

group males also appears to be maintained through parallel dispersal. C. L. Mitchell (1994) reports that males form dispersal alliances whose composition often remains constant over multiple emigration events, and this may act to ensure the relatedness of males in the face of dispersal. These data show that, regardless of ecological pressures and female dispersal patterns, males in the genus appear to have evolved a mechanism for retaining residence with their kin, regardless of dispersal patterns. A recent meta-analysis of parallel dispersal by male nonhuman primates found that this behavior may have evolved in species where it is important for males to retain coalition partners in the face of male dispersal (Schoof et al. 2009).

Additional comparative studies are needed to further our understanding of ecological pressures on social relationships, mating systems, and dispersal patterns. In addition, genetic data on the relatedness of group members (both males and females) and more detailed reports on dispersal patterns and the fates of dispersing individuals in other species are required in order to attain a more complete overview of the dynamics and interactions that these processes have on primate behavior.

Species included in this chapter are shown in Color Plates 9, 10, and 17 (*Cebus capucinus*, *Cebus apella*, and *Saimiri sciureus*).

9

Sakis, Uakaris, and Titi Monkeys

Behavioral Diversity in a Radiation of Primate Seed Predators

Marilyn A. Norconk

1. What is seed predation, and how do seeds provide both benefits and costs to sakis, bearded sakis, and uakaris?
2. How do pitheciines differ in their social group and ranging patterns using body size and group size as relevant variables?
3. How is male affiliation manifested in pitheciines and how does it compare with woolly spider monkeys, chimpanzees, and bonobos?"

INTRODUCTION

The pitheciines are a cohesive group of New World monkeys phylogenetically and in terms of diet but exhibit a range of variation in group size, use of space, and social dynamics. At one end of a continuum that ranges from small to large group sizes, titi monkeys (*Callicebus* spp.) form cohesive, pair-bonded groups that in many ways represent the "classic monogamous" pattern (Fuentes 1999b, van Schaik and Kappeler 2003) (Table 9.1). Pairs are generally territorial, adults are monomorphic in body size and color. They 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; Bales et al. 2007).

Bearded sakis (*Chiropotes* spp.) and uakaris (*Cacajao* spp.) are at the other end of the group size continuum. 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 1999a, 2003a; Veiga 2006; Bowler et al., 2009). Groups travel through large home ranges and day ranges are as long as those of any platyrrhine (Ayres 1981, 1986; Norconk and Kinzey 1994; Aquino 1998; Boubli 1999; Defler 1999a; Peetz 2001; Barnett et al. 2002). Males do not take an active part in infant care. Bearded saki and uakari males are generally larger than females (Table 9.2) and exhibit sex-specific characteristics of robusticity such as enlarged temporal muscles (Figs 9.1 and 9.2). Both male and female bearded sakis exhibit well-developed beards upon sexual maturity and colorful, relatively large external genitalia (pink scrotum

Figure 9.1 *Cacajao calvus ucayalii* adult male (photo by Mark Bowler with permission, Lago Preto Conservation Concession, Peru).

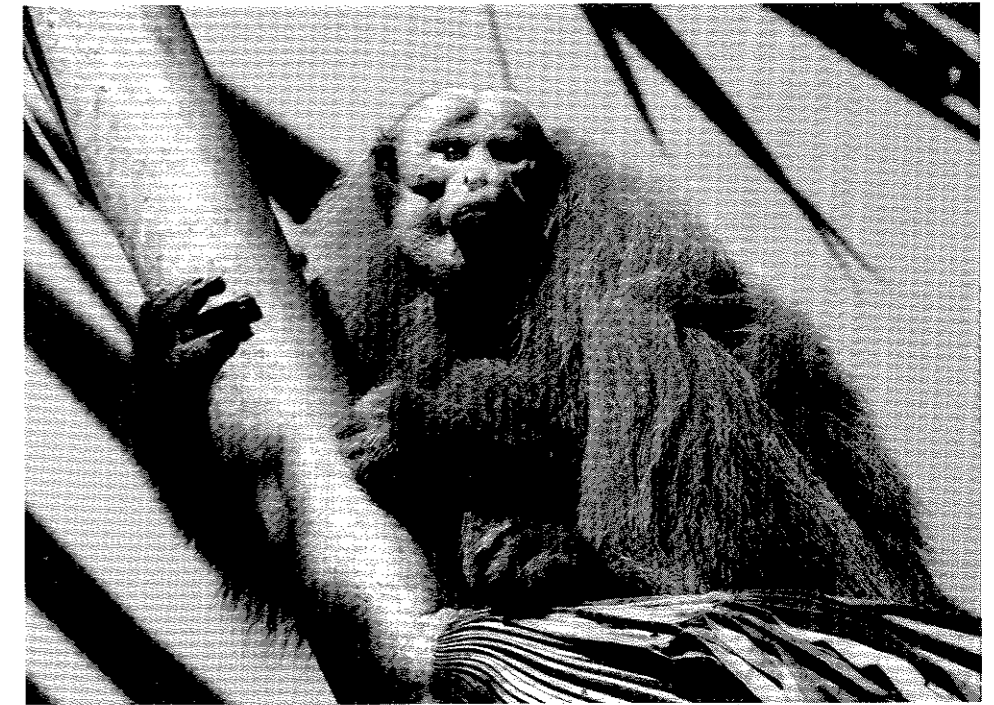


Figure 9.2 *Chiropotes sagulatus* adult male (photo by M. Norconk, Paramaribo Zoo, Suriname).

and enlarged, pink labia majora) (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 9.1), and many, but not all, conform to the "two-adult group" suggested by Fuentes (1999b). 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 caregivers (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. The expression of sexual dichromatism in sakis varies from subtle variation in the western (Amazonian) species to striking pelage differences in the eastern (Guiana Shield) *P. pithecia* spp. (Hershkovitz 1987b, Gerald 2003) (Fig 9.3). 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 non-prehensile-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 nearly

Table 9.1 Pitheciine Group Size, Group Composition, and Use of Space

SPECIES AND STUDY LOCATION AND LATITUDE, DURATION OF STUDY*	GROUP SIZE (N)	GROUP SIZE RANGE (N)	ADULT MALES	ADULT FEMALES	JUVENILES + SUBADULTS	INFANTS	HOME RANGE SIZE (HA)	DAY RANGE (KM)	POP. DENSITY (INDIVID./KM ²) OR INDIVID. SIGHTING RATE (SR)/10 KM	SOURCE
<i>Callicebus brunneus</i> Peru (c. 11° S)-ST		2-5 (6)	1(-2?)	1	0-3		1.4			Ferrari et al. 2000, Lawrence 2003
<i>Callicebus brunneus</i> Peru (c. 11° 51' S)-LT	4.6 (n = 6)	2-5					6.8 (n = 6)	349-1108	25-30/km ²	Wright 2009
<i>Callicebus brunneus</i> Bolivia (10° 35' S to 11° 31' S)-C	3	1-5 (39)								Buchanan-Smith et al. 2000
<i>Callicebus brunneus</i> Brazil (10°-12° S)-C	2.25 ± 0.97 (118)	max = 5								Ferrari et al. 2000
<i>Callicebus caligatus</i> Brazil (c. 10° S)-C	2.20 ± 0.84 (5)	max = 4								Ferrari et al. 2000
<i>Callicebus cinerascens</i> Brazil (c. 12° S)-	1.67 ± 0.33 (3)	max = 2								Ferrari et al. 2000
<i>Callicebus cupreus</i> Peru (5° 35' S)-	3.0-3.73	2-7 (18)							14.6/km ²	Bennett et al. 2001
<i>Callicebus donacophilus</i> Brazil-(c. 13° S)-	2.0 ± 1.0	max = 3								Ferrari et al. 2000
<i>Callicebus modestus</i> Peru (~11° S)-C	3.0	1-6								Martinez and Wallace 2007
<i>Callicebus moloch</i> Brazil (c. 12° S)-	2.47 ± 0.92 (15)	max = 4								Ferrari et al. 2000
<i>Callicebus moloch</i> Peru (11° 52')-T	4.1 (2)	2-5 (2)	1	1	1-2	0-1	6-8	0.55 ± 0.1, 0.67 ± 0.2	20-26/km ²	Wright 1984, 1985, 1986
<i>Callicebus moloch</i> Peru (11° 52')-T	4.0	2-7					11.5 (6-18)			Bossuyt 2002
<i>Callicebus olallae</i> Peru (~11° S)-C	2.7	1-5								Martinez and Wallace 2007
<i>Callicebus oenanthe</i> Peru (6° 01' S)-ST	4.5 ^a	4-5	1	1	2	1				DeLuycker 2006
<i>Callicebus oenanthe</i> Peru (5° 58' S)-RC	3.6	1-8							113/km ²	Aldrich et al 2008
<i>Callicebus ornatus</i> Colombia (c. 4° N)-T	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>Callicebus ornatus</i> Colombia (5° N)-LT							3.5-14			Defler 1994
<i>Callicebus personatus melanochir</i> Brazil (15° 18' S)-LT		2-6 ^a	1	1	1-4		24	1.0		Müller 1996
<i>Callicebus personatus 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>Callicebus personatus 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>Callicebus torquatus torquatus</i> Peru (4° S)-LT		3-5 ^a	1	1	1-2	1	29 (4-30)	0.8 ± 0.04 (0.5-1.4)	16/km ²	Kinzey 1978, 1981
<i>Callicebus torquatus</i> Brazil (0.24N)-LT									1.6/km ²	Boubli 2005
<i>Callicebus torquatus</i> Peru (2° 29S and 4° 15S)-C	2.9	2-5 (39)	1	1					2.5 to 2.8/km ²	Aquino et al. 2008
<i>Callicebus torquatus 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)/km ²		Defler 1983, 2003a

Table 9.1 (cont'd)

SPECIES AND STUDY LOCATION AND LATITUDE, DURATION OF STUDY*	GROUP SIZE (N)	GROUP SIZE RANGE (N)	ADULT MALES	ADULT FEMALES	JUVENILES + SUBADULTS	INFANTS	HOME RANGE SIZE (HA)	DAY RANGE (KM)	POP. DENSITY (INDIVID./KM ²) OR INDIVID. SIGHTING RATE (SR)/10 KM	SOURCE
<i>Cacajao calvus calvus</i> Brazil (3° 22' N)-LT		30-48 (3)	16	16	13	3	500-550	2.5-5.0	7-8/km ²	Ayres 1986, 1989
<i>Cacajao calvus</i> Peru (4° 23' S, 4° 30' S)-ST	41.9 ± 16.7 (21) ^b	8-70								Aquino 1998, Aquino and Encarnación 1999
<i>Cacajao calvus</i> Peru (4° 27' S)-LT	43.5 ± 24.1	max = 150+	1/3	1/3	1/3 ^c				14.3-116.8/km ² ^c	Bowler et al. 2009
<i>Cacajao calvus</i> Peru (5° 35' S)-C	15.8-33.1	2-55 (18)							7.44 and 25.78/km ²	Bennett et al. 2001
<i>Cacajao melanocephalus [hosomi]</i> Brazil (00° 24' N)-LT		c. 70						4.4	14/km ²	Boubli 1999, 2005
<i>Cacajao melanocephalus ouakary</i> Colombia (1° 5.55' S)-RC	20-30	1-108+							4.15/km ² overall, 12.0 in igapó habitat	Defler 2001
<i>Cacajao melanocephalus ouakary</i> Brazil (1° 5.55' S)-LT		5-30 (wet season), 1-100+ (dry season)								Barnett et al. 2005
<i>Chiropotes albinasus</i> Brazil (10° 10' S)-LT		19-26 (4)	8	9	8		250-350	2.5-3.5	10-11/km ²	Ayres 1981, 1989
<i>Chiropotes albinasus</i> Brazil (9-13° S)-C	4.2 ± 3.1 (7) ^d								1.6-2.5 (SR)	Ferrari, et al. 1999a-c
<i>Chiropotes chiropotes</i> Venezuela (7° 21' N)-LT		15-22 (1) ^a	1-2	8-10	3-5	1-5	180	1.6 (0.5-2.7)		Norconk 1996, Petz 2001
<i>Chiropotes sagulatus</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>Chiropotes sagulatus</i> Brazil (2° 30' S)-LT							429 ± 129.4	2.99 ± 0.02		Boyle et al. 2009a,b
<i>Chiropotes sagulatus</i> Suriname (4° 41' N)-ST	9 and 13 (2)							3.2 ± 1.1		Norconk and Kinzey 1994
<i>Chiropotes sagulatus</i> Suriname (5° 01' N)-C	32.7 (3)	22-44 (3)							37.4 (SR)	Norconk et al. 2003
<i>Chiropotes satanas</i> Brazil (multiple sites, 1-5° S)-C									1.8-10.08, 0.3 (SR)	Ferrari and Lopes, 1996
<i>Chiropotes satanas</i> , Brazil (4° 30' S)-ST		30-34 (1)	12	9	16-20	0				Silva and Ferrari 2009
<i>Pithecia aequatorialis</i> Peru (2° S)-C		1-7 (4)								Heymann et al. 2002
<i>Pithecia albicans</i> Brazil (4° 51' S)-RC	4.6 ± 1.5 (5)	3-7					172.4 (147-204)		4.1	Peres 1993a-c
<i>Pithecia hirsuta</i> Peru (c. 5° S)-RC	3.8	2-8	1-3	1-2			24.9 (9.7-42)		12.8/km ²	Soini 1986

Table 9.1 (cont'd)

SPECIES AND STUDY LOCATION AND LATITUDE, DURATION OF STUDY*	GROUP SIZE (N)	GROUP SIZE RANGE (N)	ADULT MALES	ADULT FEMALES	JUVENILES + SUBADULTS	INFANTS	HOME RANGE SIZE (HA)	DAY RANGE (KM)	POP. DENSITY (INDIVID./KM ²) OR INDIVID. SIGHTING RATE (SR)/10 KM	SOURCE
<i>Pithecia irrorata</i> Brazil (9°-13° S)-C	2.68 ± 1.38								1.3 (SR)	Ferrari et al. 1999a-c
<i>Pithecia irrorata</i> Bolivia (10° 35'S to 11° 24'S)-C	3.5	2-5 (6)								Buchanan-Smith et al. 2000
<i>Pithecia monachus</i> Peru (5° 35' S)-C	3.75	2-5 (16)							9-17.2/km ²	Bennett et al. 2001
<i>Pithecia pithecia chrysocephala</i> Brazil (2° 25'S)-LT	6 (1)	4-7a	1	1-3	0-2	0-2				Setz and Gaspar 1997, Gilbert and Setz 2001
<i>Pithecia pithecia chrysocephala</i> Brazil (c. 2° S)-ST	2.6 ± 0.5	2-3	0-2	0-2	0-1					Oliveira et al. 1985
<i>Pithecia pithecia</i> French Guiana (4° N)-LT	2.8 ± 1.0 (4)	1-4								Kessler 1998
<i>Pithecia 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>Pithecia pithecia</i> Guyana (various)-C	3.3 ± 1.7 (10)	1-5								Muckenhirn et al. 1975
<i>Pithecia pithecia</i> Suriname (4° 41'N)-RC	2.7 ± 0.8	9	1-2	1	0-1					Mittermeier 1977
<i>Pithecia 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>Pithecia pithecia pithecia</i> French Guiana (5° 04' N)-ST	2.3 (35)	1-5						1.88	0.64/km ²	Vié et al. 2001
<i>Pithecia pithecia pithecia</i> Venezuela (7° 21'N)-LT	9	5-9	3	2	2	2	15 ^c			Homburg 1997
<i>Pithecia pithecia pithecia</i> Venezuela (7° 21'N)-ST	6							1.77 ± 0.27		Cunningham 2003, Cunningham and Janson 2006
<i>Pithecia pithecia pithecia</i> Venezuela (7° 21'N)-LT	6.9 ± 1.4 (1) ^a	5-9	1-4	2-3	0-2 (m), 0-2 (f)	0-2	12.8 ^c	1.5		Norconk 2006

*C = census; RC = repeated census; ST = < 6 months of observation; LT = > 6 months of observation.

^a Range = the change in group size of one group

^b Lower number of range estimates used to calculate mean ± standard deviation. The count (100-120) of multiple groups was excluded.

^c Estimated proportion of adult males, adult females, and juveniles and infants in the entire population at Lago Preto; population density in 1999 and 2007, respectively.

^d An average of mean group sizes is reported (n = 7 locations).

^e Island-bound groups.

1,200 specimens, Hershkovitz 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. Wallace et al. (2006) added yet another

species. On one level, *Callicebus* is a highly variable and wide-ranging genus with interspecific differences in body size, pelage color, cranial dimensions, and chromosomal number (van Roosmalen et al. 2002). At another level, the genus seems remarkably uniform, particularly in mating and parenting strategies. Until recently, pelage color was treated

Table 9.2 Social and Reproductive Characteristics of the Pitheciines

SPECIES	MALE BODY MASS IN GRAMS	FEMALE BODY MASS IN GRAMS	GROUP SEX RATIO (F/M)	AGE AT SEXUAL MATURITY (MONTHS)/INTERBIRTH INTERVAL (MONTHS)	BIRTH PEAK (MONTHS) AND SEASON: WET OR DRY	PATERNAL CARE	TERRITORIAL INTERACTIONS WITH CONSPECIFIC GROUPS	LONG DISTANCE VOCALIZATIONS	SOURCE
<i>Callicebus brunneus</i>				c. 36 / 12	Copulations: Feb-June; pregnancy during dry season	Males carry, share food, and play with infants	7 encounters in 15 months of observation (females participated in 2:7)	90% calls before 0900 (calls on 15 mornings a month)	Wright 1985, 1986, 2009
<i>Callicebus 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>Callicebus discolor</i>	935	1,075		42/11.8	Winter: Dec-Mar (Davis, CA)				Hershkovitz 1990, Valeggia et al. 1999
<i>Callicebus moloch</i>	1016	877							Hershkovitz 1990
<i>Callicebus ornatus</i>	845	850	1.0		Nov-March	Males carry infants			Mason 1968, Hershkovitz 1990
<i>Callicebus personatus</i>	1,270	1,378			Oct (dry)		Vocal responses on 36 occasions to distant groups	Dawn calls given from sleeping trees	Hershkovitz 1990, Kinzey and Becker 1983
<i>Callicebus personatus personatus</i>							Rare: vocalizations only; no chasing, physical contact or threat displays	97% before 1000; not daily	Price and Piedade 2001
<i>Callicebus 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 calls and duets, from sleeping trees	Kinzey 1981, Hershkovitz 1990, Kinzey and Robinson 1983, Easley and Kinzey 1986
<i>Callicebus torquatus lugens</i>					Jan (dry)		Not daily, duetting 10-20 m apart from stable position		Defler 1983
<i>Cacajao calvus calvus</i>	3,450	2,880	1.20		Oct-Nov (dry)				Ayres 1986
<i>Cacajao calvus ucayalii</i>			Varies ^a	?/24	Aug-Nov ^a				Bowler et al. 2009
<i>Chiropotes albinus</i>	3,175 ± 185	2,518 ± 192	1.26						Ayres 1981, 1989
<i>Chiropotes albinus</i>	3,700								Ferrari 1995
<i>Chiropotes chiropotes</i>				c. 36/24+	Dec-April (late wet to dry)				Peetz 2001
<i>Chiropotes sagulatus</i>	2880	2660	1.08						Ayres 1981
<i>Chiropotes sagulatus</i>					Wet season				van Roosmalen et al. 1981
<i>Chiropotes sagulatus</i>					Late dry and short wet				T. Gregory, personal communication
<i>Chiropotes satanas</i>			0.75		March-May (late wet to dry) ^b				Silva and Ferrari 2009

Table 9.2 (cont'd)

SPECIES	MALE BODY MASS IN GRAMS	FEMALE BODY MASS IN GRAMS	GROUP SEX RATIO (F/M)	AGE AT SEXUAL MATURITY (MONTHS)/INTERBIRTH INTERVAL (MONTHS)	BIRTH PEAK (MONTHS) AND SEASON: WET OR DRY	PATERNAL CARE	TERRITORIAL INTERACTIONS WITH CONSPECIFIC GROUPS	LONG DISTANCE VOCALIZATIONS	SOURCE
<i>Pithecia albicans</i>	3000								Peres 1993a-c
<i>Pithecia irrorata</i>	2,010 (2,920)	1,875 (1,980-2,160)							Hershkovitz 1987b, Ford 1994a
<i>Pithecia hirsuta</i>				?/24-36	Sep-Dec (late dry to early wet)		Rare		Soini 1986
<i>Pithecia monachus</i>	2,795 (2,500-3,100)	1,900 (1,300-2,000)							Hershkovitz 1987b, Ford 1994a
<i>Pithecia pithecia, Venezuela</i>	1,732 (1,380-1,866)	1,515 (1,347-1,875)		Reg 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 intergroup encounters	Hershkovitz 1987b, Ford 1994a, Norconk 2006
<i>Pithecia pithecia, Suriname</i>					Oct-Jan (dry to short wet)		Primarily male		C. Thompson personal communication
<i>Pithecia pithecia, Captive</i>						Play and share food with older infants	Aggressive toward same-sex intruders		Shideler et al. 1994, Savage et al. 1992

* Population-wide, authors suggest equal numbers of males and females. Inverse correlation between group size and number of males. Smaller groups have proportionately more males or males separate from main group and spend more time in smaller groups, some of which are all-male groups. Births tend to fall in a period of low fruit availability (see text).

^b Inferred; authors witnessed copulations from October to December.



Figure 9.3 *Pithecia pithecia* adult male (photo by M. Norconk, Brownsberg Nature Park, Suriname).

as if it were a uniform character and little attention was given to within-species variation (but see DeLuycker 2007, Aquino et al. 2008). In a study of two endemic species of Bolivia, *Callicebus modestus* and *C. olallae* (often classified as subspecies of *C. donacophilus*) (Martinez and Wallace (2007:48) comment that "similar morphological features...together with variable lighting conditions during field observations make accurate identification a challenge." Nevertheless, they

suggest that pelage coloration provides the best cue to species identity.

In addition to variation in pelage color, titis exhibit small differences in body size (Table 9.2) 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 and morphological studies place *Callicebus* at the base of the pitheciine radiation, diverging from the rest of the platyrrhines about 15 million years ago (Schneider et al., 1993, Schrago, 2007, also see Kay et al., 2008).

At a proximate level, Casado et al. (2007) provide insight into how difficult it might be to sort out these species using molecular techniques. Using cytochrome *b* DNA sequence data, they sampled eight individuals (four *C. lugens* from the left bank and four *C. lugens* from the right bank of the Rio Negro—a distance of 190 km separating the two populations. Casado et al. (2007) estimated genetic distance to be much higher across large rivers than among animals on the same bank. Although their estimated time of divergence (2.2 mya) seems far-fetched, van Roosmalen et al. (2002) contend that rivers provide substantial dispersal barriers for titis, which are unlikely to cross major rivers except at their headwaters.

Callicebus spp. occupy much of the Amazon and Orinoco river basins, ranging from the foothills of the Andes to the

Atlantic Forest of southeastern Brazil (see maps in van Roosmalen et al. 2002). The only large-scale discontinuous distribution among *Callicebus* species occurs between *C. personatus* and *C. moloch* groups in central Brazil (Ferrari et al. 2000). Titis are absent from the Guiana Shield, apparently confined to the right banks of Rios Negro and Branco (Hershkovitz 1985); and their distribution is also limited by local or regional habitat variation or flooding in both *várzea* and *igapó* forests (van Roosmalen et al. 2002). In support of the view that titis express specific preferences for habitat types despite their broad distribution, Kinzey and Gentry (1979) proposed that *C. torquatus* inhabited white-sand terraces preferentially. This was questioned by Defler (1994) in Colombia but recently supported by Aquino et al. (2008) working in Peru. Interestingly, van Roosmalen et al. (2002) proposed that *Callicebus* species colonize new areas by either replacing a closely related ecospecies or accommodating sympatry in two species with different ecological preferences (i.e., they found no evidence for hybrid zones).

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 9E° N to 14E° S latitudes; see Table 9.1, Figure 9.4). 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 with two subspecies (Marroig and Cheverud 2004). L. Marsh (personal communication) is in the process of revising the taxonomy of *Pithecia*, with an expected increase in the number of species, particularly in the western Amazon Basin.

Guianan sakis (white-faced or 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 malar stripes on the side of the face. Amazonian males found south of the Amazon River (Brazil) and in the western Amazon Basin (Colombia, Ecuador, Peru) exhibit a range of variation in facial and extremity color but lack the black-white contrast exhibited by Guianan males (see Figure 9.3). Females of all *Pithecia* spp. are very similar in appearance (Hershkovitz 1987b).

According to Ford (1994a), sexual dimorphism in body mass ranges from 1.1 to 1.4 for three species of *Pithecia* sakis (see Table 9.2). *P. albicans* nearly bridges the body mass gap between *Pithecia* and larger sakis/uakaris: *Chiropotes* and

Cacajao. Peres' (1993b) research on *P. albicans* in central Amazonia suggested 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 in the absence of the two larger-bodied genera (*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) (Figure 9.5). 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 (south) bank of the Orinoco River from Brazil into southern Venezuela (state of Amazonas) and then eastward into the state of Bolívar. Their present eastern boundary in Venezuela appears to be of the Caroní River (Norconk et al. 1996b). In Brazil, they range north and south of the Amazon River, 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 saki 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 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. This revision increases the number of *Chiropotes* species to five (Silva and Figueiredo 2002, Bonvicino et al. 2003, Veiga 2006, Silva et al. 2009) (Figure 9.3) 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

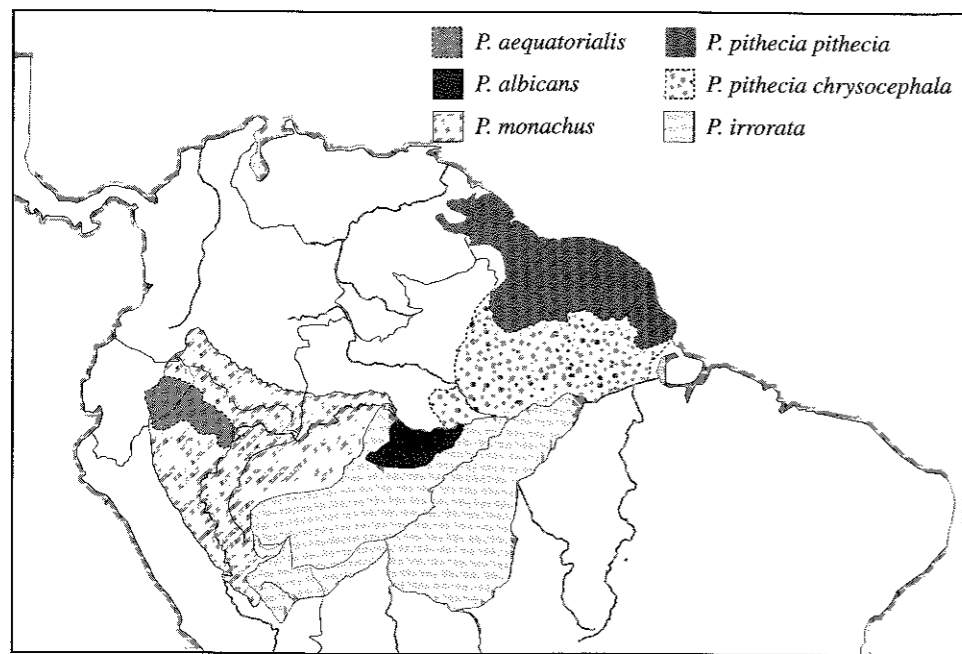


Figure 9.4 Distribution of the six current taxa of *Pithecia* spp. across the Amazon Basin and throughout the Guiana Shield and northern Brazil (map adapted from Hershkovitz 1987b and the IUCN website, <http://www.iucnredlist.org/>, by E. Bailey). Note that *Pithecia* spp. overlap throughout much of their range with larger *Chiropotes* and *Cacajao* spp. (see Figure 9.5). Overlap with *Callicebus* spp. is limited to western Amazon Basin sakis (compare figures in van Roosmalen et al. 2002).

basins, ranging from southern Venezuela and western Brazil to eastern Colombia and Peru. He designated two species, black-headed uakaris (*Cacajao melanocephalus*) with two sub-species (*C. m. melanocephalus* and *C. mouakary*), and bald-headed uakaris (*C. calvus*) with four 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) (Figure 9.2). 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 *C. 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*) (Ayres 1986, Hershkovitz 1987a, Barnett and Brandon-Jones 1997, Boubli 1999). These habitats, tributaries of the Amazon, Orinoco, and Rio Negro, 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 firma 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 throughout 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 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 variable population densities of uakaris (Table 9.1) suggest that seasonal variability in food abundance affect grouping patterns and local population densities (Bowler et al. 2009). 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

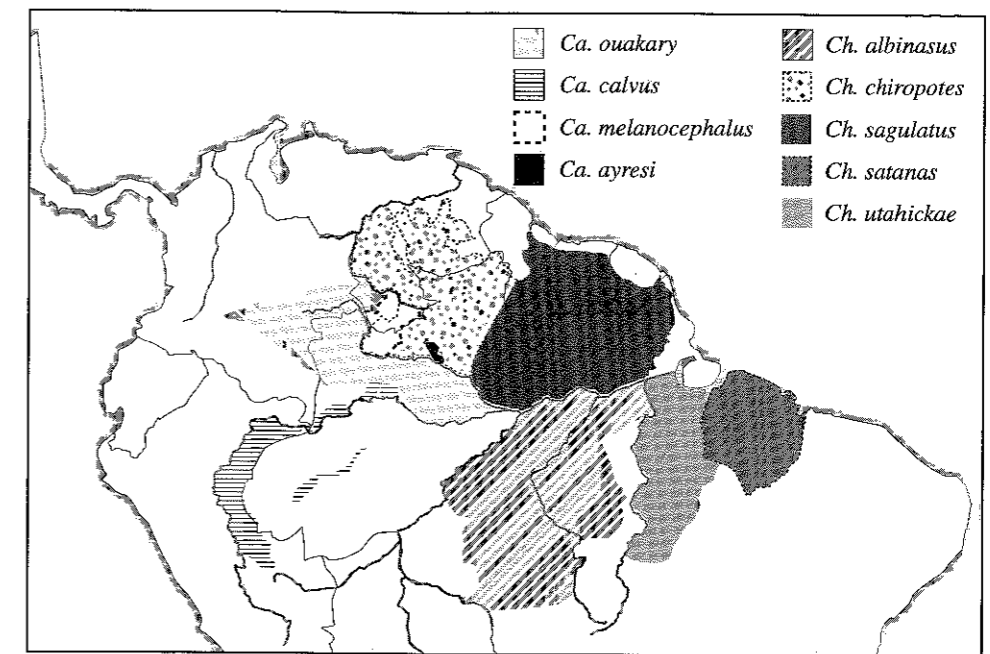


Figure 9.5 Distribution of *Cacajao* (*Ca.*) and *Chiropotes* (*Ch.*) species (adapted from Hershkovitz 1985, 1987a; Silva and Figueiredo 2002; Barnett 2005; Veiga 2006; Figueiredo 2006; Boubli et al. 2008; and the IUCN Web site, <http://www.iucnredlist.org/>, by E. Bailey). A number of these names and distributions are in flux currently. The four subspecies of bald uakaris, *Cacajao calvus* (see text), are collapsed into a single distribution. Taxonomic designations for black uakaris are expressed variously, with some authors retaining subspecies designations for *Ca. melanocephalus melanocephalus* and *Ca. m. ouakary* (e.g., Barnett 2005, Barnett et al. 2005), others raising subspecies to species status (e.g., Figueiredo 2006), or designating new species due to observations of expanded geographic ranges and molecular genetics (e.g., Boubli et al. 2008). For bearded sakis, a number of changes have been made since Hershkovitz 1985: *Ch. sagulatus* = *Chiropotes satanas chiropotes* = northern bearded saki of eastern Brazil and the Guiana Shield; *Ch. satanas* = *C. satanas satanas* = black bearded saki; *Ch. chiropotes* = *Ch. satanas chiropotes* bearded saki of western Brazil and Venezuela.

of specific plant families than that of either *Pithecia* or *Callicebus*.

PHYSICAL CHARACTERISTICS OF THE PITHECIINES

Pitheciines are small- to medium-sized platyrrhines, ranging in body size from about 850 to 3,500 g. Titis are the smallest-bodied of the pitheciines, ranging in size from approximately 800 to 1,300 g (see Table 9.2). The sexual dimorphism ratio in body mass ranges from 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 has been discussed for *Pithecia* spp. and is absent in *Callicebus* spp., *Chiropotes* spp., and *Cacajao calvus*; but there may be subtle color differences in the red faces of male and female bald-headed uakaris (Hershkovitz 1987b, Barnett and Brandon-Jones 1997) and differences in texture and golden-tipped hairs in the body pelage of male northern bearded sakis

compared with more olive-colored females (M. Norconk personal observation).

Similarities in dental anatomy unite the sakis/uakaris and distinguish them from titis (Rosenberger 1992, Kay et al. 2008). 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 9.3). Kinzey and Norconk (1990) and Norconk et al. (2009a) described them as “sclerocarpic” foragers, specialists in opening mechanically protected (i.e., brittle and/or thick-husked) fruit. The protected characteristics of fruit exocarp in their preferred plant families (Lecythidaceae, Chrysobalanaceae, Sapotaceae) contrast 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. Procumbent lower incisors are used to scrape adherent mesocarp from the inside of fruit husks and to plane or reduce the pericarp of tough or large fruit.

Table 9.3 Feeding Ecology of the Pitheciines

SPECIES AND COUNTRY OF RESEARCH	FEEDING GROUP SIZE*	% FEEDING					IMPORTANT PLANT FAMILIES (%)	SOURCE
		SEEDS	FLESHY FRUIT	FLOWERS	LEAVES	INSECTS		
<i>Callicebus brunneus</i> Peru	C				23–66 varies seasonally		Moraceae, Fabaceae, Annonaceae	Wright 1986
<i>Callicebus personatus</i> Brazil	C	21.9	54.7		17.2		Myrtaceae, Sapotaceae, Moraceae (51.4%)	Müller 1996
<i>Callicebus personatus personatus</i> Brazil			81 ^a	1	18		Sapotaceae (41%)	Kinzey and Becker, 1983
<i>Callicebus torquatus torquatus</i> Peru			71 ^b		4	20	Moraceae, Guttiferae, Fabaceae, Euphorbiaceae, Convolvulaceae, Palmae (52%)	Kinzey, 1978; 1981
<i>Callicebus torquatus lugens</i> Colombia							Euphorbiaceae	Defler 1983, 2003b
<i>Cacajao calvus</i> Brazil	8.95 (1–50) F	66.9	18.4		3.3	5.2	Lecythidaceae, Moraceae, Hippocrateaceae, Sapotaceae, Annonaceae (62.4%)	Ayres 1986, 1989; Walker and Ayres, 1996
<i>Cacajao calvus</i> Peru		46.0	50.0				Sapotaceae, Fabaceae, Apocynaceae (38%)	Aquino 1998, Aquino and Encarnación 1999
<i>Cacajao calvus ucayalii</i> Peru	F						Important resource: Mauritia flexuosa palm fruits	Bowler et al. 2009
<i>Cacajao melanocephalus [hosomi]</i> Brazil	D	67.0	28.8	5.0	4.0	2.0	Euphorbiaceae (24%), Caesalpinoidea, Fabaceae, Lecythidaceae, Sapotaceae	Boubli 1999
<i>Cacajao ouakary</i> Colombia	F						Lecythidaceae	Defler 1999a,b, 2003a
<i>Cacajao ouakary</i> Brazil							Euphorbiaceae, Lecythidaceae, Fabaceae, Combretaceae	Barnett et al. 2005
<i>Chiropotes albinasus</i> Brazil	22.5 ± 3.5	35.9	53.9	3.0	7.2 ^a		Palmae, Sapotaceae, Fabaceae, Caryocaraceae Moraceae (54%)	Ayres 1981, 1989

Table 9.3 (cont'd)

SPECIES AND COUNTRY OF RESEARCH	FEEDING GROUP SIZE*	% FEEDING					IMPORTANT PLANT FAMILIES (%)	SOURCE
		SEEDS	FLESHY FRUIT	FLOWERS	LEAVES	INSECTS		
<i>Chiropotes chiropotes</i> Venezuela ^c		50.7 (4–60)	0–52.0	0–8.1	0–1.5	1–21	Sapotaceae, Loranthaceae, Moraceae (76%)	Petz, 2001
<i>Chiropotes chiropotes</i> Venezuela ^c	F	74.8	21.6	0.4	0.2	0.5	Sapotaceae, Loranthaceae, Moraceae, Meliaceae (74.5%)	Norconk 1996, Kinzey and Norconk 1993
<i>Chiropotes sagulatus</i> Brazil	2.88	63.3	9.3	11.4	16.1 ^a		Moraceae, Fabaceae, Lecythidaceae, Sapotaceae (62%)	Ayres 1981
<i>Chiropotes sagulatus</i> Suriname	F	66.4	27.6	4.6				van Roosmalen et al. 1981
<i>Chiropotes satanas</i>	F	54.0/ 59.9 ^d	25.0/ 13.7	12.3/ 17.4	2.9/3.6	4.6/3.7	Simaroubaceae, Fabaceae, Lecythidaceae, Sapotaceae, Arecaceae	Veiga 2006, Veiga and Ferrari 2006
<i>Chiropotes utahickae</i>		75.6	5.4	18.9	0.1			Santos 2002?
<i>Chiropotes utahickae</i>		36.2	43.3	16.6	3.1	0.7		Vieira 2005?
<i>Pithecia albicans</i> Brazil	F	46.2	28.6	6.5	9.5	0.4	Sapotaceae (21%), Fabaceae (20%)	Peres 1993a–c
<i>Pithecia hirsuta</i> Peru		38.0	55.0	3.0	4.0		Lecythidaceae, Fabaceae, Annonaceae	Soini 1986
<i>Pithecia irrorata</i> Peru		83.0	15.0	0.5	1.5		Moraceae, Sapotaceae, Fabaceae, Chrysobalanaceae	Palminteri et al. 2009
<i>Pithecia pithecia chrysocephala</i> Brazil		26–31		15.9	4.0–18.4			Setz 1993
<i>Pithecia pithecia pithecia</i> Venezuela ^c		53.3	31.0	2.0	10.4	3.7	Connaraceae, Erythroxylaceae, Rubiaceae, Chrysobalanaceae (53.7)	Homburg 1997
<i>Pithecia pithecia pithecia</i> (Venezuela) ^c	C	60.6	27.8	2.2	7.1	2.3	Connaraceae, Lecythidaceae, Loganiaceae, Fabaceae, Erythroxylaceae (57%)	Kinzey and Norconk 1993; Norconk 1996

*C = primarily cohesive; D = well dispersed, no obvious fissioning; F = fission into feeding subgroups

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

^a “Fruit” did not specify seed-eating.^b “Other” category included leaves, insects, bark.^c Studies at the same site, overlapped in time.^d Study compared island and mainland groups of bearded sakis (expressed as mainland/island dietary components).

Compared with anterior dentition, saki/uakari molars are flat, with undeveloped shearing crests (Kay et al. 1988, Rosenberger 1992). The adaptations of both anterior and posterior dentition, in addition to crenulated and crack-resistant enamel on molars (Kinzey 1992, Martin et al. 2003), form a highly specialized dental apparatus that allows these monkeys to prepare and ingest fruit or seeds that are often ignored by other platyrrhines (Norconk et al. 1998, 2009a).

Both bearded sakis and uakaris are above-branch quadrupeds (pronograde clamberers) and leapers, in the upper canopy levels of the forest (Walker 1996). Vertical clinging and leaping and extensive use of the understory in *P. pithecia* differ from habitat use and locomotion of other saki species that are primarily above-branch quadrupeds (e.g., *P. albicans*, Peres 1993b; *P. monachus*, Youlatos 1999; *P. irrorata*, S. Palminteri, personal comment). Davis and Walker-Pacheco (in press) documented a distinctive morphological pattern in the postcrania of *P. pithecia*, with these smallest of the sakis clustering (statistically) well away from *Chiropotes* spp., *P. monachus*, and *P. hirsuta*.

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 1993b, 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 1993b, 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) 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 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.

In addition to scent marking branches, Gleason (personal communication) noted that adult male white-faced sakis huddled, rubbed their chests against each other, and possibly exchanged scent just prior to some intertroop encounters. Observations of group huddles occurred only in a year in which the study group had four adult males (and three females), an unusually large size for 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, but Veiga and Silva (2005) found that male bearded sakis were more likely to interact with each other socially (including hugging and lining up) than expected given group composition. They found that more than 90% of male/male interactions were affiliative. B. Bezerra (personal comment) and M. Bowler (personal comment) report that uakari adult males also engage in affiliative social interaction, although it is limited to spatial proximity, not body contact. Titi monkeys also “line up,” but they engage in lengthy periods of body contact during resting periods, unlike bearded sakis whose contact periods are brief and active, taking 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, Fabaceae, 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 9.3). 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 9.3). 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 most studies of titis have not found them to be significant seed predators (Table 9.3). Indeed, Carrillo-Bilbao et al. (2005) considered *C. discolor* to be a potentially important seed disperser. In contrast, seeds are often found to comprise a third of saki/uakari diets, sometimes more than two-thirds (see Table 9.3). Sakis and uakaris frequently ingest unripe, dull-colored (green or brown) fruit that has a woody or well-protected exocarp (Ayres 1986, 1989; Peres 1993b; Norconk et al. 1998; Boubli 1999; Barnett et al. 2005; Veiga 2006). 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), Boubli (1999), and Veiga and Ferrari (2006) 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 comment) 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 also 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 comment). Thus, incidental items are likely to provide important nutritional diversity to saki/uakari diets (also see Ayres and Nessimian 1982, Mittermeier et al. 1983, Frazão 1991, Barnett et al. 2005, Veiga 2006, and Veiga and Ferrari 2006 for information on insect eating in bearded sakis).

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 + protein/condensed tannins + acid detergent fiber. 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 equivalent to eating leaves with regard to dietary fiber intake so that (white-faced) sakis and uakaris may select fruit based on lipid value in spite of high fiber content (Ayres 1986; Norconk et al. 2002, 2009; 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 the 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) provides 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). Barnett et al. (2005:962) suggest that leaf eating “is highly seasonal and related to a dearth of fruits available in any forest type during the dry season” for golden-backed uakaris.

GROUP SIZE, USE OF SPACE, AND INTERGROUP RELATIONS

Titis and *Pithecia* spp. sakis form small social groups, have relatively small home ranges, and often exhibit behaviors that are associated with defense of territories (Tables 9.1 and 9.2). Group sizes, ranging from two to seven individuals in titis, conform to the expectation of pair-bonded primates (see Table 9.1); but *Pithecia* groups are more variable. A number of censuses have reported that *Pithecia* group sizes range from two to 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 our recent observations on individually identified, free-ranging sakis in Suriname suggest that slow dispersal of young adults may account for the “extra” adults in the group (M. A. Norconk and C. L. Thompson, personal observations). 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 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. 1999a).

Using playbacks, Robinson (1979) and Kinzey (1981, 1997a) 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 suggesting that we have not yet exhausted all of the habitat-use strategies of species in this very widespread and diverse genus.

A few studies suggest that *Pithecia* spp. are also territorial (Norconk et al. 2003, Di Fiore et al. 2007, S. Palminteri personal communication), and Shideler et al. (1994) have reported aggressive interactions with same-sex intruders among captive sakis. Territorial activities that consist of behavior-specific vocalizations and chasing (Norconk 2006, Thompson and Norconk 2009) are strikingly similar to Mason's (1968) description of behaviors associated with territoriality in *C. ornatus* and Fernandez-Duque's (see Chapter 10) description of territoriality in *Aotus*.

Chiropotes and *Cacajao* live in relatively large groups and are as far-ranging as any platyrrhine (Table 9.1) (Boyle et al. 2009b). 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 1999a, Barnett et al. 2005, Bowler et al. 2009; see Table 9.3). 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), 2.5–4.0 km for bearded sakis in Suriname (Norconk and Kinzey 1994), and 2.99 km for bearded sakis in Brazil (Boyle 2008a).

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 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. Recent studies have consistently reported group fissioning in both bearded sakis and uakaris, although the mechanism does not appear to be as simple as Norconk and Kinzey (1994) suggested.

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. 1995b; Valeggia et al. 1999). White-faced sakis have an ovarian cycle of 16–17 days, gestation of 150 days, and approximately 195 days of lactational 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 ± 9 months, $n = 6$), and first birth occurred at the age of 5 years (M. A. Norconk and S. E. Shideler unpublished data; Norconk 2006) (see Table 9.2).

The length of titi monkey ovarian cycles is very similar to that of white-faced sakis (*C. cupreus*, 17.2 ± 1.5 days), but gestation length and interbirth intervals were shorter (128.6 ± 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. (moloche) cupreus* (e.g., Mason 1971, 1974; Mendoza and Mason, 1986a,b; Mason and Mendoza 1998; Hennessy et al. 1995; Hoffman et al. 1995a). 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 (Fragasz et al. 1982). More recently, Bales et al. (2007) found significant differences between bonded vs. nonbonded titi males in the activity of neural areas that are associated with pair-bonding in rodents. Interestingly, newly bonded males were intermediate, and more variable, in glucose-uptake values, suggesting individual variation in how male/female bonds are formed in these monogamous primates.

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. moloche*. 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 became self-locomoting by their fourth month, both bearded saki and uakari infants were carried by the mother for at least 9 months. 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 provides 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 (Peetz 2001).

Uakari developmental data, reported by Fontaine (1981) on a semi-free-ranging group, are 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.

CONSERVATION STATUS

Given wide variation in habitat use, body size, geographic distribution, and ecological specializations, it is not surprising that pitheciines face a range of conservation problems. However, habitat fragmentation due to dam creation, ranching, agriculture, logging, and expansion of human populations appears to be the most widespread problem (Ferrari et al. 1999b). In addition to fragment size, long-term survival in fragments probably depends on availability of forest corridors, quality of matrix between terrestrial fragments (Boyle 2008b, Boyle et al. 2009b), and ability to move between fragments. On the positive side, studies of bearded sakis in the Biological Dynamics Forest Fragments Project (BDFFP) (Boyle 2008a,b), the Tucuruí Reservoir (Veiga 2006, Silva and Ferrari 2009), and the Celmar plantation complex (Port-Carvalho and Ferrari 2004) in Brazil and Lago Guri, Venezuela (Kinzey and Norconk 1993, Homburg 1997, Peetz 2001, Norconk 2006), found that the monkeys maintain strikingly diverse diets even with differences in activity and ranging patterns. Both Peetz

(2001) and Veiga (2006) found that bearded sakis fed on more than 100 species of plants in fragments ranging from 19 to over 1,000 ha. Veiga's study of *Chiropotes satanas* in both large and small fragments highlights the ability of sakis to shift feeding species preferences yet maintain a diet of more than 50% seeds. Feeding flexibility aside, stochastic forces operating on small group sizes and groups that receive no gene flow from immigrants eventually show population declines. For example, white-faced saki group size on the small island in Lago Guri peaked at nine and then declined to five adults 10 years later, at which time live births dropped to zero.

Unlike bearded sakis, specialized feeding and foraging strategies of uakaris may heighten their risk of extinction when forests are fragmented and migration routes are cut off. According to Barnett et al. (2005:961) black uakaris in Jaú National Park "make limited excursions far away from the igapó to exploit very specific food resources." Observations by Bowler et al. (2009) in Peru suggest that uakari birth rates are tied to *Mauritia flexuosa* palm fruit production. With the increasing number of field studies and censuses of pitheciines over the past 10 years, we are beginning to gain an appreciation for the complexity of their adaptations. The spotty distribution of white-nosed bearded sakis in southwestern Amazonia prompted Ferrari et al. (1999a) to suggest that complex interactions among several variables (e.g., soil conditions, phenology, presence or absence of key resources, and perhaps presence of a second pitheciine species) affect bearded saki survival and distribution. Hunting pressure appears to be most applicable to the larger-bodied species, and Bowler et al. (2009) describe what appears to be a stunning recovery of a uakari population in the Lago Preto Conservation Concession in Peru once hunting ceased.

Although titis should be able to handle habitat fragmentation better than larger sakis since their home ranges are much smaller, isolation of small populations seems to be their biggest conservation concern. Some species, like *Callicebus torquatus*, have specific habitat preferences that result in a mosaic of populated areas in Peru (Aquino et al. 2008) or, in the case of *C. olallae* in Bolivia (Felton et al. 2006) and *C. coimbrai* in Brazil (Jerusalinsky et al. 2006), where ranches have created open grasslands that are not easily crossed (Felton et al. 2006). Some newly named species are vulnerable because they inhabit very small areas (e.g., *C. aureipalatii*, Wallace et al. 2006) or are restricted geographically and in the path of intensive development (*C. oenanthe* in northern Peru, DeLuycker 2006, Aldrich et al. 2008). Most of these authors acknowledge that many species of *Callicebus* can tolerate degraded habitats but also state that isolation is a deepening problem. In order to address and potentially ease the pressure of persistent fragmentation coupled with development, many authors are calling for increased sizes of protected areas and active management of isolated groups at the metapopulation level.

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 saki. This view is complicated by some diversity within the small radiation of *Pithecia* species, as suggested by Peres (1993b), Walker (1996), and Davis and Walker-Pacheco (in press). 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 that appear to prefer upper forest levels.

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, territorial behavior, and home range size.

Although data on aspects of the social behavior of wild pitheciines, which require well-habituated and identifiable individuals, continue to lag behind ecological data, there are a growing number of reports suggesting that males are tolerant of, or actively cooperate with, other intragroup males. Since there is also a considerable range in the number of males in pitheciine social groups (from generally one adult male in titis and sakis to many males in bearded sakis and uakaris) (see Tables 9.1 and 9.2), the expressions of male/male behavior are variable (Table 9.4). Bossuyt (2002) and Norconk (2006) suggested that even with a single breeding male in titi and white-faced saki groups, respectively, sons are retained in the group into subadulthood, although Wright (2009) found that all subadults in the eight titi groups she monitored dispersed as subadults. Retention of sons that are willing to invest in territorial behaviors (chasing and threatening nongroup males) may improve territory maintenance (Thompson and Norconk 2009, Wright 2009). In neither titi nor saki groups do adult females regularly participate in intertroop encounters. Intertroop encounters are rare in bearded sakis and uakaris, probably because home ranges in free-ranging conditions are very large and groups often fission into subgroups.

Table 9.4 Preliminary Assessment of Male/Male Behaviors in Pitheciines

MALE-MALE CHARACTERISTICS	TITIS	SAKIS	BEARDED SAKIS	UAKARIS
Adult male tolerance of young males	x	x	x	x
Male (son) cooperation in inter-troop encounters		x		
Cohesive groups	x	x		
Well-dispersed groups			x	x
Fission-fusion			x	(x)
Sex-specific male contact behaviors			x	
Male grooming partner preferences			x	x

Ayres (1981, 1986) believed that fissioning in bearded saki and uakari groups reflected variation in resource availability. But we still do not know what it is about resource availability that affects group fissioning or determines the size of subgroups: Is it the relative abundance of fruit crops, availability of fruit-producing crowns of a particular size, seasonal availability of preferred foods like seeds (e.g., *Mauritia flexuosa*) driving either group dispersion or cohesion, diversity of fruiting species, or absolute (regional) fruit abundance? Nor do we understand the factors that affect individual decisions about which subgroup to join. Bowler et al. (2009) describe fissioning that may reflect reproductive or social preferences (i.e., all-male groups that follow larger multimale/multifemale uakari groups), and Ayres (1981) suggested that bearded saki groups may fission into male/female units. One thing seems certain however: The suggestion that bearded saki groups fission and fuse locally while feeding in nearby trees (Norconk and Kinzey 1994) is too simplistic.

Preferences expressed by male bearded sakis and uakaris for other males as social partners are now supported by quantitative data (Peetz 2001, Veiga and Silva 2005). Veiga and Silva (2005) found that more than half of the social

interactions recorded involved two or more bearded saki males and over 90% of those interactions were affiliative. Behaviors included a high incidence of male/male social resting, hugging, lining up, and grooming in bearded sakis; but Bowler (personal comment) suggests that, while uakari males are generally affiliative, they do not engage in social contact to the same degree as bearded sakis (Table 9.4). In light of the growing evidence for male/male affiliation in bearded sakis and uakaris, it is interesting to note that Hershkovitz (1993) found that males of these two genera bore large, hooked penile spines. It leads one to wonder whether the affiliation expressed by males in these large multimale groups masks a subtle form of competition. There are still many interesting discoveries to be made in feeding ecology, ranging behavior, intragroup relations, and sociosexual behavior in the pitheciines, particularly in large multimale groups of bearded sakis and uakaris—and we have not yet scratched the surface regarding female strategies.

Species included in this chapter are shown in Color Plates 14–16 (*Pithecia pithecia*, *Cacajao calvus*, and *Callicebus discolor*).