Original Article

Adult Male Replacement in Socially Monogamous Equatorial Saki Monkeys (*Pithecia aequatorialis*)

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Abstract

Sakis (genus *Pithecia*) commonly live in socially monogamous groups, but data from wild populations on group dynamics and on the turnover of reproductive-age animals are rare. Here we describe the replacement of the adult male in one group of sakis in the Ecuadorian Amazon following the death of the initial resident. We use 354 h of focal behavioral data to describe differences in the spatial relationships among group members before and after the replacement and to examine changes in the rate of male-to-female grooming, aggression, scent marking and vocalization. Interactions with extragroup individuals within the group's home range were more frequent during and after the replacement than before. The presence of such additional animals during periods of reproductive turnover may explain at least some reported observations of saki groups with more than 1 reproductive-age male or female.

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Introduction

Socially monogamous groups are characterized by the presence of only 1 reproducing adult male and 1 reproducing adult female that maintain a close sociospatial relationship and a relatively high degree of synchronization in their activities [Kleiman, 1977; Wittenberger and Tilson, 1980; Wickler and Seibt, 1983; Mock and Fujioka, 1990]. Among Neotropical primates, titis (genus *Callicebus*) and owl monkeys (genus *Aotus*) have always been reported as living in socially monogamous groups,

based on solid demographic and behavioral data [Mason, 1966; Kinzey, 1981; Aquino and Encarnación, 1986; Wright, 1986; Robinson et al., 1987; Wright, 1994, 1996; Kinzey, 1997; Fernandez-Duque, 2007]. Saki monkeys (genus *Pithecia*) have also been reported to commonly live in small social groups comprising a single male-female breeding pair and up to several young [Buchanan et al., 1981; Robinson et al., 1987; Kinzey, 1997]. Nonetheless, some researchers have described groups containing more than 1 adult male and/or female, raising the possibility of considerable variation in group structure within the genus as a whole and within local populations [Setz and Gaspar, 1997; Lehman et al., 2001; Vié et al., 2001; Norconk, 2007].

An adequate account of the typical social system of a species, and of variation around the norm, requires detailed descriptions of group size, composition and dynamics. Unfortunately, information on saki group structure is primarily derived from population surveys during which only a very limited amount of time was spent with nonindividually identified animals [Soini, 1986; Kessler, 1998; Lehman et al., 2001]. Moreover, the only significantly longer studies of any species of *Pithecia* have focused on isolated groups living on islands or in relatively small, remnant patches of forest where there have been few opportunities for observing natural changes in group composition and intergroup dynamics [Kinzey and Norconk, 1993; Setz, 1994; Norconk, 1996; Setz et al., 1999; Norconk, 2001]. As a result, information on the behavioral mechanisms regulating group size in sakis is scarce.

A thorough description of the behavioral mechanisms regulating the processes of mate choice, pair formation and pair termination are necessary for understanding how monogamous social systems are maintained because the costs and benefits to males and females of pursuing social monogamy depend heavily on the likely duration and stability of their relationship. Under the traditional view of social monogamy, it was common to assume that males and females establish strong, long-lasting and exclusive 'pair bonds' and that social groups thus consist of paired individuals plus their biological offspring [Mason, 1966; Kleiman, 1977, 1981; Palombit, 1994; Fuentes, 1999; van Schaik and Kappeler, 2003]. However, abundant information is now available from a number of primate taxa demonstrating, first, that socially monogamous groups often do not constitute such 'nuclear' families and, second, that the adults within socially monogamous groups may not enjoy extended or exclusive mating relationships [Palombit, 1994; Reichard, 1995; Palombit, 1996; Brockelman et al., 1998; Fernandez-Duque, 2007]. In general agreement with this emerging picture of 'dynamic pair bonds' in socially monogamous primates [Palombit, 1994], we describe here the replacement of the resident adult male in a well-habituated group of sakis that is being studied as part of a long-term project on the comparative socioecology of monogamous primates in the Ecuadorian Amazon and Argentine Chaco [Di Fiore and Schwindt, 2004; Schwindt et al., 2004; Hurst et al., 2005].

Methods

Study Site and Subjects
We conducted this study at the Tiputini Biodiversity Station (76°08′ W, 0°38′ S), located in the Yasuní National Park and Biosphere Reserve in Ecuador. In November of 2003, we began habituating the group of equatorial sakis *(Pithecia aequatorialis)* described in this report, which consisted of an adult male, an adult female and a male dependent juvenile estimated to be less than 1 year old. During that month, we darted and captured the adult male via remote anesthe-

tization with a tranquilizer dart fired from a CO_2-powered rifle. The male was removed from the group for approximately 3 h, during which time we collected a range of morphometric data and fitted him with a radio collar. Our capture procedures followed those we had used in the past to capture owl monkeys *(Aotus azarai)* [Fernandez-Duque and Rotundo, 2003] and titis *(Callicebus discolor)* [Di Fiore and Schwindt, 2004; Schwindt et al., 2004].

Data Collection

Between November 2003 and June 2004, we followed the animals via telemetry and direct observation to habituate them, to collect qualitative data on diet and home range use, and to develop the ethogram for systematic behavioral sampling. The quantitative data we analyze here were then collected between July 2004 and June 2005 utilizing a standardized sampling protocol that we developed for a larger, comparative study on socially monogamous primates in Argentina and Ecuador. Behavioral data were collected during 20-min 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 min. Across days, we maintained an approximate balance in the number of focal samples collected per individual. During each focal sample, we recorded the basic behavioral state ('resting', 'foraging', 'moving', 'social', 'other' and 'out of view') of the focal animal and the identity of its nearest neighbor (or neighbors, if multiple group mates were equidistant from the focal individual) as an instantaneous point sample every 2 min, and we noted all occurrences of a set of additional social behaviors of interest (e.g. approaches, leaves, grooming bouts, scent marking bouts and vocalizations) between those points. We also noted the position of the group relative to previously mapped trails and reference points 3 times per hour. Finally, we recorded ad libitum any conspicuous but rare events (e.g. intergroup encounters, fights among group members), as these occurred too infrequently for our sampling protocol to yield an adequate assessment of their rate.

Data Analysis

We divided the period of this study into 3 stages defined by the presence and identity of the adult male in the focal group: stage 1 – the tenure of the initial resident male, from July 20 to September 8, 2004; stage 2 – the transition period, from September 9 to October 4, 2004, and stage 3 – the tenure of the incoming resident male, from October 5, 2004, to July 19, 2005. Our analyses are based on approximately 49 h of focal data collected over 21 observation days in stage 1, 15 h over 11 days in stage 2, and 290 h over 104 days in stage 3.

To characterize the behavior of each individual and the relationships among group members before, during and after the replacement, we examined the proportion of instantaneous sampling points that each subject spent with each other group member as a nearest neighbor, the proportion of points they spent giving and receiving grooming, and their rates of participation in aggressive interactions, scent marking and vocalizing, where rates were calculated as the number of occurrences of the behavior of interest per focal sample. Aggressive interactions included chasing, grabbing, hitting, grasping, pulling, slapping or biting another individual. Scent marking included the behaviors 'rub face', 'rub chest' and 'rub genitals', in which the mentioned body part is moved vigorously back and forth against a stable substrate, and 'rub over', in which the focal animal was observed performing one of those same behaviors in precisely the same location where another group member had previously scent marked. To calculate the vocalization rate, we combined various distinct call types that were typically performed contagiously by several group members. These included several low-volume 'contact calls' and calls given in the context of intergroup interactions but excluded 'alarm vocalizations', which are often given by unhabituated groups in response to contact with humans.

For each of these variables, we first calculated a proportion or rate per focal sample and then computed a mean across samples for each individual. Because our data were not normally distributed, we compared the means of each variable before and after the male replacement using nonparametric Mann-Whitney U tests, treating each focal sample as an independent observation and using stage 1 (initial resident male) versus stage 3 (incoming resident male) as the grouping variable.

Results

Qualitative Overview of the Replacement

On September 9, 2004, approximately 2 months into the period of systematic data collection, the initial resident male began behaving noticeably differently. During two 8-hour follows on September 10 and 11, he was never observed with the rest of the group although other saki vocalizations were heard on occasion. On September 13, a day of intermittent heavy rain, we were unable to locate the male, but the radio collar signal was received all day from the same local area within the group's home range. The male was found dead and recovered the next day. We were unable to locate the group again until September 16, when we found the female and juvenile traveling alone and followed them for 4 h. After that, we were unable to locate the group again until the afternoon of September 25, when we saw for the first time a new male with the group just before they entered a repeatedly used sleep tree.

During two 8-hour follows of the female and juvenile on September 26 and 27, multiple unknown animals were observed within the group's home range or were seen associating intermittently with the female and the juvenile. The unknown animals included several solitary males, an adult male-subadult male pair, and at least 1 mixed-sex association. We noted no overt aggression or attempt to repulse these individuals from the range. During this time, the female also interacted vocally with several unfamiliar animals that we could not observe. The incoming resident male was first conclusively identified ranging with or near the group on October 3, although it is possible that he was one of the unfamiliar animals encountered previously. At least 1 other unfamiliar male was also seen in the group's home range on that day. The incoming resident male remained in association with the female and the juvenile for the entire day on October 4. On October 5, three weeks after the initial resident male's death, the incoming male performed jointly with the female a characteristic loud call during an encounter with another group of sakis, suggesting his full integration into the group.

Within-Group Social Interactions

Spatial relationships among members of the group were substantially different before and after the replacement. The former resident male had the juvenile as his nearest neighbor almost twice as often as he had the female, whereas the incoming male was almost twice as often near the female as he was near the juvenile (fig. 1). The incoming male spent a significantly greater proportion of scans per focal sample with the female as his nearest neighbor than did the initial resident male (Mann-Whitney U: $Z = -3.89$, $p < 0.01$) and a significantly lower proportion of scans with the juvenile (Mann-Whitney U: $Z = -3.83$, $p < 0.01$). The proportion of scans that the female spent with the incoming male as her nearest neighbor increased steadily in the months after his integration. Nonetheless, the female spent a lower proportion of scans overall with the new male as her nearest neighbor during the first 8 months of his tenure than she did with the initial resident male (Mann-Whitney U: $Z = -1.86$, $p = 0.06$), suggesting that even after 8 months of pairing, the spatial relationship of the female with the new male was qualitatively different from her relationship with her former partner.

The replacement of the adult male also impacted the spatial relationships of the juvenile with his putative mother. The female was most commonly the nearest
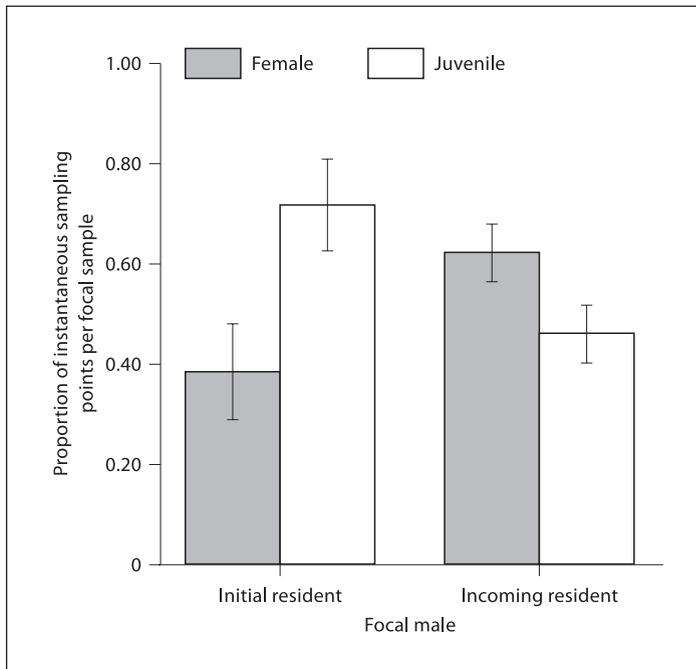
Fig. 1. Proportion of instantaneous sampling points during focal samples of the initial resident male and the incoming resident male that the female and the juvenile were his nearest neighbor. Error bars = ±2 SE.

neighbor of the juvenile both before and after replacement (fig. 2). However, the proportion of scans within each focal sample that the juvenile spent with the adult male as its nearest neighbor dropped by almost half following replacement (Mann-Whitney U: $Z = -2.94$, $p < 0.01$), while the proportion of scans it spent with the female as a nearest neighbor increased significantly (Mann-Whitney U: $Z = -3.64$, $p < 0.01$).

The differences noted in the spatial relationships of the female and the male were also reflected in their rates of grooming. Whereas grooming between the initial resident male and the female was very infrequent, it increased dramatically after the incoming male had joined the group. We only observed 1 bout of grooming (male-to-female) between the initial resident male and the female during the 2 months of systematic data collection before the replacement, and grooming was likewise only rarely seen during the preceding 8 months of pilot observations. By contrast, the incoming male spent an average of 7% of his time grooming the female during the first 8 months of his tenure in the group. The incoming resident male was seen grooming the female during 56 separate focal samples on 40 different observation days. Grooming by the male increased in the months after pairing, reaching a peak 5 months after the replacement and then decreasing (fig. 3). During this period, the female only groomed the incoming male on 5 occasions, each on different observation days.
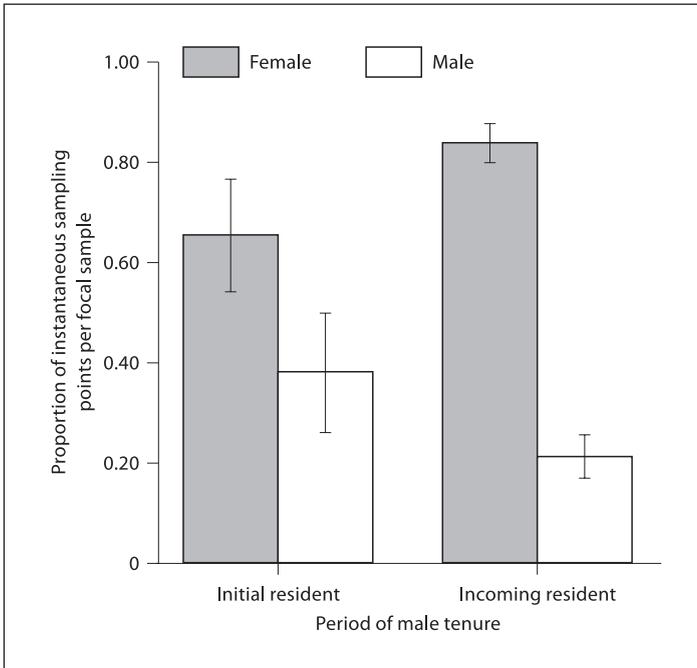
Fig. 2. Proportion of instantaneous sampling points during focal samples of the juvenile in which his nearest neighbor was the female and the resident adult male during the tenures of the initial and incoming resident males. Error bars = ±2 SE.

Aggressive interactions among group members were also more common following the replacement. Whereas aggression was never observed between the initial resident male, the female and the juvenile, we recorded at least 19 aggressive interactions between the incoming male and the other members of the group after his integration. A number of these cases involved the female aggressing against the new male soon after his integration; several others involved the new male directing aggression either against the juvenile or against an infant born in March 2005. All of these aggressive interactions were relatively minor (e.g. chases, cuffings), and none resulted in any noticeable injury to any of the participants.

Rates of scent marking and vocalizing also increased following the integration of the new male. The incoming male scent marked somewhat more than the initial resident male (mean = 0.93 vs. 0.55 scent marking events per focal sample), and scent marking by the female also increased following the integration of the new male (mean = 0.49 vs. 0.31 events per focal sample), though these differences were not statistically significant (Mann-Whitney U: $p > 0.10$ for both tests). However, the overall rate of vocalizations was significantly higher for the incoming male than for the initial resident male (mean = 10.5 vs. 3.9 vocal events per focal sample, Mann-Whitney U: $Z = -4.28$, $p < 0.01$) and significantly higher for the female after replacement than before (mean = 15.6 vs. 11.1 vocal events per focal sample, Mann-Whitney U: $Z = -2.38$, $p < 0.05$).
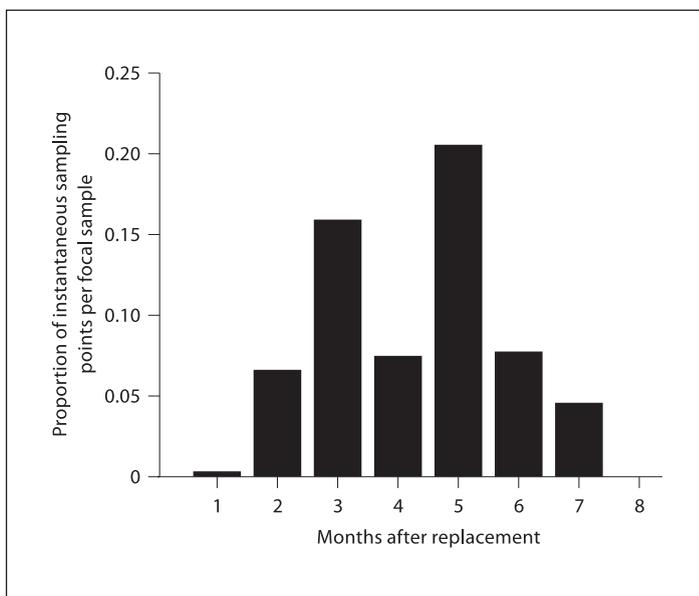
Fig. 3. Proportion of instantaneous sampling points during focal samples that the incoming resident male spent grooming the resident adult female during the first 8 months of his tenure in the group.

Encounters with Extragroup Animals

Interactions between the study group and other neighboring groups during the tenure of the initial resident male were extremely rare. Indeed, in 21 full or partial days of systematic observation over the 2 months prior to the initial resident male's death, only 1 intergroup interaction was recorded. This changed completely during the transition period, when encounters with extragroup individuals became more frequent (occurring on 6 of 11 full- or partial-day follows) and multiple unknown animals – including both adult-sized males and mixed-sex associations – were seen well within the group's range. Following the new male's integration into the group, encounters with extragroup individuals were again less frequent (occurring on 26 of 104 observation days) and were limited to peripheral portions of their home range.

Interestingly, the rate at which extragroup animals were encountered did increase on 1 subsequent occasion outside of the period of resident male replacement. It happened when we captured the replacement male in order to fit him with a radio collar. On January 15, 2005, the replacement male was darted and removed from the group for 135 min. Within just over 6 h from the time of his temporary removal, at least 1 new male was seen in the area, interacting with the group. Unknown sakis were also spotted within the group's home range on several occasions over the next few days.

Discussion

In socially monogamous taxa the replacement of one of the members of a pair can result either from desertion or death of a resident or from eviction of a resident by an incoming challenger. Although we cannot confirm the events that triggered the replacement in this case, it seems most plausible that the death of the resident male produced a vacancy that was then filled by another individual. This possibility is reinforced by the following observations: (1) no unfamiliar animals were noted interacting with the group in the weeks prior to the death of the resident male and (2) no overt aggression was noted during the transition period. Rather, we had the subjective impression that the replacement process was a 'peaceful' one (although we do note that we unfortunately had very limited contact with the female during the week and a half immediately following the death of the original resident male), and that the new male's eventual success in joining the group depended largely on his gradual acceptance by the female. This may point to a more important role for female choice than for direct male-male competition in shaping the mating system of saki monkeys.

Unfortunately, the origin of the new male is unknown. In other socially monogamous primates, it has been shown that young adults may acquire reproductive positions either within their natal territory by evicting a same-sex resident adult, by establishing a new territory with another unpaired individual, or by joining a 'widowed' or 'divorced' conspecific [Tilson, 1981; Palombit, 1994; Brockelman et al., 1998; Bossuyt, 2002; Fernandez-Duque, 2004, 2007]. No comparable data exist on sakis, but the rapidity with which multiple unfamiliar animals appeared in the female's home range following the original male's death (and during the replacement male's temporary removal) may suggest the existence of a 'floater' population that was previously (and subsequently) undetected. It remains to be determined just how floater individuals or animals in neighboring groups might detect a vacant breeding position so rapidly, but we suspect that vocal behavior plays an important role in this process.

Not surprisingly, social interactions among group members were substantially different before and after replacement. These differences were reflected in the spatial arrangement of the members, as well as in the rates of social grooming, scent marking, aggression and vocalizations. The new male spent significantly more time than the initial resident male with the female as his nearest neighbor and less time with the juvenile, and he directed more grooming towards the female than did the initial resident. Over time, the female came to spend more and more time with the new male as her nearest neighbor. The low frequency of grooming between the initial resident male and female, as well as the decrease in grooming frequency some time after the establishment of the new pair, fits nicely the expectations for a socially monogamous primate.

Our preliminary results also indicate a prominent participation of the male in intergroup vocalizations and scent marking. It remains to be examined whether the male serves an important role in territory defense and, perhaps, in suppressing the influx of extragroup animals into a group's home range. Informal playback experiments also suggest that males respond more strongly to playbacks of territorial vocalizations than do females, by vocalizing and approaching the speaker [Di Fiore, Fernandez-Duque and Hurst, unpubl. data], in agreement with similar reports on other saki species [Rosenberger et al., 1996]. Male sakis provide little direct care for

offspring [Homburg, 1998], unlike titi [Fragaszy et al., 1982; Mendoza and Mason, 1986a, b; Hoffman et al., 1995] or owl monkey males [Wright, 1984; Jantschke et al., 1996; Rotundo et al., 2002, 2005; Fernandez-Duque, 2007], who, almost exclusively, carry infants from soon after birth. Thus, territory defense may be an important alternative 'service' that males provide for female sakis.

Finally, while the modal pattern of social organization for sakis are groups containing a single adult male-female pair, there are several reports of groups containing more than 1 adult-sized individual of one or both sexes [Norconk, 2007]. This has prompted some authors to suggest that considerable variation may exist within and between saki groups in grouping patterns [Lehman et al., 2001]. While we are sympathetic to this idea, we think that our observations on sakis, as well as long-term observations of titis and owl monkeys, may provide an alternative explanation for some reported observations of multimale-multifemale groups in sakis. We suggest that at least some reported cases of multimale-multifemale groups might reflect temporary associations occurring during periods of turnover of reproductive group members. Certainly, censuses of our main study group at various times during the transition period could have yielded a range of different 'group' compositions, depending on whether the female and juvenile were interacting, for example, with a solitary individual, a pair or a whole social group. An alternative explanation for the presence of supernumerary 'adults' of one or both sexes in saki groups could be the delayed dispersal of offspring who reach adult size or coloration in their natal groups. This phenomenon has been reported for other pitheciines [Norconk, 2007] and other socially monogamous primates [Brockelman et al. 1998; Fernandez-Duque and Huntington, 2002].

These observations of the replacement of the resident adult male in a well-habituated saki group provide valuable, albeit preliminary, data on the behavioral mechanisms leading to the integration of a new male into a socially monogamous group. Still, it bears repeating that because this replacement was a singular event, interpretation of our data needs to proceed with caution. This is especially true when discussing the data that relate to interactions of members of the target group with extragroup individuals, given that the neighboring saki groups in the area are still poorly known and hard to follow and observe.

References

Aquino R, Encarnación F (1986). Population structure of *Aotus nancymai* (Cebidae: Primates) in Peruvian Amazon lowland forest. *American Journal of Primatology* 11: 1–7.

Bossuyt F (2002). Natal dispersal of titi monkeys *(Callicebus moloch)* at Cocha Cashu, Manu National Park, Peru. *American Journal of Physical Anthropology* suppl 34: 47.

Brockelman WY, Reichard U, Treesucon U, Raemaekers JJ (1998). Dispersal, pair formation and social structure in gibbons *(Hylobates lar)*. *Behavioral Ecology and Sociobiology* 42: 329–339.

Buchanan DB, Mittermeier RA, van Roosmalen MGM (1981). The saki monkeys, genus *Pithecia*. In *Ecology and Behavior of Neotropical Primates* (Coimbra-Filho AF, Mittermeier RA, eds.), pp 391–417. Rio de Janeiro, Academia Brasileira de Ciências.

Di Fiore A, Schwindt DM (2004). A preliminary study of social behavior and pair-bonding in wild titi monkeys *(Callicebus discolor)* in Amazonian Ecuador. *American Journal of Physical Anthropology* suppl 38: 87.

Fernandez-Duque E (2004). High levels of intrasexual competition in sexually monomorphic owl monkeys. *Folia Primatologica* 75(suppl 1): 260.

Fernandez-Duque E (2007). The Aotinae: social monogamy in the only nocturnal Haplorhines. In *Primates in Perspective* (Campbell CJ, Bearder S, Fuentes A, MacKinnon KC, Panger M, eds.), pp 139–154. Oxford, Oxford University Press.

Fernandez-Duque E, Huntington C (2002). Disappearances of individuals from social groups have implications for understanding natal dispersal in monogamous owl monkeys *(Aotus azarai)*. *American Journal of Primatology* 57: 219–225.

Fernandez-Duque E, Rotundo M (2003). Field methods for capturing and marking azarai night monkeys. *International Journal of Primatology* 24: 1113–1120.

Fragaszy DM, Schwarz S, Shimosaka D (1982). Longitudinal observations of care and development of infant titi monkeys *(Callicebus moloch)*. *American Journal of Primatology* 2: 191–200.

Fuentes A (1999). Re-evaluating primate monogamy. *American Anthropologist* 100: 890–907.

Hoffman KA, Mendoza SP, Hennessy MB, Mason WA (1995). Responses of infant titi monkeys, *Callicebus moloch*, to removal of one or both parents: evidence for paternal attachment. *Developmental Psychobiology* 28: 399–407.

Homburg I (1998). *Ökologie und Sozialverhalten von Weissgesicht-Sakis: Eine Freilandstudie in Venezuela*. Göttingen, Cuvillier.

Hurst D, Di Fiore A, Fernandez-Duque E (2005). Male replacement in a wild group of equatorial sakis *(Pithecia aequatorialis)*. *American Journal of Primatology* 66(suppl 1): 118–119.

Jantschke B, Welker C, Klaiber-Schuh A (1996). Rearing without paternal help in the Bolivian owl monkey *Aotus azarae boliviensis*: a case study. *Folia Primatologica* 69: 115–120.

Kessler P (1998). Primate densities in the Natural Reserve of Nourague, French Guiana. *Neotropical Primates* 6: 45–46.

Kinzey WG (1981). The titi monkeys, genus *Callicebus*. In *Ecology and Behavior of Neotropical Primates* (Coimbra-Filho AF, Mittermeier RA, eds.), pp 241–296. Rio de Janeiro, Academia Brasileira de Ciências.

Kinzey WG, ed. (1997). *New World Primates: Ecology, Evolution, and Behavior*. New York, Aldine de Gruyter.

Kinzey WG, Norconk MA (1993). Physical and chemical properties of fruits and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *International Journal of Primatology* 14: 207–227.

Kleiman D (1977). Monogamy in mammals. *Quarterly Review of Biology* 52: 39–69.

Kleiman DG (1981). Correlations among life history characteristics of mammalian species exhibiting two extreme forms of monogamy. In *Natural Selection and Social Behavior* (Alexander RD, Tinkle DW, eds.), pp 332–344. New York, Chiron Press.

Lehman SM, Prince W, Mayor M (2001). Variations in group size in white-faced sakis *(Pithecia pithecia)*: evidence for monogamy or seasonal congregations? *Neotropical Primates* 9: 96–101.

Mason WA (1966). Social organization of the South American monkey, *Callicebus moloch*: a preliminary report. *Tulane Studies in Zoology* 13: 23–28.

Mendoza SP, Mason WA (1986a). Parental division of labour and differentiation of attachments in a monogamous primate *(Callicebus moloch)*. *Animal Behavior* 34: 1336–1347.

Mendoza SP, Mason WA (1986b). Parenting within a monogamous society. In *Primate Ontogeny, Cognition and Social Behaviour* (Else JG, Lee PC, eds.), pp 255–266. Cambridge, Cambridge University Press.

Mock DW, Fujioka M (1990). Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology and Evolution* 5: 39–43.

Norconk MA (1996). Seasonal variation in the diets of white-faced and bearded sakis *(Pithecia pithecia* and *Chiropotes satanus)* in Guri Lake, Venezuela. In *Adaptive Radiations of Neotropical Primates* (Norconk MA, Rosenberger AL, Garber PA, eds.), pp 403–423. New York, Plenum Press.

Norconk M (2001). White-faced saki group dynamics in Lago Guri, Venezuela: 1990 to 2000. *American Journal of Primatology* 54(suppl 1): 41.

Norconk MA (2007). Sakis, uakaris and titi monkeys: behavioral diversity in a radiation of seed predators. In *Primates in Perspective* (Campbell CJ, Bearder S, Fuentes A, MacKinnon KC, Panger M, eds.), pp 123–138. Oxford, Oxford University Press.

Palombit R (1994). Dynamic pair bonds in hylobatids: implications regarding monogamous social systems. *Behaviour* 128: 65–101.

Palombit RA (1996). Pair bonds in monogamous apes: a comparison of the siamang *Hylobates syndactylus* and the white-handed gibbon *Hylobates lar*. *Behaviour* 133: 321–356.

Reichard U (1995). Extra-pair copulations in a monogamous gibbon *(Hylobates lar)*. *Ethology* 100: 99–112.

Robinson JG, Wright PC, Kinzey WG (1987). Monogamous cebids and their relatives: intergroup calls and spacing. In *Primate Societies* (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds.), pp 44–53. Chicago, University of Chicago Press.

Rosenberger AL, Norconk MA, Garber PA (1996). New perspectives on the pitheciines. In *Adaptive Radiations of Neotropical Primates* (Norconk MA, Rosenberger AL, Garber PA, eds.), pp 329–333. New York, Plenum Press.

Rotundo M, Fernandez-Duque E, Dixson AF (2005). Infant development and parental care in free-ranging groups of owl monkeys *(Aotus azarai azarai)* in Argentina. *International Journal of Primatology* 26: 1459–1473.

Rotundo M, Fernandez-Duque E, Giménez M (2002). Cuidado biparental en el mono de noche *(Aotus azarai azarai)* de Formosa, Argentina. *Neotropical Primates* 10: 70–72.

Schwindt DM, Carillo GA, Bravo JJ, Di Fiore A, Fernandez-Duque E (2004). Comparative socioecology of monogamous primates in the Amazon and Gran Chaco. *Folia Primatologica* 75(suppl 1): 412.

Setz E (1994). Feeding ecology of golden-faced sakis. *Neotropical Primates* 2: 13–14.

Setz EZF, Gaspar DA (1997). Scent marking behaviour in free-ranging golden-faced saki monkeys *Pithecia pithecia chrysocephala*: sex differences and context. *Journal of Zoology London* 241: 603–611.

Setz EZF, Enzweiler J, Solferini VN, Amêndola MP, Berton RS (1999). Geophagy in the golden-faced saki monkey *(Pithecia pithecia chrysocephala)* in the Central Amazon. *Journal of Zoology London* 247: 91–103.

Soini P (1986). A synecological study of a primate community in the Pacaya-Samiria National Reserve, Peru. *Primate Conservation* 7: 63–71.

Tilson RL (1981). Family formation strategies of Kloss's gibbons. *Folia Primatologica* 35: 259–287.

van Schaik CP, Kappeler PM (2003). The evolution of social monogamy in primates. In *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals* (Reichard UH, Boesch C, eds.), pp 59–80. Cambridge, Cambridge University Press.

Vié J-C, Richard-Hansen C, Fournier-Chambrillon C (2001). Abundance, use of space, and activity patterns of white-faced sakis *(Pithecia pithecia)* in French Guiana. *American Journal of Primatology* 55: 203–211.

Wickler W, Seibt U (1983). Monogamy: an ambiguous concept. In *Mate Choice* (Bateson P, ed.), pp 33–50. Cambridge, Cambridge University Press.

Wittenberger JF, Tilson RL (1980). The evolution of monogamy: hypotheses and evidence. *Annual Review of Ecology and Systematics* 11: 197–232.

Wright PC (1984). Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In *Female Primates: Studies by Women Primatologists* (Small M, ed.), pp 59–75. New York, Liss.

Wright PC (1986). Ecological correlates of monogamy in *Aotus* and *Callicebus*. In *Primate Ecology and Conservation* (Else JG, Lee PC, eds.), pp 159–167. Cambridge, Cambridge University Press.

Wright PC (1994). The behavior and ecology of the owl monkey. In *Aotus: The Owl Monkey* (Baer JF, Weller RE, Kakoma I, eds.), pp 97–112. San Diego, Academic Press.

Wright PC (1996). The Neotropical primate adaptation to nocturnality: feeding in the night *(Aotus nigriceps* and *A. azarae)*. In *Adaptive Radiations of Neotropical Primates* (Norconk MA, Rosenberger AL, Garber PA, eds.), pp 369–382. New York, Plenum Press.