female investment. Grooming patterns in nonprimary dyads varied, but were often more reciprocal. Grooming and proximity of the primary dyad also changed in relation to infant development. Our results suggest that while white-faced sakis do not show behavioral and physical traits typical of monogamy or pair-bonding, social bonds are strongest between a single male–female pair. Pitheciine social systems range from small group monogamy in *Callicebus* to large multimale–multifemale groups in *Chiropotes* and *Cacajao*. As the middle taxon in this platyrrhine radiation, behavioral strategies of white-faced sakis provide a model for how social bonds and affiliation could be influenced by and affect the evolution of larger group size in primates. Am. J. Primatol. 73:1051–1061, 2011. © 2011 Wiley-Liss, Inc.

INTRODUCTION

Cohesive social groups are a pervasive feature of most primate species, particularly anthropoids. The evolution of these groups is often viewed in the context of socioecological models in which same-sex interactions among females shape the social structure [definition following Kappeler & van Schaik, 2002] of large multimale–multifemale groups [e.g., Isbell, 2004; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980]. These models were developed largely in the context of cercopithecoids, such as baboons, which may have more than 20 adult females per group [Swedell, 2011], but sex-specific social bonds have also been observed in platyrrhines that form relatively large groups [e.g., *Ateles*: Fedigan & Baxter, 1984; Slater et al., 2009; *Brachyteles*: Strier, 1994; *Cebus*: Fragaszy et al., 2004].

Socioecological models propose that resource distribution dictates a group's competitive regime, which in turn influences female–female relationships. However, these models are not easily applied to smaller groups, which may have only one or two female(s). Theories addressing monogamy may be more helpful in these cases, as they explain the evolution of male–female bonds in the context of male parental care [Wittenberger & Tilson, 1980], infanticide prevention [van Schaik & Dunbar, 1990], mate guarding [Palombit, 1999], or female dispersion [van Schaik & van Hooff, 1983; Wrangham, 1980]. However, models of monogamy also may fail to fully predict social relationships in small groups, because many deal with gaining exclusive mating access to females (e.g., mate guarding or females as a widely dispersed resource), which often does not apply in

small multimale–multifemale groups. Developing models that can explain the environmental and social factors leading to intraspecific variation in social organization and mating systems is critical to understanding how the size and composition of primate groups affects socioecology.

White-faced saki monkey social organization ranges from groups composed of one adult male and one adult female (two-adult groups) to small multimale–multifemale groups. Group size averages 3.2 individuals (range = 2–12; for studies reporting SD, SD range = 0.8–2.4; average SD = 1.4), generally with 1–3 adult males and 1–3 adult females [reviewed in Norconk, 2011]. Multiple surveys by Lehman et al. [2001] found that 74% of bisexual groups in Guyana had multiple adult males and/or females in the group, whereas only 26% of groups consisted of a single adult male–female pair.

Multiyear observations at Brownsberg Nature Park, Suriname, suggest that newly formed groups of white-faced sakis start out as a single male–female reproductive unit that gradually accumulates off-spring over time. As offspring mature, they have been observed to mate within the group, disperse, or inherit the home range of their parents [Norconk, 2011; Thompson et al., 2010]. Despite the appreciable number of white-faced saki groups observed in a two-adult social organization (terminology following Fuentes [1999]), the species lacks most traits outlined in Fuentes' [1999] ''monogamy package'': pair-bond reinforcement behaviors, sexual monomorphism, exclusive two-adult grouping/mating patterns, and paternal care [Ford, 1994; Norconk, 2006; Rosenberger et al., 1996; Thompson, 2011].

In addition, little is known concerning how variation in white-faced saki social organization is reflected in the structure of social relationships. Do social bonds in white-faced sakis resemble pair-bonded groups or do they show sex-specific bonds as often seen in larger groups? If male–female relationships do form the group's core social bonds, is this attributable to a bond between one male–female pair or a pattern in which males and females in general are each other's strongest social partners? We assessed these questions by examining grooming and proximity patterns of three free-ranging groups of white-faced sakis at Brownsberg Nature Park, Suriname. If social bonds reflect those in other pair-bonded primates, such as titi monkeys or gibbons, then the frequency of grooming and proximity is expected to be highest between a single male–female pair, rather than between any intersexual dyads or between same-sex dyads. Data on within-group social bonds are compared with these expectations and also analyzed with regard to infant development. Last, we discuss the social behavior of white-faced sakis in the broader evolutionary context of pitheciine social diversity.

METHODS

Study Site and Subjects

Research was conducted at Brownsberg Nature Park, Suriname (5°01′N, 55°34′W) from June 2008 to November 2009 [see De Dijn et al., 2006 for site description]. Permission to conduct research at Brownsberg was granted by STINASU. All research protocols were approved by Kent State University's IACUC committee, complied with Suriname's legal requirements, and adhered to ASP's principles for the ethical treatment of nonhuman primates. White-faced sakis at Brownsberg are arboreal and free ranging. Three groups were habituated between 2003 and 2008 and are the subjects of this study (Table I). When birthdates for individuals were unknown, the age class for males was based on visual inspection of body size and fullness of the male facial mask, a sexually dimorphic trait that is variable in development but fully expressed by 3.5–4 years [Norconk, 2006]. Female age classification was based on hormonal data collected during the study period; females who consistently cycled were classified as adults, subadult individuals began cycling during the course of this study.

Junco group

TABLE I. Groups and Group Composition of White-Faced Sakis at Brownsberg Nature Park, Suriname

Group	Junco		Mazaroni		Peach	
Sex	♀	♂	♀	♂	♀	♂
Adult	JF1[a] (A2005) JF2 (SA2005)	JM1[a] (A2005)	MF1[a] (A2005) MF2[a] (A2008)	MM1[a] (A2008)	PF[a] (A2008)	PM[a] (B2003)
Subadult	JF3 (B2005)	JM2 (SA2005)		MM2[a] (SA2008)		
Juvenile		JJ (B2007)		MM3[b] (J2008)		
Infant		FP (B2009)		MM4 (B2009)		HD (B2008)

[a]Individual was observed copulating during the study period. For the Mazaroni group, all possible pairings of copulating males and females were observed and pairs engaged in roughly equal numbers of copulations (range: 10–16) [Thompson, 2011].
[b]MM3 was an older juvenile at the beginning of the study and a young subadult by the end.
In parentheses: year the individual was either A = initially observed as an adult, SA = observed as a subadult, J = observed as juvenile, B = born. See text for dates of birth/death.

First observed in 2005 when this group consisted of JM1 and JF1 as adults, JF2 (as a subadult), and a female infant (presumably current group member JF3); JF1 was the mother. JM1 was the only adult male present in the group at the time of the infant's birth. This group remained stable from 2005 to the end of this study, gradually accumulating offspring (JM2, born c.a. late 2005 to early 2006). In June 2008, a juvenile male (JJ) was present in the group (last seen nursing June 30, 2008); JF1 was the mother. JF1 also gave birth during the study period to a male (FP) between January 19 and 28, 2009.

Mazaroni group

This group was habituated for this study, with data collection conducted from June 2008 to October 2009. When observations began, MM3 appeared to be an older juvenile, but was likely better classified as a young subadult by the end of the study. MM2 was estimated as an older subadult or young adult male, and was not yet as large as MM1 (MM2 was smaller and had a less developed facial mask than JM2), but did engage in copulations during this study. Of the group's two adult females, MF1 gave birth during the study period (between September 20 and November 29, 2008), but the infant died between 4 and 5 months of age. MF1 was known to be a member of this group for ~3 years before the start of this study.

Peach group

Observed from 2003–2007. Between May and August 2007 five individuals disappeared and in August 2007 only an adult male and a subadult male (PM, an infant in 2003) remained. By the onset of this study (May 2008), the adult male had disappeared, and PM had "inherited" the group/range. A new female (PF) had also immigrated into the group. This pair comprised Peach group for this study; a male infant (HD) was born between September 25 and October 8, 2008.

Data Collection

Each group was followed in rotating 4-day observation blocks (contact hours: Junco = 1,295.5 hr; Mazaroni = 658.4 hr; Peach = 860.1 hr) by one to three observers. Data were collected by focal sampling; focal order was predetermined randomly but could not always be adhered to due to limited visibility. When the focal animal's behavior could not be seen, observers switched to the next randomly predetermined focal animal that was visible. Focal animals were sampled for 1 hr and not resampled until all group members had been sampled that day. Only adults and subadults were used as focal animals; social interactions with juveniles/infants were excluded in order to focus on adult relationships.

Instantaneous scan samples were conducted at 15 min intervals on focal animals, in which the focal's distance to all other visible group members was recorded as: within arm's reach, <1, 1–5, 6–10, 11–15, 16–20, or 20+ m. This yielded 3,924 estimates of interindividual distances (Junco: 2,430; Mazaroni: 777; Peach: 717). Five-minute continuous focal samples were taken every 15 min, in which all occurrences of the following behavioral events were recorded: (1) approaches and leaves (within 1 m) to/from the focal and by the focal and (2) the start and end time of grooming bouts and the individuals involved. Focal samples were dictated into a voice recorder (WS-110, Olympus, Global) and converted to a sound file; grooming bout duration was recorded (in seconds) from the sound file. A total of $N = 313.6$ focal hours were collected (Junco = 132.9 hr; Mazaroni = 58.3 hr; Peach = 122.4 hr) from which 9.2 hr of grooming data were obtained (Junco: 6.27 hr; Mazaroni: 2.28 hr; Peach: 0.61 hr) and 2,728 approach/leave events (Junco: 1,338; Mazaroni: 324; Peach: 1,066). All occurrences of copulations were recorded; dyads that engaged in copulations are termed "sexual dyads" (Table I).

Data were collected by C.L.T. and six field assistants, who entered into the project sequentially. There were never more than three observers involved in the project at once. Observers were trained by estimating distance between two objects in the forest and then comparing to actual distance. Formal tests of interobserver reliability were conducted by comparing all data (subject identification, distance, approaches/leaves, and grooming) collected by a new field assistant to C.L.T. (who collected data throughout) during one full day follow. Interobserver reliability reached 95% for all measurements before formal data collection by field assistants began. All observers followed all three study groups.

Data Analysis

Within-group social bonds

Proximity data are presented by dyad as the percentage of samples in which both members of the dyad were within 1 m and within arm's reach. Grooming data are presented as the percentage of a dyad's total sampling time spent grooming. For each group, the dyad with the highest proximity and grooming levels were termed the "primary dyad." The proximity (percent samples in which dyads were ≤1 m) and overall grooming time (regardless of directionality) of these dyads were compared using an ANCOVA, with identities of each individual in the dyad as covariates in order to control for the nonindependence of dyads. It should be noted that the small number of primary dyads ($N = 3$) make these statistics problematic; however, a comparison of primary vs. nonprimary dyads via t-tests (i.e., not controlling for nonindependence of dyads) for all variables yielded similar statistical outcomes.

Directionality of grooming

The grooming index, a measure of asymmetry in grooming reciprocity within a dyad, was calculated for all dyads [from Silk et al., 2006]:

$$1 - \left| \left(\frac{Gi \to j}{Gi \leftrightarrow j} \right) - \left(\frac{Gj \to i}{Gi \leftrightarrow j} \right) \right| \qquad (1)$$

where G = time spent grooming, and i, j are the individual members of the dyad. The index reflects grooming reciprocity within a dyad, where an index of one reflects completely equal levels of grooming and an index of zero denotes grooming directed solely by one individual toward the other (no reciprocity). The grooming equality index was compared between primary dyads and all other dyads via an ANCOVA with identities of each individual in the dyad as covariates (see note on ANCOVA above).

Changes in the intersexual relationship with infant development

Three females gave birth during the study period. Two infants born to females PF and JF1 survived until the end of the study period (aged 14 and 10 months, respectively); the third infant (born to female MF1) died between 4 and 5 months of age. In order to learn more about the influence of reproduction on intersexual relationships over time, we compared grooming and proximity patterns of the primary dyad before the infant's birth, during locomotor dependency (birth through last date the infant was observed riding on mother), and locomotor independence (after last date seen riding on mother). The duration of infant dependency was 90 days (Junco infant) and 144 days (Peach infant). Independent infants were observed nursing until the end of the study. The proportion of sampling time spent grooming by each member of the primary dyad was compared between periods of infant development (prebirth vs. dependent, dependent vs. independent) via two-sample proportions tests, using a Bonferroni correction to account for multiple comparisons (modified α = 0.0125). For MF1, sample size during the infant's life was too low to analyze separately. A χ^2 was conducted to determine the relationship between proximity of primary dyads and infant dependency. All tests were nondirectional with α set at 0.05, except as noted above.

Hinde's Index was calculated to assess responsibility for proximity maintenance within the primary dyad for the above categories of infant dependency [Hinde & Atkinson, 1970]. H is given as:

$$H = \frac{U_a}{U_a + U_b} - \frac{S_a}{S_a + S_b} \qquad (2)$$

where U_a and U_b are the number of occasions in which the dyad was united by individual a's and b's movements, respectively, and S_a and S_b are the equivalent for separation of the dyad. H ranges from $+1.0$ to -1.0, with each extreme denoting complete responsibility for proximity maintenance by either individual and zero reflecting equal proximity maintenance. For the MF1-MM1 dyad, sample size of approaches/leaves was too low before birth to calculate H separately.

RESULTS

Social Bonds

The primary dyad for each group consisted of the oldest sexually active male and a breeding female (Fig. 1). These dyads (MM1 & MF1; JM1 & JF1; PM & PF) spent significantly more time within 1 m than other dyads (ANCOVA: $F = 7.88$, $P = 0.012$; covariates NS). Similarly, the majority of grooming between adults and subadults for Junco and Mazaroni groups was largely attributable to the primary dyad (Fig. 2). The percent of sampling time primary dyads spent grooming was likewise higher
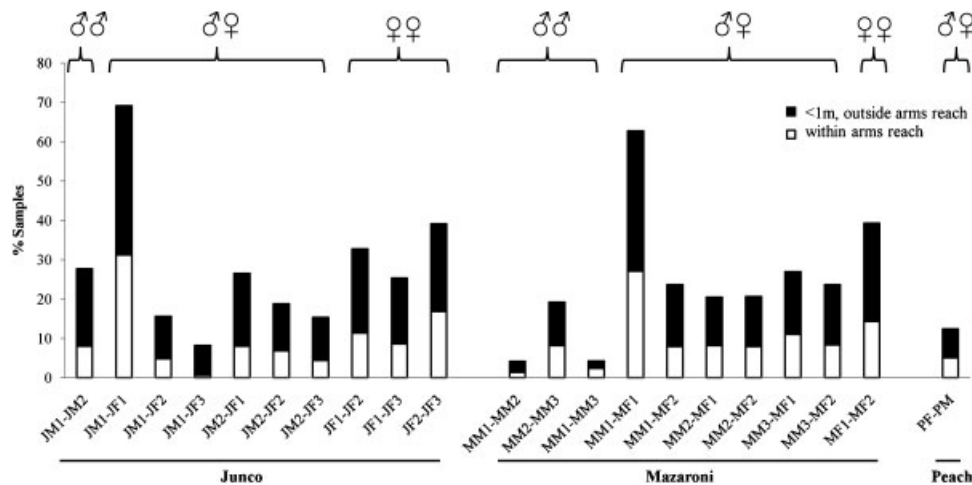

Fig. 1. Proximity within 1 m by dyad. JM1-JF1 and MM1-MF1 are classified as primary dyads; PF-PM is the only adult dyad in Peach group and is deemed a primary dyad by default.
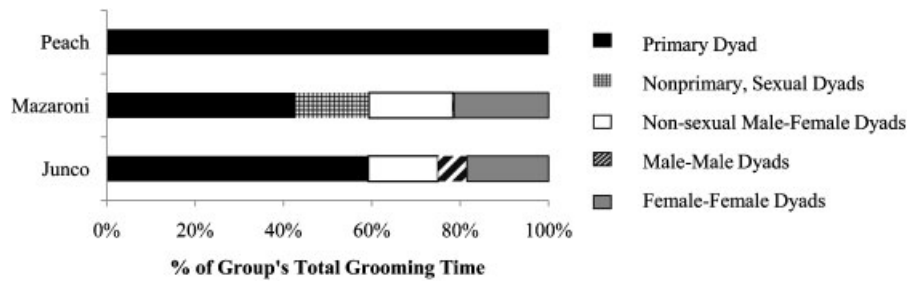
Fig. 2. Percent of each group's grooming time attributable to each type of dyad. Note that Peach has only one adult dyad, and hence 100% of grooming time was performed by this dyad. Categories may contain the cumulative groom time of a variable number of dyads [the primary dyad (black) is always only one dyad; see Fig. 1 for identity of dyads].
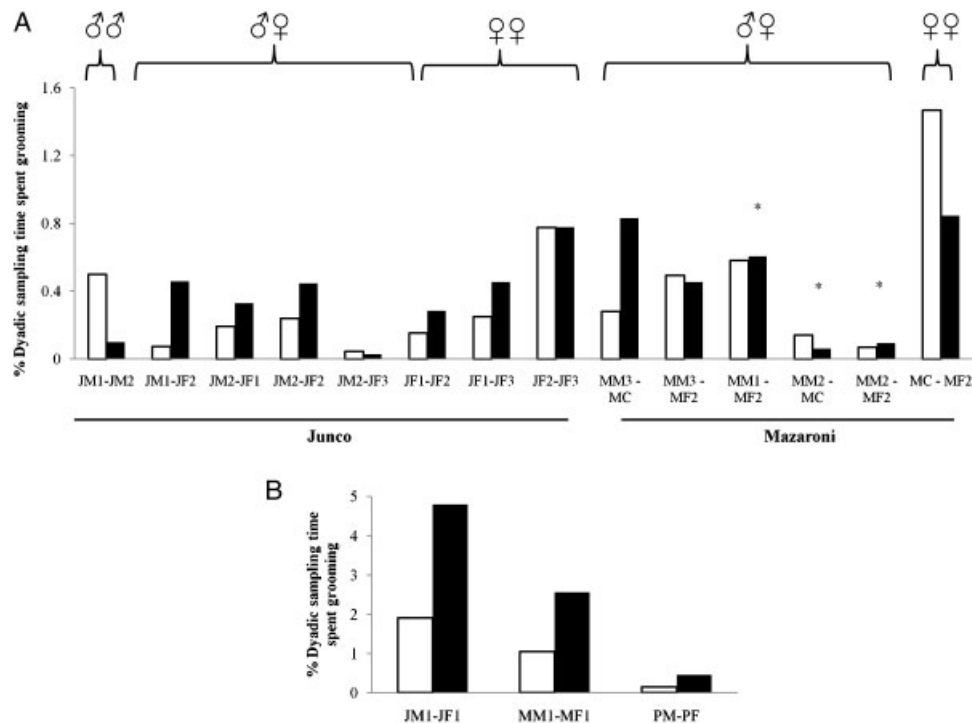

Fig. 3. Grooming reciprocity of (**A**) nonprimary dyads, (**B**) primary dyads. In (A) male–male relationships in Mazaroni group and one Junco male–female (JM1-JF3) dyad are omitted as values were <0.03. *Denotes nonprimary sexual dyads. Note difference in scale.

than recorded for other dyads (Fig. 3A and B; ANCOVA: $F = 26.91$, $P < 0.001$; covariates NS).

Female–female bonds ($N = 4$ dyads) were variable, with the strongest bond between the two adult females in Mazaroni group. For Junco group, the female–female sibling bond (JF2-JF3) showed higher levels of grooming and proximity than the adult/subadult mother–offspring bond (JF1-JF2, JF1-JF3) (Fig. 1), as well as more reciprocal grooming (Fig. 3A).

Male–male bonds ($N = 4$) were also variable, with the two adult males in Junco group exhibiting the highest levels of grooming and proximity (Figs. 1 and 3A). Grooming between Junco males was directed more often by the older (JM1) toward the younger (JM2). All adult male–male bonds in Mazaroni exhibited low levels of proximity, with MM2-MM3 being the highest for the group. Male–

male grooming in Mazaroni group was essentially nonexistent (Fig. 2).

Groups differed in their social habits. Total sampling time spent grooming ranged from 11.79% and 9.55% in Junco and Mazaroni groups respectively, to 0.60% in the Peach group. Controlling for variation in group size (as having more potential grooming partners may increase time spent grooming), the pattern is the same, although less pronounced. Junco dyads spent on average 1.31% of sampling time grooming, Mazaroni 0.96%, and Peach 0.60%. Constraints in activity budget (i.e., time spent resting) did not account for this pattern because between-group differences in activity budget were negligible (51.9% of activity budget spent resting in Peach group vs. 51.8% in Mazaroni and 49.9% in Junco). The Peach group dyad also spent compara-

tively less time in proximity than most dyads in other groups (Fig. 1). One possible explanation for this is the fact that Peach was a recently formed group (see group history), although in many primate species social affiliation, sexual behavior, and bonding can be more intense during the initial stages of group formation [e.g., Savage et al., 1988]. In white-faced sakis, grooming usually occurred during resting periods, with 73% of grooming occurring between 10:00 and 14:30 hr.

Directionality of Grooming

Grooming in primary dyads was biased toward female investment in all groups (Fig. 3B). Grooming relationships in nonprimary, but sexual dyads (MM1-MF2; MM2-MF1; MM2-MF2) were (1) considerably less frequent, (2) not strongly female biased, and (3) more reciprocal (Fig. 3A). The grooming equality index was relatively low for primary dyads (Table II), indicating nonreciprocity of grooming, with females grooming males more than vice versa. However, there was no significant difference between primary and nonprimary dyads in the grooming equality index (ANCOVA: $F = 1.97$, $P = 0.184$; covariates NS).

Changes in the Intersexual Relationship With Infant Development

There was a significant association between primary dyad proximity and stage of infant development in Junco ($\chi^2_{10} = 27.7$, $P = 0.002$) and Peach group ($\chi^2_{10} = 61.9$, $P < 0.001$; Fig. 4). These dyads spent more time than expected within 1 m before birth and while the infant was dependent, but less time than expected in proximity after the infant became independent. However, in Junco group, of the six possible dyads, including the primary individuals, only one (JF1-JF3: the primary female and her known offspring) showed a similar significant relationship between proximity and infant development ($\chi^2_8 = 17.3$, $P = 0.027$). Peach group

had only one adult dyad, and hence no equivalent comparison. Too few samples were available for Mazaroni group before and during the infant's life to calculate meaningful summations.

Hinde's Index for the primary dyad increased while the infant was dependent in both Peach and Junco groups, indicating increased proximity maintenance by the male (Table III). The male decreased proximity maintenance once the infant became independent. Hinde's Index between the primary individuals and other group members could often not be calculated separately across infant development categories due to small sample sizes (which reflects the comparatively lower frequency of social interactions of nonprimary dyads). However, for those dyads ($N = 3$) with sufficient samples, there were no consistent changes in Hinde's Index with regard to the presence of a dependent infant.

For both JF1 and PF, grooming directed toward the primary male was relatively high prebirth and while the infant was dependent, but dropped significantly when the infant became independent (two-sample proportions test: JF1, $z = 4.75$, $P < 0.001$; PF, $z = 3.55$, $P < 0.001$; Fig. 5). For both dyads, female-directed grooming by the male de-
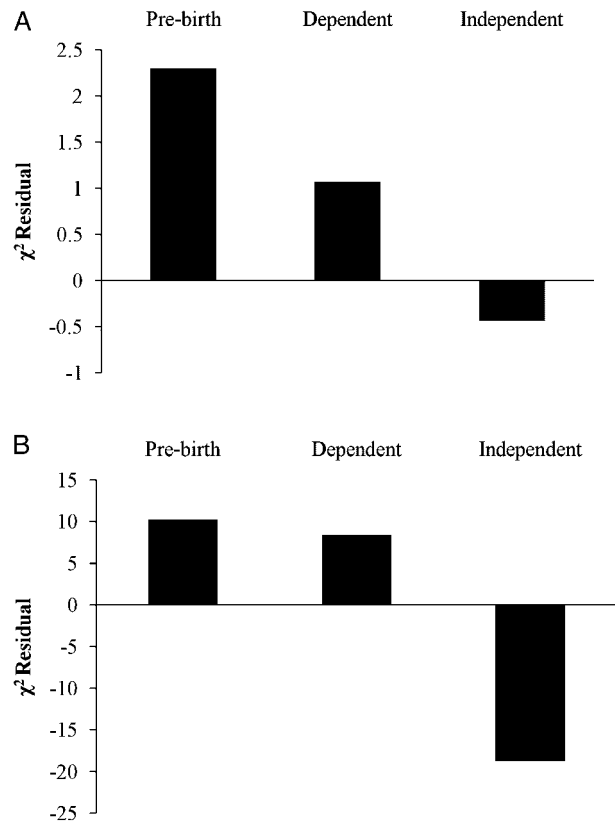

Fig. 4. χ^2 Residuals for primary dyad proximity changes by infant status. (**A**) Junco group primary dyad (JM1-JF1), (**B**) Peach group primary dyad (PM-PF). Sign was added to denote direction of deviation from expected; positive values reflect closer proximity than expected by chance, negative values lower frequencies of proximity than expected by chance.

TABLE II. Grooming Equality Indexes for Junco and Mazaroni Groups

		Junco group					
		JM1	JM2	JF1	JF2	JF3	
	MM1		0.33	0.57*	0.27	–	**JM1**
Mazaroni	**MM2**	–		0.74	0.70	0.78	**JM2**
Group	**MM3**	–	–		0.70	0.68	**JF1**
	MF1	0.58*	0.60	0.48		1.0	**JF2**
	MF2	0.98	0.86	0.96	0.73		
		MM1	**MM2**	**MM3**	**MF1**	**MF2**	

Grooming equality indexes for all primary dyads are reported separately by infant development stage in Table III. Values reported here are for all observed grooming during study period. Indexes close to 1.0 reflect complete reciprocity and values close to 0 reflect strongly nonreciprocal grooming. Primary dyads are indicated by an asterisk (*).

TABLE III. Responsibility for Intersexual Proximity Maintenance Between Sexual Dyads

Dyad	Infant development period	H	Responsible for maintaining proximity	Grooming equality index
JM1-JF1 (Junco group)	Prebirth	−0.18	F	0.75
	Infant dependent	0.40	M	0.17
	Infant independent	0.46	M	0.39
PM-PF (Peach group)	Prebirth	−0.20	F	0.52
	Infant dependent	−0.08	Equal	0.03
	Infant independent	−0.17	F	0.89
MM1-MF1[a] (Mazaroni group)	Total	0.30	M	Prebirth: 0.23
				A.D.: 0.61
MM1-MF2[b] (Mazaroni group)	Total	0.16	M	0.98

H = Hinde's index; equation given in methods. F = Female; M = Male.
[a]Sample size was too low to separate H and proximity data before and after infant birth.
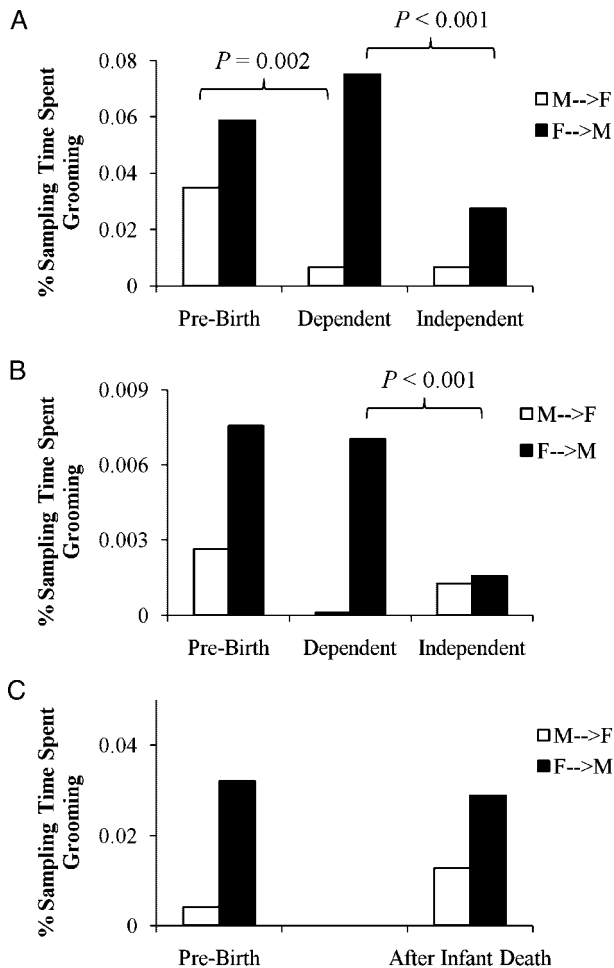[b]Nonprimary, sexual dyad.

Fig. 5. Changes in grooming time and reciprocity of primary dyads with infant status. (**A**) Junco primary dyad (JM1-JF1), (**B**) Peach primary dyad (PM-PF), and (**C**) Mazaroni primary dyad (MM1-MF1). Note difference in scales.

creased after the infant was born, but this difference was only significant for JM1 (two-sample proportions test: $z = 3.15$, $P = 0.002$). Increased grooming of other group members did not account for these changes. In Junco group, male grooming of other group members decreased slightly during infant dependency and the male was never observed to groom the infant. The Peach male was observed grooming the infant for <30 sec during dependency; no other grooming partners were present in the group. Males were not observed to have any other social interactions with dependent infants.

Once infants became independent, adult male PM increased grooming of the primary female, whereas JM1's grooming remained constant. These changes are reflected by the increase in grooming reciprocity (decrease in grooming index) during infant dependency (Table III). The drop in grooming reciprocity (increase in grooming index) after the infant became independent resulted from the female grooming less (Fig. 5). These results indicate that although males increased proximity maintenance to the primary female after the birth of an infant, they groomed her less than before the infant's birth. After the infant became independent, overall grooming and proximity between the dyad decreased significantly.

In the case of the deceased infant in the Mazaroni group, female grooming of the primary male remained roughly constant after the death of the infant, although male grooming increased, causing an increase in grooming reciprocity (Table III; Fig. 5C). However, it should be noted that the prebirth sample is based on a smaller data set than the after death sample (148 min of continuous sampling vs. 1,279 min).

DISCUSSION

Patterns in White-faced Saki Monkey Social Bonds

On the basis of this 17-month study, within-group social structure of white-faced sakis can be characterized as follows: (1) social bonds (as illustrated by proximity and grooming) were strongest for a single male-female dyad for each group, regardless of the presence of other sexually active group members; (2) male and female (sex specific)

bonds were variable in strength, but generally less intense than the primary dyad's (male–female) bond, and (3) grooming and proximity of the primary dyad changed with infant development, with increased male proximity maintenance toward females after infants were born and decreased proximity and grooming when infants became independent. Because females with dependent infants still groomed males, there is no reason to believe that the presence of an infant would constrain a male's ability to groom the female. Furthermore, the rarity of male–infant social interactions suggests that increased proximity maintenance is not due to attraction to the infant for social interaction (e.g., desire to handle infant), although it does seem likely that the presence of the infant is in some way the catalyst for these changes. These results indicate that among white-faced sakis living in one-male, one-female groups or small multimale–multifemale groups, the strongest social bond is between a single male and a single female.

For primary dyads, grooming was largely non-reciprocal and biased toward female investment in all groups. Nonprimary dyads (including other sexual dyads) showed a fundamentally different relationship in terms of grooming patterns, suggesting that the relationship of the primary dyad is unique. Primary dyads may represent the primary breeders in the group, although this has not been confirmed by genetic data. All primary dyad females gave birth during the study period, whereas nonprimary females did not although one nonprimary female (MF2) was pregnant at the end of the study period [Thompson CL, unpublished data].

The patterns of grooming observed here differ from many monogamous species as well as other platyrrhines living in small multimale–multifemale groups, where males invest more heavily in the intersexual relationship, with large amounts of grooming directed toward the female [gibbons: Palombit, 1999; *Indri*: Pollock, 1979; saddleback tamarins: Goldizen, 1989; *Callimico*: Porter & Garber, 2009; grooming between *Aotus* pairs is rare: Rotundo et al., 2005]. Notably, the monogamous primate that does show male-directed grooming by the female is the genetic sister taxa of *Pithecia*, *Callicebus* (titi monkeys) [Kinzey & Wright, 1982].

Intersexual Social Bonds and Infant Development

Male white-faced sakis increased proximity maintenance to females while infants were dependent, but simultaneously decreased the amount of grooming directed at the female. Once infants became independent, overall proximity and male-directed grooming by the female decreased significantly. We discuss four potential explanations for the observed pattern.

1. *Infant protection from infanticide*: Infanticide models predict that females should maintain intersexual relationships during times of infant vulnerability [Palombit, 2000; van Schaik, 1996]. This is consistent with our results, and such a pattern has also been reported for gorillas [Harcourt, 1979] and baboons [Weingrill, 2000]. A floater population (male and female) was present at the study site (pers. obs.) and has also been documented for *P. aequatorilis* [Di Fiore et al., 2007], and floater males could pose a legitimate risk for infanticide. Nevertheless, infanticide has not yet been observed in this species (although there have been few long-term studies in free-ranging populations). It is also unclear if persistent male–female proximity would prevent infanticidal attacks in this population, because threats would come during infrequent encounters between established groups and floater males (three observed encounters over this 17-month study). Additionally, in the absence of genetic data, we cannot be assured that the primary males in this study are indeed the sires of the primary female's offspring. However, as there are few or no other breeding males within groups and females were not observed to mate with extragroup males, primary males may develop a strong sociosexual bond with primary female and thus act to protect her (and likely his) infant.

2. *Protection from predation* [Treves et al., 2003]: Increased male–female proximity during infant dependency could protect infants from predation. Indeed, de Luna et al. [2010] found that male equatorial sakis and titis were more likely to mob predators than females and juveniles. However, it seems somewhat unconvincing to us that an infant clinging to its mother (i.e., a dependent infant in this study) would be at a higher risk of predation than a small, locomotor inexperienced juvenile that is not on/near a larger adult (i.e., an independent infant in this study).

3. *Infant attraction* [Hrdy, 1977]: A model of infant attraction is not consistent with our data. No other dyads showed increased proximity, proximity maintenance, or grooming of females with a dependent infant nor a decrease in these variables when infants became independent. The actions of primary males are inconsistent with this idea as well: despite increased proximity maintenance by males, they actually groomed females less, did not handle infants, and only minimally groomed infants.

4. *Females invest in the male–female relationship in order to obtain benefits from males*: Although direct paternal care is absent in white-faced sakis, males may be providing indirect benefits to females through territory defense. Males are the primary participants in between-group aggression [Norconk, 2006; Thompson, 2006, 2011], and there is some evidence to suggest that males serve as "hired guns" [sensu Wrangham & Rubenstein, 1986] that defend

access to feeding resources for females: between-group aggression increased in response to decreases in whole fruit consumption [Thompson, 2011]. This defense of resources may be comparatively more important while females are pregnant, lactating, and carrying offspring than when infants are independent, as the female's energetic costs would be higher. Accordingly, high levels of grooming and proximity prebirth and during infant dependency could be taken as a female's increased value of this service; the decrease in female investment in the primary social bond when infants become independent (i.e., when her energetic expenditure is lower) may likewise represent a decrease in her value of this service.

Evolution of Social Diversity Within the Pitheciines

As a subfamily, Pitheciines exhibit a broad range of social and mating patterns—from classical monogamy to large polygynously breeding multimale–multifemale groups. *Pithecia*, in the middle, exhibits more flexibility in adult group membership than titis, but still retains territorial defense and small home ranges [Norconk, 2011; Thompson, 2011]. The phylogenetic relationships among these taxa are well known, based on both fossil [Kay, 1990; Kay et al., 2008; Rosenberger et al., 2009] and molecular data [Finotelo et al., 2010; Wildman et al., 2009], and support the view that titis are at the base of the pitheciine radiation (Fig. 6). As such, the specialized traits associated with seed predation evolved after *Pithecia* and the larger bodied pitheciins diverged from the titis [Kinzey, 1992]. Socially, *Chiropotes* and *Cacajao* diverge sharply from both *Callicebus* and *Pithecia*, having large multimale–multifemale groups, predominantly male–male bonds, and no between-group aggression [Ayres, 1986; Boubli, 1999; Gregory, 2011]. Ecologically, the evolution of specialized morphology for seed predation provided pitheciins with access to a relatively reliable and aseasonal resource, which may have facilitated relaxation of constraints on social strategies and promoted male–male tolerance.
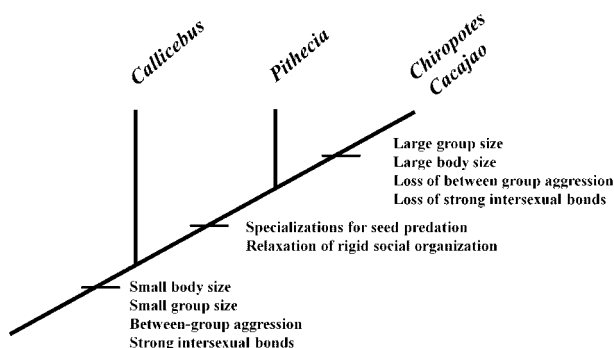
Strong male–female social bonds in *P. pithecia* still resemble the monogamous condition in titis, but the social organization and sexual behavior of the group has become more flexible through the retention of adult offspring in the group and/or by accepting immigrants. This evolutionary shift may have been driven by the benefits of male intragroup cooperation. Younger male white-faced sakis often assist older males during aggressive intergroup encounters [Norconk, 2006; Thompson, 2011]. If this assistance increases the breeding male's tenure length, then selection for greater male intrasexual tolerance could lead to the retention of offspring in the group into adulthood, as well as the possibility of male immigration. The incentive for helper males to engage in risky between-group aggression may include: tolerance of their mating activity [one helper male (MM2) in this study engaged in copulations], benefits of kin selection (if related to the primary male), avoiding the costs of dispersal/solitary living, and/or serve a learning function for future territory defense. It is also notable that, in past observations of this study population, a young subadult male (PM) who helped during between-group encounters inherited his natal home range.

Pitheciines may provide clues to how social systems change evolutionarily, what mechanisms might be retained at intermediate stages (e.g., territoriality and patterns of social bonding), and how social tolerance of adult offspring may lead to the evolution of large group size. Among pitheciines, bearded sakis and uakaris are the least well known socially, although the data available indicate that male intrasexual tolerance has been taken to the extreme in this clade, with male–male affiliation being the norm [Bowler & Bodmer, 2009; Gregory, 2011; Peetz, 2001; Veiga & Silva, 2005]. However, details of intragroup relatedness and dispersal patterns are currently unknown. More detailed studies of the larger pitheciines as well as other species of *Pithecia* are necessary before we fully understand the range of adaptations in this primate clade.

ACKNOWLEDGMENTS

Fig. 6. Phylogenetic relationships of the Pitheciines.

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