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Variations in Group Size in White-Faced Sakis (*Pithecia pithecia*): Evidence For Monogamy or Seasonal Congregations?

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Introduction

There are few longitudinal data on the social structure and behavior of white-faced sakis (*Pithecia pithecia pithecia*). Synecological studies have found that they tend to live in small groups of 2–4 animals (Buchanan *et al.*, 1981; Mittermeier, 1977; also Oliveira *et al.*, 1985, who studied the golden-faced subspecies, *P. p. chrysocephala*), which have led some researchers to suggest that white-faced sakis are monogamous (e.g., Napier and Napier, 1986; Robinson *et al.*, 1986; Dunbar, 1988). Besides group size, support for monogamy in white-faced sakis comes from field studies in which males and females responded in a territorial manner to loud calls during vocal playback experiments (Rosenberger *et al.*, 1997).

Data from historic accounts and recent surveys indicate that some groups of white-faced sakis contain more than four individuals. There have been reports as early as the mid-19th century of groups with 6–10 members (Schomburgk, 1848; Schomburgk, 1876). More recent field accounts confirm that some groups have more than one adult member of each sex (Buchanan, 1978; Oliveira *et al.*, 1985; Kinzey and Norconk, 1993; Gleason and Norconk, 1995; Ryan, 1995; Norconk *et al.*, 1997; Norconk *et al.*, 1998), leading to suppositions that this species may not be monogamous. It has been suggested that groups with more than four animals may represent seasonal congregations of smaller groups (Buchanan, 1978; Fleagle and Meldrum, 1988). Therefore, it is not surprising that Rosenberger and coworkers (1997) recommended that

we reevaluate the white-faced saki as a "typical" monogamous primate.

Although preliminary surveys have provided invaluable data on the size and composition of white-faced saki groups (e.g., Mittermeier, 1977; Oliveira *et al.*, 1985; Kessler, 1998), they are difficult to interpret because the studies were typically conducted during only one season, and few sightings were made due to the shy and cryptic nature of the animals. Moreover, there are few recent data for populations of white-faced sakis in Guyana (Muckenhirn *et al.*, 1975; Sussman and Phillips-Conroy, 1995), where there are, surprisingly, some of the earliest descriptions of large group sizes (Schomburgk, 1848; Schomburgk, 1876).

If there is a seasonal effect influencing group congregations in white-faced sakis, then surveys conducted throughout the year may provide important preliminary data on their social structure. In this report we present longitudinal survey data on group size for white-faced sakis in Guyana and summarize results from previous surveys. We then suggest directions for future studies.

Methods

The data analyzed in this paper are from a literature review and 1,725 km of surveys we conducted at sixteen sites in Guyana (Fig. 1). Guyana is a small country of 215,000 km^2 situated on the northeastern coast of South America, between 56°20' and 61°23'W and 1°10' and 8°35'N. Mean annual precipitation is between 2,000 and 3,400 mm (ter Steege, 1993). There are generally two wet seasons (May to August and December to January) and two dry seasons (September to November and February to April).

Data were collected during three periods: (1) November 1994 to June 1995; (2) September 1995 to June 1996; and (3) June to August, 1997. When surveying forests, we used randomly selected and predetermined transect lines. Although most studies of the distribution of animals use only random selection of transects (e.g., Anderson *et al.*, 1979; Burnham *et al.*, 1980; Krebs, 1989; Peres, 1997), we also used predetermined transect lines to ensure that biogeographic features, such as rivers that may be barriers to dispersal, were included in the data set. Predetermined transect lines often ran along paths in the forest to maximize survey time in remote areas. Two types of surveys were conducted: (1) unique and (2) repeat. Unique surveys were made along transects, such as trails or riverbanks, where one to two transits were made during a census. During repeat surveys we conducted more than two transits of a transect line. Repeat surveys were conducted along paths at five locations: (1) Timehri; (2) Dubulay Ranch; (3) Kaieteur Falls National Park; (4) Mabura Hill Ecological Reserve and (5) Sebai River. We walked slowly along unique and repeat transects lines at a rate of 1.0 km/h, stopping every ten minutes to listen for the sounds of movement in the forest.

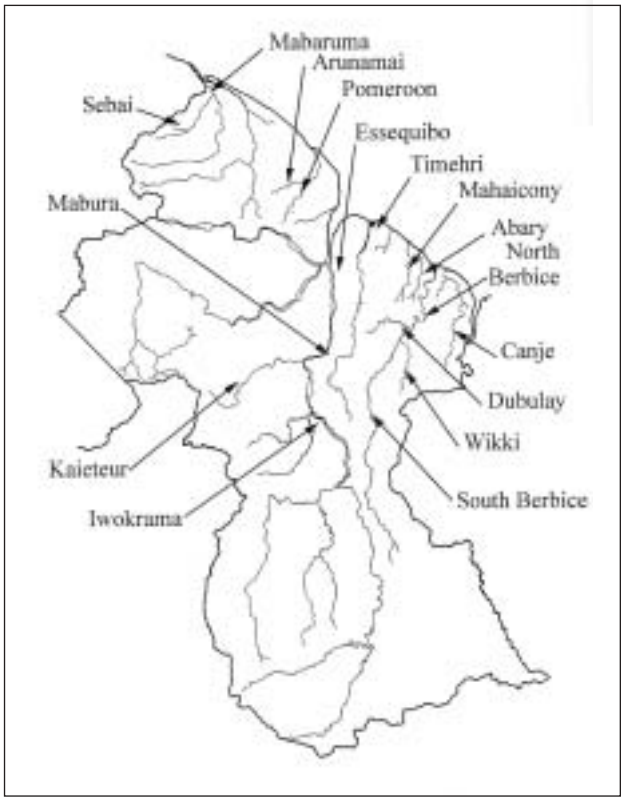

Figure 1. Locations of study sites.

We surveyed rivers by paddling slowly (1.5–2.0 km/h) along riverbanks. During river surveys, randomly selected areas were chosen on each bank for land surveys. Non-linear transect lines in the forest were used because travel costs are very high in Guyana. Thus, it was cost-prohibitive to cut and mark trails when only 2–4 weeks were available for data collection. Furthermore, in protected areas such as Kaieteur Falls National Park, Mabura Hill Forest Reserve, and Iwokrama Forest Reserve, it is illegal to cut trails. Hence, established trails were used in these protected areas.

During surveys, data were recorded on: (1) primate species; (2) time of day; (3) weather; (4) vegetation height; (5) general height of group; (6) number of animals in group; (7) cue by which animals were detected; (8) activity; (9) perpendicular distance from the transect [meters]; (10) sighting angle; and (11) habitat type. When a primate group was seen, a standardized time of 10 minutes was spent observing the behavior of individuals in the group (NRC, 1981). *Ad libitum* notes on behavior, obvious individual physical characteristics, and vocalizations were also collected. The location of primate groups seen during surveys was determined using LANDSAT-5 satellite photographs, 1:50,000 topographic maps of the region, and a Magellan NAV 5000D GPS. If monkeys were observed feeding, then fruit and/or voucher specimens were collected. Specimens were placed in plastic zip-lock bags and preserved with 80% ethanol. They were deposited for identification at the Center for the Study of Biological Diversity at the University of Guyana. Habitat descriptions were made using soil features, a vegetation map (Huber *et al.*, 1995), various monographs on Guyanese flora

(Van Roosmalen, 1985; de Granville, 1988; Mennega *et al.*, 1988; ter Steege, 1990, 1993), and LANDSAT-5 satellite imagery of survey areas.

Group sizes are given as the mean ± one standard deviation. Nonparametric statistics were used because survey data violate assumptions of normality (Ludwig and Reynolds, 1988). Spearman correlation coefficients (r_s) were computed for monthly data on mean group size (dependent variable) versus rainfall and fruiting records (independent variables) in Guyana. Rainfall and fruiting records are based on 100 years of data collected in Guyana (ter Steege, 1993). Data on group sizes from the three groups seen by Kinzey (1988) and Norconk (1997) in Venezuela were combined to facilitate comparisons. A Kruskal-Wallis (H) test was used to determine variations in group sizes between studies. Mann-Whitney U (U) tests were run to document pair-wise differences in group sizes for each of the published studies. Statistics were computed using SPSS 8.0 statistical software. All statistical tests were two-tailed and the alpha level was set at $p<0.05$.

Results

Table 1 shows the group size and composition of white-faced sakis we sighted in Guyana. We observed a total of 21 groups. Group size ranged from 2–12, with a mean of 4.8 ± 2.4 animals. The total average sex ratio was 1.1:1. Of the 21 groups censused, 52.3% (N = 11) contained more than one adult of each sex. A total of 71.4% (N = 15) groups contained more than one adult male or adult female. Mean monthly group size was not correlated with either rainfall (r_s = -0.145, p = 0.78) or fruiting records (r_s = 0.464, p = 0.35).

Table 1. Size and composition of *Pithecia pithecia pithecia* groups censused in Guyana.

Group Number	Number of Animals					
	Adult males	Adult females	Juvenile males	Juvenile females	Infants	Total
1	1	1				2
2	2	2	1			5
3	2	2				4
4	3	3	1			7
5	1	1			1	3
6	2	2				4
7	2	1				3
8	2	2			1	5
9	1	2		1	1	5
10	5	5	1		1	12
11	3	3				6
12	2	2	1		1	6
13	2	0				2
14	1	0	1	1		3
15	1	2				3
16	3	2	1	2	1	9
17	1	1	1		1	4
18	2	2			1	5
19	1	1	1		1	4
20	3	2	1			6
21	1	1				2
Total	41	37	9	4	9	100
Range	1-5	0-5	0-1	0-2	0-1	2-12
Mean	2.0	1.8	1.0	1.3	1.0	4.8
1 SD	1.0	1.1	0.0	0.6	0.0	2.4

On April 17, 1996, a group of twelve white-faced sakis were sighted by SML in riparian forest near the Madewini River in northern Guyana (6°29'N, 58°13'W). The animals were not shy and were followed easily for one hour. The group was composed of five adult males, five adult females, a juvenile male, and a juvenile female. The animals were traveling slowly as a cohesive group in the understorey at a height of 15 m. Two adult males foraged for ripe fruits in a *kokerite* palm (*Attalea maripa*) within 1 m of each other. Each male bit into and dropped fruits over a 45-second period before moving off to join the rest of the group. No social interactions were observed among any of the group members.

Average group size for all records of white-faced sakis was 3.8 ± 2.1 animals (Table 2). There is significant variation in group size for white-faced sakis across the study sites in NE South America (Kruskal-Wallis $H_{(5)}$ = 12.650, p = 0.027). This variation is driven by significantly larger group sizes in Guyana compared to those reported by Mittermeier (1977) in Suriname (Table 3).

Discussion

Some groups we surveyed in Guyana contained only one adult of each sex, whereas others contained more than one adult of each sex. We found no evidence of a seasonal effect on group size. Our data on group size are comparable to those collected by Kinzey *et al.* (1988) in eastern Venezuela and Muckenhirn *et al.* (1975) in Guyana. This continuity in grouping patterns for white-faced sakis in the western Guiana shield (eastern Venezuela and Guyana) indicates that the observations we made are not a phenomenon unique to only our study sites and time period. Surprisingly, average group size for white-faced sakis in Suriname, which is also part of the Guiana Shield (Norconk *et al.*, 1997), was significantly smaller than that seen for conspecific groups in Guyana. The reasons for these regional differences in social structure are poorly documented, but may be due to variations in plant species composition and diversity (Terborgh and Andresen, 1998). Therefore, our data support white-faced sakis as not being representative of a "typical" monogamous primate (Rosenberger *et al.*, 1997). However, it must be noted that only limited interpretations of social behavior can be made based on survey data. Detailed data on the feeding ecology and behavior of habituated groups are needed to determine the causal factors affecting intraspecific variation in group structure.

It should not be assumed that white-faced sakis are alone in challenging our views on primate monogamy. Fuentes (1999) conducted a review of primate monogamy and found that many supposed monogamous species exhibit a variety of grouping types and mating patterns. A notable example

Table 2. Size and composition of *Pithecia pithecia* groups censused in South America.

Country	Group Size			Group Composition					Sources
	Mean ± 1 SD	Range	N	AM	AF	SA	J	I	
Guyana	4.8 ± 2.4	2-12	21	1-5	0-5		0-2	0-2	Present study
Guyana	3.3 ± 1.7	1-5	10						Muckenhirn *et al.* (1975)
Venezuela	9.0		1	3	1	1-2	0-1		Norconk (1997)
Venezuela	5.5 ± 2.5	3-8	2						Kinzey *et al.* (1988)
Suriname	2.7 ± 0.8	2-4	9	1-2	1		0-1		Mittermeier (1977)
French Guiana	2.8 ± 1.0	1-4	4						Kessler (1998)
Brazil	2.6 ± 0.5	2-3	3	0-2	0-2	0-1		0-1	Oliveira *et al.* (1985)
Brazil	6		1	1	1-3	0-2	0-2	0-2	Setz and Gaspar (1997)

AM=adult male, AF=adult female, SA=subadult, J=juvenile, I=Infant

Table 3. Mann-Whitney U scores for intersite differences in group size for *Pithecia pithecia pithecia*. Sites are expressed by country to facilitate comparisons. Numbers above the diagonal refer to the U score. Numbers below the diagonal indicate the corresponding p value for each test.

Country	Venezuela	Guyana[a]	Guyana[b]	Suriname	French Guiana	Brazil
Venezuela		25.5	6.0	48.0	1.5	2.0
Guyana[a]	0.214		60.0	68.5	32.5	11.5
Guyana[b]	0.155	0.053		33.0	15.5	10.0
Suriname	0.042	0.019	0.310		17	12.5
French Guiana	0.105	0.119	0.509	0.865		6.0
Brazil	0.142	0.076	0.370	0.364	0.544	

[a] Present study, [b] Muckenhirn *et al.* (1975)

of this social diversity can be found among hylobatids. Despite gibbons being described as invariably monogamous (Leighton, 1986), recent field studies indicate that some species are not exclusively monogamous and/or pair-bonded (Jiang *et al.*, 1999; Palombit, 1994; Palombit, 1999; Sommer and Reichard, 2000). For example, Jiang and colleagues (1999) report the coexistence of monogamy and polygyny in black-crested gibbons (*Hylobates concolor*). Therefore, contrary to assumptions of obligate monogamy in gibbons, the social system of these primates may be characterized by flexible grouping and mating patterns (Sommer and Reichard, 2000).

How then can we interpret a social system for white-faced sakis that contrasts large group size, at least in some parts of its range, and monogamy? Monogamy in primates has been explained as: (1) an anti-infanticide strategy (Van Schaik and Dunbar, 1990; Palombit, 1999); (2) a strategy to elicit male parental care (Kleiman, 1977); (3) a means of protecting resources that are scarce and uniformly dispersed (Wittenberger and Tilson, 1980); and (4) a response to human predation (Kinzey, 1987). Fuentes (1999) reviewed these models and identified the following six characteristics of monogamy: exclusive one-male/one-female groups; pair bond and reinforcement behavior; sexual monomorphism; exclusive mating; territoriality; and paternal care. White-faced sakis do not meet the criteria for three of the six monogamous characteristics: exclusive one-male/one-female groups (present study; Kinzey *et al.*, 1988; Norconk, 1997; Rosenberger *et al.*, 1997); pair bond/reinforcement behavior (Gleason and Norconk, 1995); and paternal care (Ryan, 1995). Monomorphism is the only one of Fuentes' (1999) criteria that *P. p. pithecia* meets. The lack of longitudinal data on territoriality and the exclusivity of mating between two adults highlight some of the directions to be undertaken in future studies of this species. Social systems in white-faced sakis will be better understood when longitudinal data are also collected on: (1) demography and social behavior, (2) population genetics and paternity, and (3) ecological correlates to social structure.

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Diurnal Activity Budgets of Black Spider Monkeys, *Ateles chamek*, in a Southern Amazonian Tropical Forest

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Introduction

In the last twenty years an increasing number of field studies have demonstrated the potential behavioral flexibility within individual primate species. Until recently few published studies existed for any one primate genus, and thus all populations of a given species were inevitably 'tarred with the same behavioral brush' of just one focal study group. Whilst detailed behavioral studies of some primate genera are still scarce, for example the incredibly wide ranging *Cacajao* in the Neotropics (but see Ayres, 1989), today many primate genera have been studied at a number of long-term field sites. In this paper, I present data on diurnal variations in black spider monkey activity budgets from a previously unstudied focal study group in eastern Bolivia, and compare these results with other long-term *Ateles* study sites.

Study Site

The study was conducted in the Noel Kempff Mercado National Park of 15,300 km² in the north-eastern corner of Departmaento Santa Cruz, Bolivia (see Fig. 1). The Río Iteñez defines the park's eastern and northern edges, and represents the border with the neighboring Brazilian states of Rondônia and Mato Grosso. The region is situated on the Brazilian Shield geological formation, which is characterized by poor kaolinitic clay and podsol soils (PLUS-CORDECRUZ, 1994; Peres, 1997). The region has been characterized by a marked dry season in the austral winter, a mean annual temperature of *c.*26°C, and an annual precipitation of *c.*1,600 mm (Wallace, 1998).

Figure 1. Map showing the location of the Noel Kempff Mercado National Park, Bolivia.

Research was based at Lago Caiman (13°36'S, 60°55'W), a large oxbow lake at the base of the northern tip of the Huanchaca escarpment, and approximately 21 km upstream from an international tourist centre "Flor de Oro". A 400 ha study plot (2 x 2 km) with a grid system of trails spaced every 100 m was set up approximately 3.5 km from camp. Subsequently, trails were cut to include a further *c.*100 ha to cover parts of the focal spider monkey community range not encompassed by the 400-ha grid. The Lago Caiman study plot contained a number of structurally and floristically distinct habitats: tall forest, low vine forest, *sartenejal* or swamp forest, piedmont forest and cerrado forest (Wallace, 1998).