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## 8

## Sakis, Uakaris, and Titi Monkeys

## Behavioral Diversity in a Radiation of Primate Seed Predators

Marilyn A. Norconk

## INTRODUCTION

The pitheciines are a cohesive group of platyrrhines phylogenetically and ecologically but exhibit a range of variation in group size and social dynamics. At one end of the continuum, titi monkeys (*Callicebus* spp.) form small, cohesive, pair-bonded groups that in many ways represent the “classic monogamous” pattern (Fuentes 1999, van Schaik and Kappeler 2003). Pairs are generally territorial, adults are monomorphic in body size and color, adults exhibit social and physiological mechanisms that promote and reinforce attachment between mates, and males are strongly paternalistic (Mason 1968, 1971; Fragaszy et al. 1982; Kinzey 1981;

Menzel 1986; Mendoza and Mason 1986a,b; Mason and Mendoza 1998; Schradin et al. 2003).

Bearded sakis (*Chiropotes* spp.) and uakaris (*Cacajao* spp.) are at the opposite end of the continuum from titi monkeys. They form large, more loosely structured groups that may fission into smaller feeding parties (Ayres 1986; Norconk and Kinzey 1994; Kinzey and Cunningham 1994; Defler 1999, 2003a). Groups travel through large home ranges and day ranges as long as those of any platyrrhine (Ayres 1981, 1986; Norconk and Kinzey 1994; Aquino 1998; Boubli 1999; Defler 1999; Peetz 2001; Barnett et al. 2002). Males do not take an active part in infant care, and there is little sexual dimorphism in body mass (Ford 1994) and



minimal difference in pelage color (for uakaris, Hershkovitz 1987a). Uakari males do exhibit sex-specific traits (enlarged frontal and parietal areas, Fontaine 1981), but sex-specific cues in bearded sakis are minimal. Both male and female bearded sakis exhibit well-developed beards upon sexual maturity and colorful, relatively large external genitalia (pink scrotum and enlarged, pink vaginal lips) (van Roosmalen et al. 1981, Peetz 2001).

Members of the genus *Pithecia* are intermediate between titis and bearded sakis/uakaris. Groups are usually reported as being small (Table 8.1), and many, but not all, conform to the "two-adult group" suggested by Fuentes (1999). White-faced sakis (*Pithecia pithecia*) exhibit aggressive intergroup behavior both in the wild and in captivity (Homburg 1997, Savage et al. 1992, Shideler et al. 1994, Norconk et al. 2003). Mothers are primary care-givers (Brush and Norconk 1999), but adult male interest increases as infants mature; and adult males have been observed to play and share food with older infants (Buzzell and Brush 2000). Ryan (1995) reported that white-faced saki males carried infants, but Homburg (1997) did not find that to be the case. *Pithecia* adult males vary from subtle sexual dichromatism in the western (Amazonian) species to striking pelage differences in the eastern (Guiana Shield) *P. pithecia* ssp. (Hershkovitz 1987b, Gerald 2003). Small group size, small body mass, and territorial behavior ally *Pithecia* with *Callicebus*, whereas diet and dental anatomy, relatively low level of male infant care, and bushy tails ally them with *Chiropotes* and *Cacajao*.

## SYSTEMATICS AND GEOGRAPHIC DISTRIBUTION OF THE PITHECIINES

### *Callicebus* (Titis)

In the process of preparing the second volume of *Living New World Monkeys (Platyrrhini)*, Hershkovitz wrote six taxonomic reviews of nonprehensile-tailed platyrrhines including the four genera reviewed here (Hershkovitz 1985, 1987a,b, 1990). Of the four genera of the Pitheciinae, *Callicebus* is the largest and the most complex group. Ten taxa distributed in two species were recognized in an earlier review (Hershkovitz 1963), but in 1990, after examining close to 1,200 specimens, he raised the number of taxa in the genus *Callicebus* to 25, which he distributed into 13 species (Hershkovitz 1990). Van Roosmalen et al. (2002) reexamined the genus, named two new species, raised all subspecific taxa to species level, and divided the genus into five groups—for a total of 28 species. Thus, *Callicebus* has become the second most speciose genus of platyrrhines after *Saguinus*.

Titi monkey species are largely distinguished by pelage color, small differences in body size (Table 8.2), and chromosome number ( $2n = 20$  in *Callicebus torquatus*, 46 in *C. cupreus*, 48 in *C. brunneus* and *C. moloch*, and 50 in *C. dubius donacophilus*) (Hershkovitz 1990: Table 12). Molecular studies place *Callicebus* (as represented by *C.*

*torquatus* and *C. moloch*) as the sister group of the sakis/uakaris, supporting the view that the four genera represent a single clade (Schneider and Rosenberger 1996; but also see Ford 1986, Kay 1990, Marroig and Cheverud 2001).

*Callicebus* species groups are distributed throughout the western and southern Amazon Basin (*cupreus*, *donacophilus* *moloch* groups) and southern Orinoco River Basin (*torquatus* group), with a disjunct distribution between the Atlantic coastal forests of southeastern Brazil (*personatus* group) and central Bolivia (Ferrari et al. 2000, van Roosmalen et al. 2002 and distribution maps therein). They are absent from the northern Guiana Shield forests. Amazonian and Orinoco Basin titis are sympatric with one or more species of the larger pitheciines (see below).

Some species of titis, as well as uakaris, have been called "habitat specialists." Kinzey and Gentry (1979) proposed that *C. torquatus* was a white-sand specialist in Peru, but this hypothesis was reviewed and rejected by Defler, working in Colombia. Defler (1994, 2003b) found that two species, *C. cupreus* (*moloch*) and *C. torquatus*, were broadly sympatric in Colombia. Each exhibited habitat preferences, the former in low forests along streams and the latter in tall, well-stratified forests; but neither was restricted to these habitats. This view conforms with the recent review of *Callicebus* spp. by van Roosmalen et al. (2002). They suggest that *moloch* and *cupreus* groups are tolerant of habitat disturbance, due to both human activity and seasonal flooding. These two groups are comprised of species that are ecologically very similar and allopatric, but both species are broadly sympatric with the *C. torquatus* group in the sense suggested by Defler above (van Roosmalen et al. 2002). *C. donacophilus* may express a preference for grassland habitats in the state of Rondônia, Brazil (Ferrari et al. 2000).

### *Pithecia* (Sakis)

*Pithecia* spp., like *Callicebus*, have a broad geographic distribution and occupy a range of habitats from tropical wet to tropical dry forests throughout the Amazon Basin and north into the Guianas and eastern Venezuela (approximately to 9° N to 14° S latitudes; see Table 8.1). Hershkovitz (1987b) revised the systematics of *Pithecia* and divided them into two groups based on geographic distribution: a Guianan group (two taxa) and an Amazonian group (six taxa). The distinction between these groups is partly based on pelage color. A recent study of cranial morphology advocates raising all members of the Amazonian (Monacha) group to species status and leaving the Guianan (*Pithecia*) group as subspecies (Marroig and Cheverud 2004).

Guianan sakis (white-faced and pale-faced sakis) found north of the Amazon River and ranging into the Guianas are strongly sexually dichromatic: male body pelage is entirely black with a white or yellowish face; females are gray-brown with white or off-white facial markings above the brow and stripes on the side of the face. Amazonian males found south of the Amazon River (Brazil) and in the western Amazon



Table 8.1 Group Size and Composition and Use of Space by the Pitheciines

SPECIES <sup>1</sup>	GROUP SIZE (N)	GROUP SIZE, RANGE (N)	ADULT MALES	ADULT FEMALES	JUVENILES + SUBADULTS	INFANTS	HOME RANGE SIZE (HA)	DAY RANGE (KM)	POPULATION DENSITY (INDIVIDUALS/KM <sup>2</sup> ) OR INDIVIDUAL SIGHTING RATE (SR)/10 KM	SOURCE
<i>Calliobus brunneus</i> , Peru (c. 11°S) ST		2-5 (6)	1(-2?)	1	0-3		1.4			Ferrari et al. 2000, Lawrence 2003
<i>C. brunneus</i> , Bolivia (10°35'S to 11°31'S) C	3	1-5 (39)								Buchanan-Smith et al. 2000
<i>C. brunneus</i> , Brazil (10°-12°S) C	2.25 ± 0.97 (118 sightings)	max = 5								Ferrari et al. 2000
<i>C. caligatus</i> , Brazil (c. 10°S) C	2.20 ± 0.84 (5 sightings)	max = 4								Ferrari et al. 2000
<i>C. cinerascens</i> , Brazil (c. 12°S) C	1.67 ± 0.33 (3 sightings)	max = 2								Ferrari et al. 2000
<i>C. cupreus</i> , Peru (5°35'S) C	3.0-3.73	2-7 (18)							14.6	Bennett et al. 2001
<i>C. donacophilus</i> , Brazil (c. 13°S) C	2.0 ± 1.0	max = 3								Ferrari et al. 2000
<i>C. moloch</i> , Brazil (c. 12°S) C	2.47 ± 0.92 (15 sightings)	max = 4								Ferrari et al. 2000
<i>C. moloch</i> , Peru (11°52'S) LT	4.1 (2 sightings)	2-5 (2)	1	1	1-2	0-1	6-8	0.55 ± 0.1 and 0.67 ± 0.2	20-26/km <sup>2</sup>	Wright 1984, 1985, 1986
<i>C. moloch</i> , Peru (11°52'S) LT	4.0	2-7					11.5 (6-18)			Bossuyt 2002
<i>C. ornatus</i> , Colombia (c. 4°N) ST	3.2 (9)	2-4 (9)	1	1	0-1	0-1	4.4 (3.2-5.1)	0.57 (0.3-0.87)		Mason 1968
<i>C. ornatus</i> , Colombia (5°N) LT							3.5-14			Defler 1994
<i>C. personatus melanochir</i> , Brazil (15°18'S) LT		2-6 <sup>2</sup>	1	1	1-4		24	1.0		Müller 1996
<i>C. p. personatus</i> , Brazil (19°S) ST		6 (1)	1	1	3	1	4.7	0.69 ± 0.04 (0.52-0.80)		Kinzey 1981, Kinzey and Becker 1983
<i>C. p. personatus</i> , Brazil (c. 20°S) ST		3-5 (2)	1(-2?)	1(-2?)	1	1	10.7-12.3	1.0 ± 0.2 (0.8-1.3)		Price and Piedade 2001
<i>C. torquatus torquatus</i> , Peru (4°S) LT		3-5 <sup>2</sup>	1	1	1-2	1	29 (4-30)	0.8 ± 0.04 (0.5-1.4)	16	Kinzey 1978, 1981
<i>C. t. lugens</i> , Colombia (1°5.55'S) RC	4.8 (10)	3-5 (10)	1	1	0-1	1	14.2 (9-22)		6.08 (8 groups)	Defler 1983, 2003a
<i>Cocajao calvus calvus</i> , Brazil (3°22'N) LT		30-48 (3)	16	16	13	3	500-550	2.5-5.0	7-8	Ayres 1986, 1989
<i>C. c. ucayalii</i> , Peru (4°23'S and 4°30'S) ST	41.9 ± 16.7 (21) <sup>3</sup>	8-70								Aquino 1998, Aquino and Encarnación 1999
<i>C. c. rubicundus</i> , Peru (5°35'S) C	15.8-33.1	2-55 (18)							7.44 and 25.78	Bennett et al. 2001
<i>C. melanocephalus melanocephalus</i> , Brazil (00°24'N) LT		c. 70						4.4		Boubli 1999
<i>C. m. ouakary</i> , Colombia (1°5.55'S) RC	20-30	1- >108							4.15 overall, 12.0 in <i>igapó</i> habitat	Defler 2001
<i>Chirapates albinus</i> , Brazil (10°10'S) LT		19-26 (4)	8	9	8		250-350	2.5-3.5	10-11	Ayres 1981, 1989
<i>C. albinus</i> , Brazil (9-13°S) C	4.2 ± 3.1 (7) <sup>4</sup>								1.6-2.5 (SR)	Ferrari et al. 1999

Table 8.1 (cont'd)

SPECIES <sup>1</sup>	GROUP SIZE (N)	GROUP SIZE, RANGE (N)	ADULT MALES	ADULT FEMALES	JUVENILES + SUBADULTS	INFANTS	HOME RANGE SIZE (HA)	DAY RANGE (KM)	POPULATION DENSITY (INDIVIDUALS/KM <sup>2</sup> ) OR INDIVIDUAL SIGHTING RATE (SR)/10 KM	SOURCE
<i>C. satanas chiropotes</i> , Suriname (4°41'N) and Brazil (2°N) LT		8-27+ (4)	8	9	5	2-3	200-250	2.5		van Roosmalen et al. 1981, Ayres 1981
<i>C. s. chiropotes</i> , Suriname (4°41'N) ST	9 and 13 (2)							3.2 ± 1.1		Norconk and Kinzey 1994
<i>C. s. chiropotes</i> , Venezuela (7°21'N) LT		15-22 <sup>2</sup> (1)	1-2	8-10	3-5	1-5	180	1.6 (0.5-2.7)		Norconk 1996, Peetz 2001
<i>C. s. chiropotes</i> , Suriname (5°01'N) C	32.7 (3)	22-44 (3)							37.4 (SR)	Norconk et al. 2003
<i>C. satanas</i> , Brazil (multiple sites, 1-5°S) C									1.8-10.08, 0.3 (SR)	Ferrari and Lopes 1996
<i>Pithecia aequatorialis</i> , Peru (2°S) C		1-7 (4)								Heymann et al. 2002
<i>P. albicans</i> , Brazil (4°51'S) RC	4.6 ± 1.5 (5)	3-7					172.4 (147-204)		4.1	Peres 1993
<i>P. hirsuta</i> , Peru (c. 5°S) RC	3.8	2-8	1-3	1-2			24.9 (9.7-42)		12.8	Soini 1986
<i>P. irrorata</i> , Brazil (9°-13°S) C	2.68 ± 1.38								1.3 (SR)	Ferrari et al. 1999
<i>P. irrorata</i> , Bolivia (10°35'S to 11°24'S) C	3.5	2-5 (6)								Buchanan-Smith et al. 2000
<i>P. monachus</i> , Peru (5°35'S) C	3.75	2-5 (16)							9-17.2	Bennett et al. 2000
<i>P. pithecia chrysocephala</i> , Brazil (2°25'S) LT	6 (1)	4-7 <sup>2</sup>	1	1-3	0-2	0-2				Setz and Gaspar 1997, Gilbert and Setz 2001
<i>P. p. chrysocephala</i> , Brazil (c. 2°S) ST	2.6 ± 0.5	2-3	0-2	0-2	0-1					Oliveira et al. 1988
<i>P. p. pithecia</i> , French Guiana (4°N) LT	2.8 ± 1.0 (4)	1-4								Kessler 1998
<i>P. pithecia</i> Guyana (various) C	4.8 ± 2.4 (21)	2-12	2.0	1.8	1.0 (m) 1.3 (f)	1.0				Lehman et al. 2001
<i>P. p. pithecia</i> , Guyana (various) C	3.3 ± 1.7 (10)	1-5								Muckenhirn et al. 1975
<i>P. p. pithecia</i> , Suriname (4°41'N) RC	2.7 ± 0.8	9	1-2	1	0-1					Mittermeier 1977
<i>P. p. pithecia</i> , Suriname (5°01'N) C	3.7 (10)	2-6	1-2	1-3	1		10.3		14.1 (SR)	Norconk et al. 2003
<i>P. p. pithecia</i> , French Guiana (5°04'N) ST	2.3 (35)	1-5						1.88	0.64	Vie et al. 2001
<i>P. p. pithecia</i> , Venezuela (7°21'N) LT	9	5-9	3	2	2	2	15 <sup>5</sup>			Homburg 1997
<i>P. p. pithecia</i> , Venezuela (7°21'N) LT	6.9 ± 1.4 (1) <sup>2</sup>	5-9	1-4	2-3	0-2 (m) 0-2 (f)	0-2	12.8 <sup>5</sup>	1.5		Norconk, in press

<sup>1</sup> In addition to species name, data in column one include country of study, latitude, and study length. These data are not repeated for Tables 8.2 and 8.3. C, census; RC, repeated census; ST, short term (<1 year); LT, long term (≥1 year).

<sup>2</sup> Range = the change in group size of one group.

<sup>3</sup> Lower number of range estimates used to calculate mean ± standard deviation. The count (100-120) of multiple groups was excluded.

<sup>4</sup> An average of mean group sizes is reported (n = 7 locations).

<sup>5</sup> Island population.

Table 8.2 Social and Reproductive Characteristics of the Pitheciines

SPECIES	MALE BODY MASS (G)	FEMALE BODY MASS (G)	GROUP SEX RATIO	AGE AT SEXUAL MATURITY (MONTHS)/ INTERBIRTH INTERVAL (MONTHS)	BIRTH PEAK (MONTHS) AND SEASON (WET OR DRY)	PATERNAL CARE	TERRITORIAL INTERACTIONS WITH CONSPECIFIC GROUPS	VOCALIZATIONS	SOURCE
<i>Callicebus brunneus</i>				c. 36/12		Males carry, share food, and play with infants	7 encounters in 15 months of observation (♀♀ participated in 2:7)	90% calls before 0900 (calls on 15 mornings a month)	Wright 1985, 1986
<i>C. ornatus</i>	1,178	1,163	1.0				Calling, chasing, piloerection, tail lashing, chest rubbing (5%–7% HR overlap). Rate = 1.67/day	Regular dawn calls and during ITEs	Mason 1968, Hershkovitz 1990
<i>C. discolor</i>	935	1,075		44.4 ± 15.6 /11.8	Winter: Dec–Mar (Davis, CA)				Hershkovitz 1990, Valeggia et al. 1999
<i>C. moloch</i>	1,016	877							Hershkovitz 1990
<i>C. ornatus</i>	845	850	1.0		Nov–March	Males carry infants			Mason 1968, Hershkovitz 1990
<i>C. personatus</i>	1,270	1,378			Sept–Oct (dry)		Vocal responses on 3:6 occasions (no other groups in forest patch)	6:16 mornings, dawn calls given in sleeping trees	Hershkovitz 1990, Kinzey and Becker 1983
<i>C. p. personatus</i>							Rare: vocalizations only; no chasing, physical contact, or threat displays	97% before 1,000, not daily	Price and Piedade 2001
<i>C. torquatus torquatus</i>	1,110	1,310		c. 36	Nov–March	Males carry infants	Vocalizations and movement away from intruders (playbacks), occasional active encounters (10% overlap of HR)	Solo male and duets, from sleeping trees	Kinzey 1981, Hershkovitz 1990, Kinzey and Robinson 1983, Easley and Kinzey 1986
<i>C. t. lugens</i>					Jan (dry)		Not daily, duetting 10–20 m apart from stable position		Defler 1983
<i>Cacajao calvus</i>	3,450	2,880	1.20		Oct–Nov (dry)				Ayres 1986
<i>Chiropotes albinus</i>	3,170	2,520	1.26						Ayres 1981, 1989
<i>C. satanas chiropotes</i>	2,880	2,660	1.08						Ayres 1981
<i>C. s. chiropotes</i>					wet season				van Roosmalen et al. 1981
<i>C. s. chiropotes</i>				c. 36/24+	Dec–April (late wet to dry)		Only one group in forest patch		Peetz 2001
<i>Pithecia albicans</i>	3,000								Peres 1993
<i>P. irrorata</i>	2,010 (2,920)	1,875 (1,980–2,160)							Hershkovitz 1987b, Ford 1994
<i>P. hirsuta</i>				? / 24–36	Sept–Dec (late dry to early wet)		Rare		Soini 1986
<i>P. monachus</i>	2,795 (2,500–3,100)	1,900 (1,300–2,000)							Hershkovitz 1987b, Ford 1994
<i>P. pithecia</i>	1,732 (1,380–1,866)	1,515 (1,347–1,875)		Regular cycles (birth)/23.2 (15–34)	Nov–April (dry)	Play starting c. 4 months of age	Calling (roaring), chasing, piloerection, neck rubbing, urine marking. Rate: 9/100 hr	During travel and ITEs	Hershkovitz 1987b, Ford 1994, Norconk in press
<i>P. pithecia</i>						Play and share food with older infants	Aggressive toward same-sex intruders		Shideler et al. 1994, Savage et al. 1992
<i>P. p. chrysocephala</i>							Neck rubbing unrelated to territorial behavior		Setz and Gaspar 1997

HR, home range; ITE, inter-troop encounters.



Basin (Colombia, Ecuador, Peru) exhibit a range of variation in facial color but are more subtly marked than Guianan males. The range of variation may have taxonomic significance (L. Marsh personal communication, A. Rylands personal communication), but there is not yet sufficient evidence to make such an assessment. Females of all *Pithecia* spp. are very similar in appearance (Hershkovitz 1987b).

According to Ford (1994), sexual dimorphism in body mass ranges from 1.1 to 1.4 for three species of *Pithecia* sakis (see Table 8.2). *P. albicans* nearly bridges the body mass gap between *Pithecia* and larger sakis/uakaris: *Chiropotes/Cacajao*. Peres' (1993) research on *P. albicans* in central Amazonia suggests that relatively larger body size compared with other *Pithecia* spp., in addition to a preference for higher canopy travel and larger home ranges, may reflect competitive release of *P. albicans* in the absence of both *Cacajao* and *Chiropotes*.

### *Chiropotes* (Bearded Sakis)

Bearded sakis (*Chiropotes* spp.) are found primarily in upland, nonflooded habitats in eastern Amazonia, both north and south of the Amazon River (Hershkovitz 1985, Walker 1996, Auricchio 1995). In the Guianas, they are absent from the region west of the Essequibo River in Guyana and their presence in Venezuela may have been due to their ability to follow the right bank of the Orinoco River from Brazil into southern Venezuela (state of Amazonas) and then east into the state of Bolívar. Their present eastern boundary in Venezuela appears to be the left bank of the Caroní River (Norconk et al. 1996). In Brazil, they range north and south of the Amazon, east of Rio Madeira and throughout eastern Amazonia (66° to 44° W latitude) (Ferrari and Lopes 1996 and distribution maps therein). The Rio Tocantins provides a boundary between two subspecies of *Chiropotes satanas*, *Ch. s. satanas* and *Ch. s. utahicki*.

It is unclear why bearded sakis are absent from western Guyana and why their distribution is spotty in French Guiana. They are not found at the Nouragues Research Station in French Guiana (Bongers et al. 2001) despite geological similarities to sites in Suriname and Guyana and high species diversity of one of their most important plant food families, the Lecythidaceae (Mori 1989). de Granville's (1982) description of the forests of southern French Guiana as xeric and scrubby may constitute a barrier to the northern migration of bearded sakis from Brazil. If vegetation or riverine barriers do exist for *Chiropotes*, they have not limited *Pithecia* dispersal into either Guyana or French Guiana. Having a wider tolerance for seasonally dry habitats, *P. pithecia* is apparently broadly distributed across the entire region.

Hershkovitz (1985) reviewed the systematics of *Chiropotes*, dividing the genus into two species, *C. satanas* (with three subspecies) and *C. albinasus*, but the group was reevaluated recently by Bonvicino et al. (2003). Based on pelage coloration and karyotypic analysis, they suggested that the most westerly group could be a different species

and recommended raising the present subspecies to species status. If accepted, this would increase the number of *Chiropotes* species to five (Bonvicino et al. 2003) and perhaps more if the Guianan bearded sakis (from Venezuela and the Guianas) are included in future genetic analyses.

### *Cacajao* (Uakaris)

Hershkovitz (1987a) summarized data from collection localities for uakaris in the Orinoco and western Amazon Basins, ranging from southern Venezuela and western Brazil to eastern Colombia and Peru. He designated two species, black-headed uakaris (*C. melanocephalus*) with two subspecies and bare-headed uakaris (*C. calvus*) with three subspecies. *Chiropotes* and *Cacajao* are generally found to be allopatric, with *Cacajao* inhabiting the western Amazon Basin and *Chiropotes* inhabiting the eastern Amazon Basin (Hershkovitz 1985, 1987a; Auricchio 1995 and distribution maps therein). A permeable species boundary apparently exists on the eastern edge of Pico de Neblina National Park, Brazil (c. 65° W latitude), where Boubli (2002) found a few *Chiropotes* individuals in an area also occupied by *Cacajao melanocephalus*.

Uakaris appear to range widely on a daily and seasonal basis but particularly inhabit areas that flood seasonally along white-water rivers (*várzea*) and black-water rivers (*igapó*). These habitats are flooded up to 9 months of the year to a depth of 6–20 m (Ferreira and Prance 1998) and support fewer primate species year-round than terra firme forests occupied by bearded sakis. Ayres et al. (1999) found that both uakaris and squirrel monkeys were endemic to the *igapó* habitats of the Mamirauá Reserve in central Amazonia but only uakaris traveled through the entire extent of the reserve, moving deeply into flooded forest.

Low concentrations of suspended nutrients and a low pH of black-water rivers result in relatively lower plant species diversity in *igapó*, although plant diversity is still much higher in flooded tropical forests than in temperate forests (Junk 1989). Plant strategies related to growth and reproduction differ in *várzea* and *igapó* forests. Parolin (2000, 2001) found that habitats flooded by white-water rivers originating from the Andes (*várzea*) have rich soils due to a high load of suspended sediments. Selection for fast-growing stems allows young plants to reach sufficient height and to survive seasonal floods. Rapid stem growth is replaced by high maternal investment in large seeds in the habitats drained by black-water streams (*igapó*) (Parolin 2000, 2001). It is not yet understood how these differences in plant growth rates and maternal investment might translate into habitat and dietary differences among populations of uakaris.

*Várzea* and *igapó* habitats may provide reliable resources for primate seed predators with few competitors, but long day ranges, large home ranges, and reports of low population densities of uakaris suggest that something about these resources is limiting. Population density estimates of bearded sakis are also relatively low. Stevenson (2001)



found that fruit production (as estimated by fruit traps) did not predict either pitheciine biomass or number of species found at 30 neotropical field sites (he excluded *Callicebus* in this analysis). Indeed, “the most striking result [of the study] was the association between the abundance of pitheciine species and *Eschweilera* trees” (Stevenson 2001:172). This observation accords well with research on the biogeography of the family Lecythidaceae. Mori (1989) suggested that many Lecythidaceae species had their origin in the ancient Guiana Shield forests and have recently migrated into the alluvial habitats of the Amazon Basin. *Eschweilera* and other Lecythidaceae genera are now abundant in *várzea* forests, with *E. turbinata* documented as the most abundant tree species by Ayres (1986). The geographic distribution of *Cacajao* and possibly *Chiropotes* may be more dependent on and limited by seed availability of specific plant families than either *Pithecia* or *Callicebus*.

## PHYSICAL CHARACTERISTICS OF THE PITHECIINES

Pitheciines (including *Callicebus*) are small- to medium-sized platyrrhines, ranging in body size from about 850 g to 3,500 g. Titis are the smallest-bodied of the pitheciines, ranging in size from approximately 800 to 1,300 g (see Table 8.2). The sexual dimorphism ratio in body mass ranges 0.85–1.16. Adult females are heavier than males in four of six species for which body mass data exist, although Hershkovitz (1990:37) remarked that there were “no appreciable morphological differences between the sexes at comparable ages.” In the other three genera, males are slightly larger than females (1.08–1.26 in *Chiropotes* and *Cacajao*,  $n = 3$  species, and 1.07–1.47 in *Pithecia*,  $n = 3$  species). Sexual dichromatism was discussed above for *Pithecia* spp.; is absent in *Callicebus* spp., *Chiropotes* spp., and *Cacajao calvus*; but is expressed to varying degrees in *Cacajao melanocephalus* (Hershkovitz 1987b, Gerald 2003).

Similarities in dental anatomy unite the sakis/uakaris and separate them from titis. Titis lack the highly derived incisor/canine complex of the larger pitheciines but exhibit (with *Aotus*) tall incisors and enlarged incisor roots that suggest heavy use of anterior dentition during food acquisition or processing (Kinzey 1992).

Dental adaptations in the sakis/uakaris are strongly correlated with a high incidence of seed predation (see Table 8.3). Kinzey and Norconk (1990) described them as “sclerocarpic” foragers, specialists in opening mechanically protected (i.e., hard and/or thick-husked) fruit. The protected characteristics of fruit exocarp contrasts with the relatively soft seeds, particularly if they are young seeds. Mechanically protected fruits are breached using robust, widely flaring canines; but the canines of *P. pithecia* are also used very precisely to open small, multiloculed fruit, like many species of the Euphorbiaceae, to extract tiny seeds (M. A. Norconk, personal observation). Procumbent incisors are used to scrape adherent mesocarp from the inside of fruit husks.

Compared with anterior dentition, saki/uakari molars appear to be unspecialized—low-crowned with thin enamel. However, two specializations in the enamel have been noted. First, Kinzey (1992) described the well-crenulated enamel of molars, particularly in *Chiropotes* and *Cacajao*, and proposed that the uneven surface of the tooth facilitated positioning seeds during mastication. Second, Martin et al. (2003) examined the microstructure of saki/uakari enamel and found it to be infused with Hunter-Schreger bands, which enable the teeth to resist the propagation of cracks. This finding, they believe, fits well with a diet that requires mastication of “tough, pliable, and generally soft seeds, rather than hard food items” (Martin et al. 2003:360–361). The lack of crack-resistant properties in the enamel of *Callicebus* correlates with the lower proportion of seeds in their diet (Martin et al. 2003).

Both bearded sakis and uakaris are above-branch quadrupeds (pronograde clamberers) and leapers, dropping between tree crowns (Walker 1996). White-faced sakis are vertical clingers and leapers and above-branch quadrupeds. Body proportions and use of the tail as a rudder to “direct turning of the body in the mid-air phase” of vertical clinging and leaping distinguish *Pithecia* from bearded sakis and uakaris (Walker 1996:346).

All sakis/uakaris have bushy tails—long and bushy in *Pithecia* and *Chiropotes*, short and bushy in *Cacajao*. Despite the reduced tail length in uakaris, tail wagging occurs in both bearded sakis and uakaris (Fontaine 1981, Fernandes 1993, Defler 2003a). Tail wagging, whether below branch or arched over the head (in bearded sakis) and accompanied by vocalizations, occurs in a variety of contexts from mild to severe agitation (e.g., predator sightings and in response to alarm calls, reunion of group members, and group reorganization after rest or feeding periods) (Fernandes 1993, Walker and Ayres 1996, Peetz 2001, Defler 2003a). Tail wagging is absent in *Pithecia* and titi monkeys, but tail twining among group members is common in titis. Rather than providing a medium-distance visual cue, as it may in bearded sakis and uakaris, titi monkey tail twining provides a tactile cue “which, it seems reasonable to suppose, contribute[s] to the formation and maintenance of the bond between male and female” (Mason 1974:7).

Kinzey (1986:136) reviewed the available literature on scent marking in platyrrhines and observed that scent marking “plays a major role in regulating social behavior in the marmosets and tamarins, and almost all species of platyrrhines utilize specialized skin scent glands and/or urine for chemical communication.” To date, however, there is little information on the function of scent marking in pitheciines. White-faced sakis (*P. pithecia*) possess scent glands in the gular, sternal, and anogenital areas and at times combine scent marking with urine washing (Brumloop et al. 1994, Setz and Gaspar 1997, Gleason 1998). Adult males were scored more often than adult females in scent-marking activities by all of these observers. Gleason (1998) found that the frequency of scent marking peaked in an overlap



Table 8.3 Feeding Ecology of the Pitheciines<sup>1</sup>

SPECIES AND COUNTRY OF RESEARCH	FEEDING GROUP SIZE (RANGE)	% FEEDING					TOP PLANT FAMILIES	SOURCE
		SEEDS	FLESHY FRUIT	FLOWERS	LEAVES	INSECTS		
<i>Callicebus brunneus</i> , Peru	Cohesive group				23–66, varies seasonally		Moraceae, Leguminosae, Annonaceae	Wright 1986
<i>C. personatus personatus</i> , Brazil	Entire group	21.9	54.7		17.2		Myrtaceae, Sapotaceae, Moraceae (51.4%)	Müller 1996
<i>C. p. personatus</i> , Brazil			81 <sup>3</sup>	1	18		Sapotaceae (41%)	Kinzey and Becker 1983
<i>C. torquatus torquatus</i> , Peru			71 <sup>3</sup>		4	20	Moraceae, Guttiferae, Leguminosae, Euphorbiaceae, Convolvulaceae, Palmae (52%)	Kinzey 1978, 1983
<i>C. t. lugens</i> , Colombia							Euphorbiaceae	Defler 1983, 2003
<i>Cacajao calvus calvus</i> , Brazil	8.95 (1–50), small subgroups	66.9	18.4		3.3	5.2	Lecythidaceae, Moraceae, Hippocrateaceae, Sapotaceae, Annonaceae (62.4%)	Ayres 1986, 1989; Walker and Ayres 1996
<i>C. c. ucayalii</i> , Peru		46.0	50.0				Sapotaceae, Leguminosae, Apocynaceae (38%)	Aquino 1998, Aquino and Encarnación 1999
<i>C. melanocephalus melanocephalus</i> , Brazil	Dispersed	67.0	28.8	5.0	4.0	2.0	Euphorbiaceae (24%), Caesalpinoidea, Fabaceae, Lecythidaceae, Sapotaceae	Boubli 1999
<i>C. m. ouakary</i> , Colombia	Fission–fusion						Lecythidaceae	Defler 1999, 2003
<i>Chiropotes albinus</i> , Brazil	22.5 ± 3.5	35.9	53.9	3.0	7.2 <sup>4</sup>		Palmae, Sapotaceae, Leguminosae, Caryocaraceae, Moraceae (54%)	Ayres 1981, 1989
<i>C. satanas chiropotes</i> , Brazil	2.88	63.3	9.3	11.4	16.1 <sup>4</sup>		Moraceae, Leguminosae, Lecythidaceae, Sapotaceae (62%)	Ayres 1981
<i>C. s. chiropotes</i> , Suriname	Fission–fusion (especially when fruit trees are within 100 m)	66.4	27.6	4.6				van Roosmalen et al. 1981
<i>C. s. chiropotes</i> , Venezuela <sup>2</sup>		50.7 (4–60)	0–52.0	0–8.1	0–1.5	1–21	Sapotaceae, Loranthaceae, Moraceae (76%)	Petz 2001
<i>C. s. chiropotes</i> , Venezuela <sup>2</sup>	Travel together, fission when in the vicinity of several feeding trees	74.8	21.6	0.4	0.2	0.5	Sapotaceae, Loranthaceae, Moraceae, Meliaceae (74.5%)	Norconk 1996, Kinzey and Norconk 1993
<i>Pithecia albicans</i> , Brazil	Often fragmenting	46.2	28.6	6.5	9.5	0.4	Sapotaceae (21%), Leguminosae (20%)	Peres 1993
<i>P. hirsuta</i> , Peru		38.0	55.0	3.0	4.0		Lecythidaceae, Leguminosae, Annonaceae	Soini 1986
<i>P. pithecia chrysocephala</i> , Brazil		26–31		15.9	4.0–18.4			Setz 1993
<i>P. p. pithecia</i> , Venezuela <sup>2</sup>		53.3	31.0	2.0	10.4	3.7	Connaraceae, Erythroxylaceae, Rubiaceae, Chrysobalanaceae (53.7)	Homburg 1997
<i>P. p. pithecia</i> , Venezuela <sup>2</sup>	Entire group	60.6	27.8	2.2	7.1	2.3	Connaraceae, Lecythidaceae, Loganiaceae, Leguminosae, Erythroxylaceae (57%)	Kinzey and Norconk 1993, Norconk 1996

<sup>1</sup> Percentage feeding on various resources was taken directly from sources; no attempt was made to total the “% feeding” resources to equal 100%.

<sup>2</sup> Studies at the same site, overlapped in time.

<sup>3</sup> “Fruit” did not specify seed eating.

<sup>4</sup> “Other” category included leaves, insects, bark.



zone between two groups, and most of his samples occurred while the sakis were traveling. Setz and Gaspar (1997) concluded that scent marking was related to sexual behavior, but there was only one group at their site, a forest fragment in central Amazonia. Neither Gleason (1998) nor Setz and Gaspar (1997) found sakis to scent mark while feeding.

In addition to scent marking branches, Gleason (personal communication) noted that adult males huddled, rubbed their chests against each other, and possibly exchanged scent just prior to some inter-troop encounters. Group huddles were seen only in a year in which the study group had four adult males, an unusual composition for most wild white-faced saki groups.

Bearded sakis do not scent mark branches, but they may exchange scent through body contact. Peetz (2001:146) observed "ritualized behavior patterns of hugging and lining up." The behaviors were not limited to adult males. Of 44 incidences of hugging, half involved four or more individuals. Peetz treated hugging and lining up as separate activities, but both involved body contact during which scent may have been exchanged. Titi monkeys also "line up," but they engage in lengthy periods of body contact during resting periods (see above), unlike bearded sakis whose contact periods are brief and active and often take on characteristics of a "reunion" (M. A. Norconk, personal observation).

## FEEDING ECOLOGY AND DIET

Fleshy fruit comprises the largest component of titi monkey diets, particularly fruit of the Moraceae, Leguminosae, and Sapotaceae families. Leaves are the second highest food category, but leaf composition of the diet ranges 4%–66% depending on the season and titi monkey species (Table 8.3). The *moloch* and *cupreus* groups of titis appear to have a higher proportion of leaves in the diet than the *torquatus* and *personatus* groups (Table 8.3). Insect eating represented 20% of the diet of *C. torquatus* in a study by Kinzey (1978, 1981).

Only a few studies have examined *Callicebus* diets in a long-term, comprehensive manner (Wright 1986, Müller 1996); but titis do not appear to ingest a high proportion of seeds (Table 8.3). In contrast, seeds are often found to comprise a third of saki/uakari diets, sometimes more than two-thirds (see Table 8.3). Sakis and uakaris frequently ingest unripe, dull-colored (green or brown) fruit that has a woody or well-protected exocarp (Ayres 1986, 1989; Peres 1993; Norconk et al. 1998; Boubli 1999). Mature seeds and fruit pulp are also eaten, but they usually make up a smaller proportion of the diet.

Leaves, flowers or nectar, insects, bark, pith, termite nests, and wasp nests are secondary resources for sakis and uakaris but may be important seasonally. Ayres (1989), Norconk (1996), and Boubli (1999) found that these secondary resources make up only about 10% of the annual diet; but Peetz (2001) found that insects made up over 20% of the diet of bearded sakis seasonally. B. Urbani (personal

communication) suggests that secondary resources provide an intermittent nutritional boost to the white-faced saki diet. *Polistes* spp. wasp nests, taken opportunistically whether or not the wasps had deserted the nest, were higher in crude protein (10.9% dry matter, DM) than most other resources ingested by white-faced sakis. Grasshoppers (*Tropidacris* spp.) had the highest crude protein value (58.4% DM) and were relatively high in lipids (8.0% DM). Nothing is known about the specific mineral requirements of wild sakis, but iron and manganese were found to be in significantly higher concentrations in termite nests than in fruit and leaves ingested by the sakis (B. Urbani, personal communication). Thus, incidental items are likely to provide important nutritional diversity to saki/uakari diets.

Venezuelan white-faced sakis ingest a diet rich in seeds, but they also ingest young leaves daily and insects and fleshy fruit seasonally (Norconk and Conklin-Brittain 2004). This combination of items provided an intake that was calculated, primarily from fruit, to be seasonally rich in lipids (11.4%–27.5% estimated DM basis), high in total dietary fiber (25.4%–40.8% DM), and seasonally low in both free simple sugars (4.0%–21.3% DM) and crude protein (4.0%–12.6% DM) (Norconk and Conklin-Brittain 2004).

Bearded sakis and uakaris may also have a high intake of and preference for lipid-rich seeds. Ayres (1986:191–192) found that lipid value was higher in large seeds than small seeds. Large seeds also had a significantly higher ratio of lipids plus protein content to condensed tannin plus acid detergent fiber content. This finding correlates well with the high proportion of large seeds found in *igapó* habitats, where plant maternal investment is high and compensates for poor nutrient availability in the soils of black-water river basins (Parolin 2001). Seed eating is similar to leaf eating with regard to dietary fiber intake so that (white-faced) sakis and uakaris may be forced to accept a trade-off between high lipids and high fiber as part of their seed-eating strategy (Ayres 1986, Norconk et al. 2002, Norconk and Conklin-Brittain 2004).

The major advantage of a diet rich in seeds may lie in the ability to reduce or shift the impact of seasonal fruit shortages relative to that experienced by other platyrrhine frugivores. For both bearded sakis and white-faced sakis inhabiting the tropical dry forests of Lago Guri, Venezuela, seeds represented more than 60% of the diet in the early and late dry seasons. Both species shifted to fleshy fruits in the late wet season, and their seed intake fell (Norconk 1996). The period of food shortage as measured by low food species diversity seems to occur at the end of the wet season and beginning of the dry season in Lago Guri. At this time, many seeds are small, still early in their maturation, and fleshy fruits have declined in abundance. Ayres (1986:206) provided support for this observation by noting that *Cacajao calvus* "seem to accumulate extensive fat tissues, comparable to that reported in *Saimiri*" at a time when other frugivorous primates have difficulty finding fleshy fruits in the white-water flooded forests of Lake Teiú, Brazil.



A second advantage of seed eating is the duration of availability of at least some seed species. Boubli (1999) and Norconk (1996) noted that uakaris and sakis, respectively, can gain access to seeds in well-protected fruits that have slowly maturing seeds. Third, these pitheciines have the dental and gnathic strength to break open large, woody young pods of the Bignoniaceae, a family of primarily wind-dispersed seeds, fruiting in the dry season. Winged seeds are largely ignored by other primate frugivores and as such may be an important fallback food for sakis (Norconk and Conklin-Brittain 2004).

## GROUP SIZE, USE OF SPACE, AND INTERGROUP RELATIONS

Titis and *Pithecia* sakis form small social groups, have relatively small home ranges, and often exhibit behaviors that are associated with defense of territories (Tables 8.1 and 8.2). Group sizes, ranging from two to seven individuals in titis, conform to the expectation of pair-bonded primates (see Table 8.1), but *Pithecia* groups are more variable. A number of censuses have reported *Pithecia* group sizes between two and five individuals, consistent with a pair-bonded primate (e.g., Ferrari et al. 2000, Buchanan-Smith et al. 2000, Bennett et al. 2001). However, Lehman et al.'s (2001) extensive survey in Guyana documented a wide range of variation in group size. They observed 21 groups, of which one had 12 individuals. Only five groups had the expected one adult male:one adult female ratio typical of pair-bonded primates, but slow dispersal of young adults may account for the "extra" adults in the group. Studies exceeding a year in length reported group sizes as high as nine individuals, with stable compositions of multiple males and multiple females (Peres 1993, Setz 1993, Norconk 1996); but the Setz and Norconk studies were in habitat fragments with limited dispersal opportunities. In the absence of genetic data on paternity and long-term studies in intact (nonfragmented) habitats, it is best to interpret *Pithecia* social groups as usually small but flexible and responsive to variables such as population density, food distribution, and perhaps sympatry with the two larger-bodied pitheciines, *Chiropotes* and *Cacajao* (see Ferrari et al. 1999).

Using playbacks, Robinson (1979) and Kinzey (1981, 1997) defined two distinctive patterns of home range use and defense by *Callicebus* spp. *C. (moloch) ornatus* gave early-morning calls regularly followed by intertroop encounters depending on the proximity of callers to their territorial boundary (Robinson 1979, Robinson et al. 1987). In contrast, a *C. torquatus* group moved away from playbacks of both adult males and male-female pairs using, what Kinzey and Robinson (1983) called, "proximity-dependent avoidance." *C. personatus* seems to be closer to the *C. torquatus* pattern of group dispersion (Ferrari et al. 2000), but other behavioral and spatial use differences may exist among these species to suggest that we have not

exhausted all of the habitat use strategies of species in this very widespread and diverse genus.

A few studies suggest that white-faced sakis in Venezuela and Suriname are also territorial (Norconk et al. 2003; M. A. Norconk personal observation), and Shidele et al. (1994) have reported aggressive interactions with same sex intruders among captive sakis. Territorial activities consist of behavior-specific vocalizations and chasing and are strikingly similar to Mason's (1968) description of behavior associated with territoriality in *C. ornatus* and Fernandez-Duque's (see Chapter 9) description of territoriality in *Aotus*.

*Chiropotes* and *Cacajao* live in relatively large groups and are as far-ranging as any platyrrhine. Daily travel distance appears to be driven by the density and dispersion of seed crops, and some authors have reported extensive group fissioning and wide variations in feeding group sizes seasonally (Ayres 1986, Defler 1999). Most authors report minimum estimates of home range instead of defining use of space in precise terms. Ayres (1986) estimated white uakari home ranges to be 500–550 ha, with daily path lengths up to 5 km. Path lengths averaged 4.4 km for black-headed uakaris in Brazil (Boubli 1999) and 2.5–4.0 km for bearded sakis in Suriname (Norconk and Kinzey 1994).

The difficulty of tracking fast-moving, widely ranging bearded saki and uakari groups, as well as the paucity of studies on captive groups, has resulted in little information on how *Chiropotes* and *Cacajao* groups are organized socially. Ayres (1981) suggested that the organization of bearded saki groups may be based on an underlying structure of multiple male-female units. This hypothesis might provide information on how groups fission during feeding and travel, but logistical difficulties have thus far precluded the ability to address the question. To my knowledge, there have been no studies of wild bearded sakis or uakaris with individually identified animals.

Defler (2003b) documented seasonal variation in group size for black-headed uakaris in Colombia, but Boubli (1999) found them to be more cohesive in Brazil. Van Roosmalen et al. (1988) and Norconk and Kinzey (1994) found that bearded sakis often fissioned when multiple feeding trees were within about 100 m, but they traveled cohesively between feeding sites. That view may have to be modified as recent work in Suriname suggests that there may be seasonal variation in group patterns for bearded sakis (M. A. Norconk personal observation) similar to what Defler (2003b) noted for uakaris.

To cautiously summarize the socioecology of pitheciines using available data from 9–15 studies (see Tables 8.1–8.3 for raw data), there is a strong positive correlation between group size and day range (Fig. 8.1:  $\tau = 0.66$ ,  $p < 0.01$  two-tailed,  $n = 14$ ) and between group mass and home range size (Fig. 8.2:  $\tau = 0.69$ ,  $p < 0.01$ ,  $n = 18$ ). Diet and home range size were not correlated, either in terms of the percentage of seeds in the diet (Fig. 8.3:  $\tau = 0.42$ ,  $p$  not significant,  $n = 9$ ) or as a percentage of all fruit resources in the diet (Fig. 8.4:



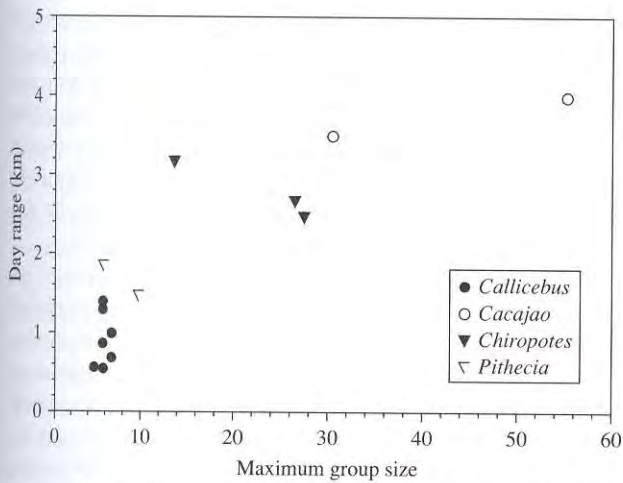


Figure 8.1 Maximum group size is plotted against estimated day range. The maximum group size was used since group sizes are underestimated for many of the pitheciine census samples. Home ranges are also estimates, particularly for the larger-bodied species. *Pithecia* and *Callicebus*, whose group size is smaller than 10 individuals, have smaller home ranges (<40 ha) than *Chiropotes* and *Cacajao* (except *P. albicans*). Data taken from Tables 8.1 and 8.2.

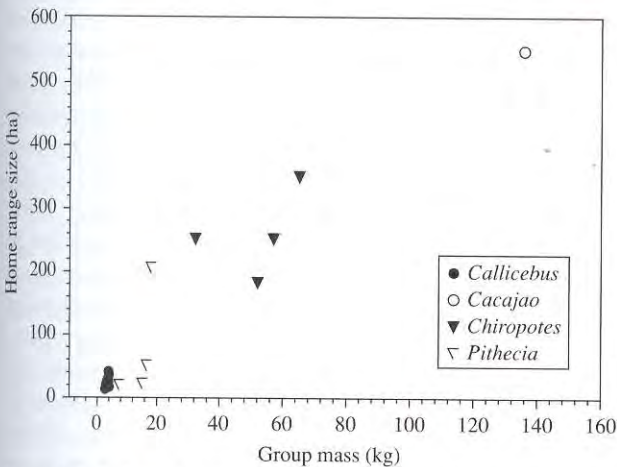


Figure 8.2 Estimated group mass is plotted against estimated home range size. Calculation of group mass: [(male body mass (kg) \*  $n$  males) + (female mass \*  $n$  females) + ( $n$  immatures \* (0.75) female body mass)]. *Pithecia* sakis are intermediate between *Callicebus* and the two larger-bodied sakis. Sample sizes are low for all taxa but particularly for *Cacajao*. The outlier for *Pithecia* is *P. albicans* (see Tables 8.1 and 8.2).

$\tau = 0.28$ ,  $p =$  not significant,  $n = 11$ ). The latter analysis is influenced by the striking reliance on fruit resources (>70%) by pitheciines.

## REPRODUCTION AND DEVELOPMENT

Pitheciine female reproductive physiology has been studied for the smaller members of the group: white-faced sakis (*P. pithecia*, Savage et al. 1992, Shideler et al. 1994) and titis (*C. cupreus*, Hoffman et al. 1995, Valeggia et al. 1999). White-faced sakis have a 16- to 17-day ovarian cycle, gestation of 150 days, and approximately 195 days of lacta-

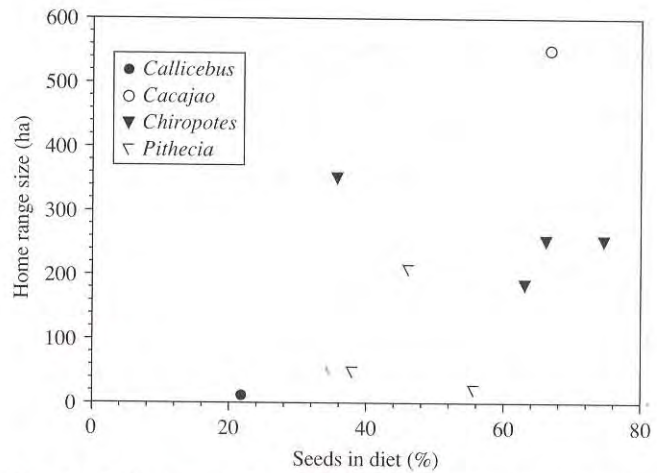


Figure 8.3 Percentage of seeds in diet is plotted against estimated home range size. Data on seed eating are available for only one species of *Callicebus* (*C. personatus*), but seed eating does not increase with larger home ranges for those populations with sufficient data.

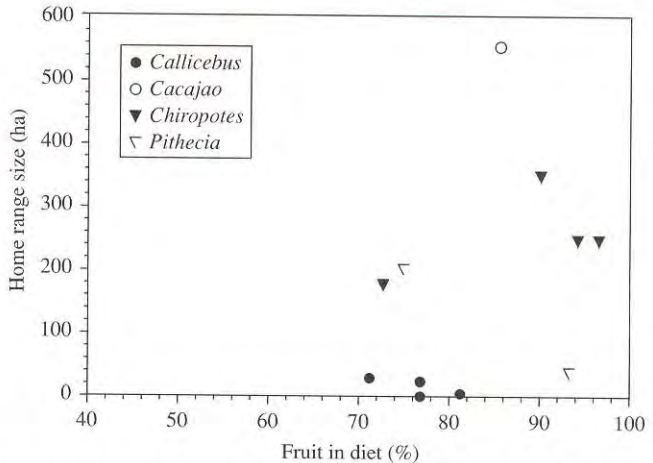


Figure 8.4 Percentage of fruit (including seeds) in diet is plotted against estimated home range size. All pitheciines have a total fruit intake of >70% of their diets.

tional amenorrhea. The interbirth interval in captivity was 15.1 months, and sexual maturity occurred at about 30 months. Interbirth intervals are longer in wild sakis ( $21.5 \pm 9$  months,  $n = 6$ ), and first birth occurred at the age of 5 years (M. A. Norconk and S. E. Shideler unpublished data; Norconk in press; see Table 8.2).

The length of titi monkey ovarian cycles is very similar to that of white-faced sakis (*C. cupreus*,  $17.2 \pm 1.5$  days), but gestation length and interbirth intervals were shorter ( $128.6 \pm 4.4$  days and 11.8 months, respectively) (Valeggia et al. 1999). Titi monkey females housed with an unfamiliar male had their first infants at the age of 3.7 years (range 2–6 years) (Valeggia et al. 1999).

Mason, Mendoza, and colleagues conducted a number of elegant studies on the behavior and physiology of filial attachment in *C. (molech) cupreus* (e.g., Mason 1971, 1974; Mendoza and Mason, 1986a,b; Mason and Mendoza 1998; Hennessy et al. 1995; Hoffman et al. 1995). They found that



titi monkey infants exhibit preferences for fathers (Mason and Mendoza 1998) and that separation from the father, but not the mother, elicited a strong cortisol response (Hoffman 1998). Male caretaking peaked in the second month and continued until the sixth month (Fragaszy et al. 1982).

In a series of experiments, Hoffman (1998) studied physiological and behavioral parameters in the interaction between nearly mature titi monkeys and their parents. His experimental studies on captive *C. cupreus* "dispersal" accord well with data collected by Bossuyt (2002) on wild *C. moloch*. Hoffman's data suggested that sons were more reticent to leave the family group than daughters, but both daughters and sons showed strong behavioral attachment to parents until they were 3.5–4 years of age (Hoffman 1998:92). Bossuyt (2002), working in Cocha Cashu, Peru, found that both daughters and sons dispersed from their natal groups between 3 and 4 years of age, that daughters tended to disperse earlier than sons, and that, in light of high juvenile mortality, parents may benefit from retaining subadults in the group as individuals that could provide "critical aid" to siblings. Existing data on dispersal patterns in titis appear to be similar to preliminary data on white-faced sakis: both sons and daughters appear to leave their natal group but do not do so until they are mature (at least 3 years of age). Like titis, white-faced sakis appear to retain affiliative relations within their natal group prior to dispersal (M. A. Norconk, personal observation).

Homburg (1997) documented developmental patterns for the first 5 months of life for wild white-faced sakis in Lago Guri, Venezuela. The mother was the only carrier for the first 8 weeks. In the third month, two other adult females carried the infant for 15–85 min once or twice a day (Homburg 1997:131). Distance between mother and infant increased in the fourth month, and solitary play was observed in the fifth month. Infants made brief contact with males, but no male infant carrying was observed (but see Ryan 1995). A wild white-faced saki infant was observed to spend about 50% of its time off the mother's back by the fifteenth week of life (Buzzell and Brush 2000). Captive infants showed an accelerated level of independence and were on the mother in only 3% of the samples at the end of the twelfth week of life. Carrying by other group members was seen during week 12 in the wild but was not seen in the captive sample (Buzzell and Brush 2000). Whereas white-faced saki infants become self-locomoting by their fourth month, both bearded saki and uakari infants were carried by the mother for at least 9 months (see below). Larger body mass may account for the slower developmental pattern in bearded sakis and uakaris, but longer daily travel paths for these species may also influence the duration of maternal carrying.

The transition to the white face and black body pelage characteristic of adult male white-faced sakis (*P. pithecia*) appears to follow a prolonged but variable developmental path. Some young males in Lago Guri, Venezuela, exhibited the dark body pelage of adult males within a few months, and others maintained the orange–brown agouti coloration

of females into their third year (M. A. Norconk, personal observation). Homburg (1997) estimated that body pelage changed at about 20 months of age but body hair was not entirely black until the third year. Development of the white facial mask appears to proceed at a variable rate with respect to changes in body pelage in Guianan sakis (M. A. Norconk, personal observation), but nothing is known about the development of pelage differences in Amazonian sakis.

Peetz (2001) provides the only information available on the development of wild bearded sakis, but Hick provided developmental data on captive sakis (cited in van Roosmalen et al. 1981). According to Peetz, bearded saki births peaked in the dry season (December to April); however, van Roosmalen et al. (1981) correlated the birth season with the beginning of the wet season in Suriname. Peetz (2001) estimated a minimum interbirth interval of 2 years, that infants were carried ventrally for the first 2 months of life and dorsally through the fifth month, and that they were still carried in the ninth month whenever mothers leapt between widely spaced tree crowns. Older juveniles traveled independently by age 10–13 months (Peetz 2001) but continued to suckle into the second year. Testes descended at about 3 years of age.

Peetz (2001) did not document any courtship behavior pre- or postcopulation. After copulation, both males and females resumed precopulation activities (Peetz 2001). Adult male care of infants is not as extensive in bearded sakis; it was limited to grooming and playful interactions between adult males and young bearded sakis (Peetz 2001).

Uakari developmental data, reported by Fontaine (1981) on a semi-free-ranging group, is remarkably similar to Peetz's description for bearded sakis. Suckling continued until 22 months of age, and mothers persisted in carrying 12-month-old infants across wide gaps between tree crowns (Fontaine 1981). Phenotypic changes from young uakari to adult began at about 2 years of age: "a darkly pigmented glandular field develops in the sternal area, alopecia of the scalp develops, and the general body pelage of the dorsal torso and lateral limb surfaces fills out to form a mantle" (Fontaine 1981:457). Sexually dimorphic traits develop slowly in red uakaris as they do in white-faced sakis. Infant red uakaris are born with only a trace of pink in the face, and color change begins gradually in the juvenile period (3–12 months). Over a period of 2 years, Fontaine (1981) observed young male uakaris to increase in body mass and musculature relative to females and to develop the characteristic paired muscle masses overlying the frontal and parietal areas of the skull. *P. pithecia* saki males complete the developmental process by about 3 years of age, when uakaris are just beginning it. Fontaine (1981) also noted that the developmental process in male red uakaris is remarkably plastic, as it appears to be in male white-faced sakis.

## CONCLUSIONS

I opened this chapter with the view that the pitheciines represent a closely related group of species arrayed along a



continuum of smaller to larger body mass, with group compositions ranging from pair-bonded and territorial to multimale and relatively nomadic. *Pithecia*, *Chiropotes*, and *Cacajao* are clearly a very cohesive group from the perspective of feeding adaptations. Body size aside, they share the same dental adaptations. *Pithecia*, the smallest of the three, may have a broader diet that includes leaves on a regular basis as well as fewer habitat restrictions. Tropical dry and savanna habitats probably limit the distribution of bearded sakis and uakaris but do not seem to be a barrier to *Pithecia* dispersal, particularly for *P. pithecia*, the white-faced sakis. This view is complicated by some diversity within the small radiation of *Pithecia* species, as suggested by Peres (1993) and Walker (1996). The smaller-bodied, vertical clinging and leaping white-faced sakis of the Guianas are well adapted to moving through low- to middle-canopy levels compared with the Amazonian sakis.

There also appears to be a size-related continuum among titi monkeys, with the smaller ones (*C. moloch*, *donacophilus*, *cupreus*) inhabiting small, well-defended territories using voice and movement toward territorial boundaries and *C. torquatus* and *C. personatus* using voice to announce their presence in a larger home range. *Callicebus* contrasts with the other three pitheciines in aspects of feeding ecology, but *Pithecia* is closer to *Callicebus* in aspects of body size, group size, and perhaps home range size.

The larger sakis (bearded sakis and uakaris) are very similar in diet and dentition, ranging patterns, group size, and slow developmental patterns. Their primary difference lies in habitat preferences: bearded sakis are found more often in nonflooded forests and uakaris, while not limited to flooded forests, use those habitats extensively.

One can make the case that, for most primates, more wild studies will improve the resolution with which we interpret their social behavior, but this is particularly true for the pitheciines. Long-term studies are rare even for *Callicebus*, even though wild studies began in the 1960s (Mason 1968). No long-term free-ranging studies have been conducted on *Pithecia*, and our understanding of social behavior in the bearded sakis and uakaris is hindered not only by the difficulty of studying social behavior in these relatively nomadic primates but also by the few opportunities to study them in captivity. We must begin to shift from the more easily gathered data on feeding ecology and develop methods to study behavioral mechanisms that serve to coordinate large groups of bearded sakis and uakaris, to explore ecological and social differences that may underlie the diversity of *Pithecia* populations, and to further investigate the seemingly cohesive pattern of behavior in the 28 species of *Callicebus*.

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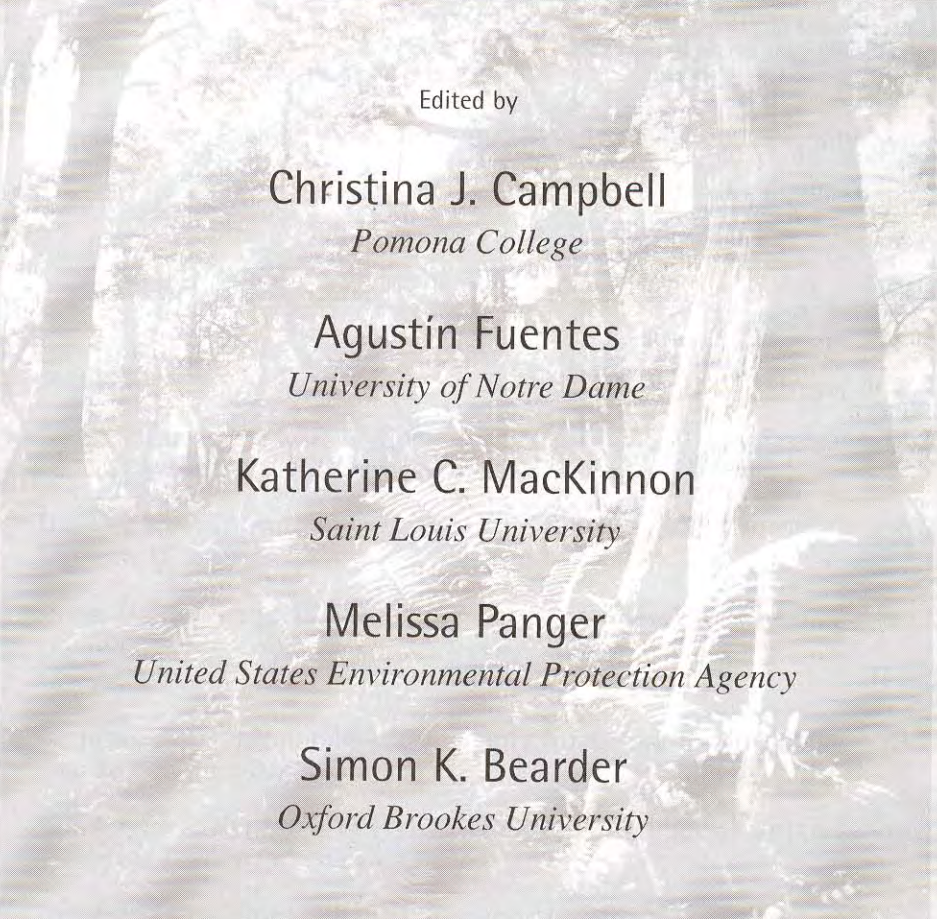


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# PRIMATES IN PERSPECTIVE



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