Part II Comparative Pitheciid Ecology

Chapter 9

Male cooperation in Pitheciines: the reproductive costs and benefits to individuals of forming large multimale/multifemale groups

Paul A. Garber & Martin M. Kowalewski

> Primates differ from many other animal lineages in that they show rather good evidence of cooperation, especially in long-term relationships. (van Schaik & Kappeler 2006, p. 13)

Introduction

Traditional approaches to the study of primate sociality have highlighted predator protection as a primary benefit of group living, and argue that factors such as aggression, dominance and feeding competition constrain or determine group size, group composition and the nature of social interactions among individual group members (van Schaik 1983, 1989; Janson & Goldsmith 1995; Sterck *et al.* 1997; Chapman & Chapman 2000; Janson 2000; Kappeler & van Schaik 2002). In particular, both the socioecological model and the ecological constraints model describe a set of resource conditions (clumped and monopolizable resources of intermediate size relative to group size) and competitive regimes under which within-group contest competition for food, especially among females and unrelated individuals, is expected to be severe, agonistic and frequent (van Schaik 1989; Sterck *et al.* 1997).

Moreover, it is argued that the costs of feeding competition increase with group size, as individuals are required to travel greater distances to locate more productive feeding sites or experience elevated predation risk by foraging in small, scattered parties in order to encounter sufficient resources (Janson & Goldsmith 1995; Sterck *et al.* 1997; Koenig *et al.* 1998; Chapman & Chapman 2000; Janson 2000). Even under conditions in which food patches are small, dispersed, and nonmonopolizable, these models suggest that group members compete through a process of avoidance and scramble competition (Sterck *et al.* 1997; Chapman & Chapman 2000; Steenbeek & van Schaik 2001; Snaith & Chapman 2005). The major limitations of these approaches are their focus on competition and aggression as the main factors driving within-group social relationships and primate social organization, and their lack of attention to the joint reproductive benefits both males and females receive as members of a functioning, integrated, cooperative and stable social unit (Sussman & Garber 2007).

Over the past few years, a series of papers have been published (Dugatkin 1997; Nunn 2000; Chapais 2006; van Schaik & Kappeler 2006; Sussman & Garber 2007) that provide strong empirical and theoretical support for models of primate sociality based on patterns of affiliation, cooperation, reciprocity and mutualism. These studies build on the work of Hamilton (1964), Trivers (1971) and Axelrod and Hamilton (1981) in defining and expanding the set of social and ecological conditions under which cooperative behaviors are expected to evolve and be maintained as an evolutionary stable strategy.

Here we define cooperation as coordinated "actions or traits that benefit other individuals" (van Schaik & Kappeler 2006, p. 3). Cooperation can take several forms, including altruism, reciprocity or mutualism. Altruism is a unilateral interaction with high benefits for the recipient and high costs for the donor, and no expectation of reciprocation, which is usually explained through kin selection (Hamilton 1964). In reciprocity, benefits to the recipient are variable, and immediate costs to the donor are low to moderate. In this case, the donor receives eventual benefits through future reciprocal actions of the recipient. Where the immediate costs to the donor are low [Trivers's (1971) tit-for-tat strategy] or the long-term benefits are high (e.g. friendships, cooperative hunting, alliance partners: Boesch *et al.* 2006; Smuts 1997), reciprocally cooperative relationships are expected to be based more on partner competency than kinship (Goldberg & Wrangham 1997; Noë 2001; Chapais 2006; Mitani 2006). Mutualism brings either benefits to both actors, or benefits the recipient at no cost to the donor (Dugatkin 1997). As returns are immediate, such relationships do not require book-keeping of cost–benefit ratios or sanctions against defectors. We argue that mutualisms and reciprocity, based principally on partner competency, represent a critical factor driving affiliative social interactions and social organization in many primate species (Chapais 2006; Sussman & Garber 2007).

Evolutionary Biology and Conservation of Titis, Sakis and Uacaris, eds. Adrian A. Barnett, Liza M. Veiga, Stephen F. Ferrari and Marilyn A. Norconk. Published by Cambridge University Press.

Pitheciines

In this chapter we examine the published literature on patterns of social interactions and cooperative behavior among adult male pitheciines (*Pithecia*, *Chiropotes* and *Cacajao*). Compared to most other New World primate taxa, bearded sakis and uacaris live in relatively large social units that contain as many as 10–16 adult males (Table 9.1). Although it is often assumed that resident adult male primates compete aggressively for access to reproductive partners, in several species of New World monkeys there is evidence of high levels of within-group tolerance among males (Table 9.1). We explore several theories of social cooperation in order to evaluate the set of factors that promote adult male affiliation in pitheciines.

Pithecia

Pithecia appears to represent a basal member of the pitheciine clade (Bonvicino *et al.* 2003; Schneider & Rosenberger 1996). Although once considered to mate monogamously and live in a pair-bonded social system (Buchanan *et al.* 1981), there is growing evidence, at least in *Pithecia pithecia* (Lehman *et al.* 2001; Norconk 2011), *Pithecia hirsuta* (Soini 1986) and *Pithecia albicans* (Peres 1993), that stable groups may contain as many as 8–12 individuals including 1–4 adult males and 1–3 adult females (Table 9.1).

Pithecia are characterized by a well-developed set of scent glands (Buchanan *et al.* 1981; Norconk 2011) and, in the case of white-faced sakis (*P. pithecia*), males are reported to scent mark more than females. Norconk (2011, p. 131), citing a personal communication from T. Gleason, writes "… adult males huddled, rubbed their chests against each other, and possibly exchanged scent just prior to some inter-troop encounters". In addition, monk sakis (*Pithecia monachus*) have been observed to engage in frequent allogrooming involving most group members (Moynihan 1976). Scent marking and allogrooming appear to represent important tactile and olfactory mechanisms used by male sakis to promote affiliative bonds, coordinate social interactions and maintain group cohesion.

Table 9.1 Demographic, social and reproductive characteristics of pitheciine and atelid genera. Based on a compilation of data from Masterson and Hartwig (1998), Ford (1994), Di Fiore and Campbell (2007), Kowalewski (2007), and Norconk (2006, 2007).

Variable	Pitheciinae			Atelidae			
	Pithecia	***Chiropotes***	***Cacajao***	***Alouatta***	***Lagothrix***	***Ateles***	***Brachyteles***
Group size	1–12	19–44	1–>108 (200?)	6–40	10–49	12–42	7–63
# of males per group	1–4	1–8	16	1–6	2–11	3–6	4–21
# of females per group	1–3	8–10	16	1–15	3–15	5–18	3–28
Within-group male affiliation and social tolerance (grooming, proximity, lining up, tail wagging)	Low/medium	High	High	Low/medium	Medium	High	High
Within-group contest feeding competition (aggressive)	Low	Low	Low	Low	Low	Low	Low
Dispersal	Bisexual	Female-biased	?	Bisexual	Bisexual (?)	Female-biased	Female-biased
Sexual dimorphism – body mass	Medium/high 1.02–1.47	Low 1.08–1.26	Low 1.08–1.26	High 1.31–1.48	Low–medium 1.04–1.45	Low 0.85–1.2	Low 1.283
Sexual dimorphism – canine size[2]	1.17	1.06	1.19	1.25–1.33	1.07–1.22	1.10–1.13	1.15
Sexual dichromatism	Yes (some species)	No	Very low to some (1 species)	Yes (some species)	No	No	No
Testis size/color difference	?	Yes (color)	?	Yes (color)	?	No	Yes (size)
Testis size/body mass[3]	5.8×10^{-4}	?	1.7×10^{-3}	3.2×10^{-3}	2.1×10^{-3}	1.7×10^{-3}	?
Intergroup encounter (collective male defense)	Yes	Yes	?	Yes	Yes	Yes	Yes
Females receptive across year	?	Yes	?	Yes	Yes	Yes	Yes

Table 9.1 *(cont.)*

Variable	Pitheciinae			Atelidae			
	Pithecia	*Chiropotes*	*Cacajao*	*Alouatta*	*Lagothrix*	*Ateles*	*Brachyteles*
Female promiscuity	?	?	Some evidence	Yes	Yes	Yes	Yes
Within-group male intrasexual tolerance during copulations	?	?	Yes (limited data)	In some species	Yes	No (?)	Yes
Groups with within-group adult sex ratios approaching 1 : 1 (female : male)	Yes (0.67–3)	Yes (1.12–5)	Yes (1)	Yes (0.7–4.2)	No (1.3–2.8)	Yes (0.8–4.4)	Yes (0.9–2.4)
Interbirth interval (months)	15–36	24	?	15.9–22.5	36.7±4.7	31.9–50	36.4±4.3
Female mate choice	Weak	Strong	Strong	Weak in some species and strong in others	Strong	Strong	Strong
Seasonality of births	Dry season (also late dry to early wet)	Wet season (also late wet to dry)	Oct–Nov (dry season)	Depends on the site (with and without)	Late wet/ early dry season	Some (it varies)	Dry season
Expected forms of male social cooperation	Mutualism	Mutualism/ reciprocity	Mutualism/ reciprocity	Mutualism	Mutualism/ reciprocity	Reciprocity/ mutualism	Reciprocity/ mutualism

[1] Kay *et al.* (1988), Bowler (pers. commun.); [2]canine dimorphism index (CDI) from Kay *et al.* (1988). If this index is 1.00, there is no canine dimorphism and it would be 2.00 if male canines are twice as large as those of females; [3]Harcourt *et al.* (1995).

Chiropotes

Species of the genera *Chiropotes* live in multimale/multifemale groups containing up to 44 individuals, although groups of approximately 20 individuals are more common (Table 9.1). van Roosmalen *et al.* (1981) and Norconk (2007) indicate that *Chiropotes* social groups travel as a cohesive unit, although they may divide into smaller subgroups to exploit nearby feeding trees. This has been described as a type of fission–fusion social system (Peetz 2001; Veiga *et al.* 2006). In *Chiropotes albinasus* and *Ch. satanas*, stable groups composed of as many as 15 adult males and 13 adult females have been reported (Norconk 2011; Veiga & Ferrari 2006). Regardless of group size, the ratio of adult males to adult females is often close to 1 : 1 (Table 9.1; see also table 8.1 in Norconk 2011). Although only a few long-term studies of bearded saki social organization exist, observations of lone females in *Ch. chiropotes* (Peetz 2001) and *Ch. satanas* (Veiga & Silva 2005) suggest the probability of female dispersal. Male dispersal is less clear, but it is possible that as in atelines (Strier 2000; Di Fiore & Campbell 2007), male bearded sakis either are philopatric or disperse less frequently than females (Veiga, pers. commun.).

Recent studies indicate high levels of affiliative behavior among male *Chiropotes*. In a 16-month study of a group containing 12–15 adult male and 9–13 adult female *Ch. satanas* in Brazil, Veiga *et al.* (2006) found that males were consistently more affiliative to each other than they were to females. In addition, adult males were each other's nearest neighbors 63.7% of the time compared to 15.9% for adult females. In addition to social proximity, over 90% of adult male social interactions were affiliative and included social resting, allogrooming, alliance formation and "lining-up" behavior. Lining-up is a highly ritualized behavioral pattern of body contact between adults which appears to include the exchange of tactile and olfactory information through scent-marking and grooming. In a second study, Peetz (2001) also observed lining-up behavior in male *Ch. chiropotes* in Venezuela. In this study, 17.9% of the activity budget involved social interactions, and 83.7% of which were affiliative.

A second ritualized behavioral pattern described for *Chiropotes* (and *Cacajao*) is tail wagging, which is "accompanied by vocalizations, occurs in a variety of contexts from mild to severe agitation … [and functions during the] … reunion of group members, and group reorganization after rest or feeding periods" (Norconk 2011, p. 129). Both behavioral patterns function to reinforce social bonds, reunite group members, and promote affiliative and cooperative behaviors.

Finally, recent observations by Veiga (pers. commun.) of *Ch. satanas* at Tucuruí in Brazil indicate that females are sexually receptive throughout the year, including periods in which they are transporting small infants and lactating. Female receptivity during non-fertile periods is likely to have an important effect on reproductive strategies, male–female social and reproductive bonds, and the degree to which any single male can monopolize access to females.

Cacajao

Uacaris are the largest-bodied pitheciines, and live in extremely large multimale/multifemale groups (Ayres 1989; Defler 1999; Barnett 2005). In *Cacajao calvus*, groups can be as large as 70–150 individuals, including possibly 30 adult males (Bowler 2007). Defler (2001) indicates that, although most groups of *Cacajao oukary* contain 20–30 animals, he observed a temporary group that may have approached 200 animals. Bowler (2007) reported an average group size of 43.5 at Largo Preto, Peru. Despite their large size, uacari troops appear to be relatively stable, traveling and foraging together "in a coordinated fashion for several days" (Defler 1999, p. 6).

Uacari social interactions and spatial organization have been described as a type of fission–fusion social system, possibly in response to changes in the distribution, availability and productivity of feeding sites (Barnett 2005). In comparison to chimpanzees and spider monkeys (*Ateles*), however, uacari (*Cacajao melanocephalus*) subgroups are relatively large, with counts of 21–30 animals the most common, and subgroups containing 31–100 animals were as common as those of 11–20 (Defler 1999).

In *C. calvus*, larger subgroups or fission–fusion parties occur during periods of mature fruit abundance and smaller and more scattered foraging parties are reported in the dry season (Ayres 1989). Subgroups may disperse over an area of 1–2 km, but coordinate their activities using an extensive repertoire of contact vocalizations.

Despite large group size and the presence of many resident adult males, Boubli (1999) observed virtually no aggressive interactions during a 16-month study of *C. melanocephalus* in Brazil. Similarly, Cunha and Barrett (1989, cited in Barnett & Brandon-Jones 1997) indicate high levels of male–male tolerance in their study groups of *C. ouakary*. Male–male tolerance and cooperation may play a role in predator protection and intergroup encounters. In *C. ouakary* and *C. melanocephaus*, Barnett *et al.* (2005) report that males may remain behind after the rest of the group has left to distract or confront a potential threat. In captivity, same-sex adult uacaris (*C. c. calvus*) also are reported to be highly tolerant of one another (Barnett & Brandon-Jones 1997).

In a recent study of *C. calvus ucayalii*, Bowler (2007) observed all male subgroups of up to 10 individuals on the periphery of large bisexual groups. This author suggests that similar-aged males develop strong social bonds as juveniles which continue when they form bachelor groups. While at least some of these males are almost certainly related (as sibs, half sibs or cousins), the absence of genetic studies impedes a more systematic understanding of the role of kinship in the cooperative relationships of male uacaris.

Discussion

The pitheciines are characterized by social groups containing multiple adult males and females. Direct evidence of within-group contest competition at feeding sites is extremely limited, whereas affiliative and cooperative social interactions among same-sex adult group members, especially males, appears to be common (Peetz 2001; Veiga & Silva 2005). Given the paucity of long-term studies of individually marked pitheciines, the discussion that follows is best considered a starting point from which to examine the social and reproductive costs and benefits of forming large multimale–multifemale ("multi") groups. The presence of stable multi groups across a wide range of primate taxa highlights the reproductive advantages for both males and females of residing in a large troop (Table 9.2).

Why form multimale–multifemale groups?

Due to the relatively high costs and slow rate of reproduction, related primate females may tend to aggregate in an attempt to increase their access to feeding sites, reduce predation risk and enhance offspring survival (van Schaik 1983, 1989). Although this may help to explain the spatial distribution of many matrilineal species, it is less clear how it applies to primates with male philopatry (Strier 1999; Kowalewski 2007). Females may benefit from the presence of several adult males if this guarantees them access to high-quality feeding sites, protection from predators, group stability (reduction in the invasion of potentially infanticidal males) and increased mate choice (van Schaik *et al.* 1999; Crockett & Janson 2000; Pereira *et al.* 2000; Kowalewski 2007; Kowalewski & Garber 2010).

Males, in contrast, may respond to the distribution of females by developing strategies for increasing their access to mating partners (Altmann 1990; Nunn 2000). This can occur in several ways, including (a) forming a pair bond or harem (monopolization), (b) forming small multi groups in which access to fertile females is constrained by a rigid male dominance hierarchy or mate guarding, and (c) forming larger multi groups in which male social interactions are cooperative, non-hierarchical, and all or most resident males have access to receptive females (Table 9.2) and act collectively to exclude extragroup males (Nunn 2000; Pereira *et al.* 2000; Strier 2000; Kowalewski 2007).

Nunn (2000) describes a set of alternative models for examining within-group cooperative behaviors in male primates that promote what he terms the "collective good". Under conditions in which multimale groups are characterized by a rigid linear male hierarchy, the dominant male is the primary breeder and females are receptive only during ovulation, subordinate resident males obtain few direct benefits (possibly long-term expectation of inheriting the dominant breeding position) while incurring potential costs (e.g. injuries) when aiding the dominant male to repel intruders. Under

Table 9.2 Expected effects of within-group male intrasexual social tolerance on reproductive strategies and biology in species characterized by different dispersal patterns. We assume that the majority of new groups form by the fissioning of established groups and therefore individuals may receive benefits from maintaining long-term social bonds with natal group members. In species in which males have reduced intrasexual tolerance, the number of co-resident males will be relatively small.

Dispersal pattern:	**Bisexual dispersal**		**Female dispersal/ male philopatry**
Sociosexual parameter / **Level of male tolerance within group:**	**Intolerant or lower male intrasexual tolerance**	**Higher male intrasexual tolerance**	**Higher male intrasexual tolerance**
Per capita cost of female defense	Higher	Lower	Lower
Risk of infanticide	Higher	Low	Lowest
Per-capita cost of predator detection	Higher	Lower	Lower
Male reproductive tenure	Lower	High	Highest
Ability of males to monopolize matings	Highest	Lower	Lower
Access to a larger number of females	Lower	Higher	Higher
Mate guarding	Higher	Lower	Lower
Cost to male of entering a new group	High	Lower	Highest
Body/canine size dimorphism	Higher	Lower	Low
Testis size/sperm competition	Lower	Higher	Higher
Opportunities for long-term social bonds among males	Low	High	Highest
Opportunities for male–male cooperation	Low	High	Highest
Opportunities for female mate choice	Low	Highest	High
Increased genetic diversity of a female's successive offspring	Lower–higher depending on male tenure in group	Higher	High
Effects of female receptivity during non-mating periods in strengthening male–female social bonds	Lower	Higher	High
Opportunities for females to mate promiscuously	Lower	Higher	Higher

these conditions, male cooperation will have little effect on reproductive skew, as the dominant male is the principle breeder. In contrast, in species characterized by less-rigid hierarchies in which all or most males have at least some access to receptive females, all resident males benefit from the collective defense of receptive females. Assuming that collective action is more effective than individual defense, each male increases his probability of siring offspring in the group (Table 9.2), while the per-capita costs of collective action, whether fighting, chasing, or vocal battles, decrease.

A model of benefits and costs of male cooperation in pitheciines

We begin with the assumption that group size, social organization and behavioral interactions in many primate lineages are determined more by reproductive strategies and demographic parameters than foraging constraints. Bisexual dispersal and female-biased dispersal are common in platyrrhines (Strier 1999, 2000; Steenbeek & van Schaik 2001; Jack 2007). Whereas in the former both males and females must make dispersal decisions, in species with male philopatry, the selection of target groups for dispersal is the responsibility of females.

Within this framework, comparisons with the atelids (Table 9.1) may provide important insights into male cooperation and social strategies in pitheciines, especially considering that this platyrrhine group probably represents the sister taxon of the Pitheciidae (Schneider & Rosenberger 1996). In *Brachyteles* and *Ateles*, dispersal is female-biased, established groups are largely composed of male patrilines with unrelated adult females, and within-group social bonds among adult males are highly affiliative and cooperative (Strier 1992; Di Fiore & Campbell 2007). In these taxa, females are promiscuous, actively solicit copulations from males, appear to exercise mate choice and are receptive outside of their fertile periods (Table 9.1). Female receptivity during non-fertile periods may reinforce male cooperative mate defense, as well as strengthen sociosexual bonds between males and females. In the case of the northern muriquis (*Brachyteles* *hypoxanthus*), Strier (2000, p. 72) reports that "male kin display tolerance toward one another's sexual activities in exchange for cooperation in competitive contests with other male kin groups over access to females".

In *Ateles*, adult males are each other's closest social partners (Symington 1990). Resident females mate with multiple males, and males jointly patrol the borders of their range and act collectively to repel intruders (Table 9.1). Although kinship may play an important role in understanding the benefits of male mating tolerance in spider monkeys and muriquis, many cooperative behaviors such as tolerance at feeding sites, minimal within-group intrasexual aggression, greeting behaviors, and cooperative group or mate defense may be best classified as mutualisms – relatively low-cost behaviors from which several individuals receive immediate benefits.

In contrast with *Ateles* and *Brachyteles*, dispersal in woolly monkeys (*Lagothrix*) appears to be bisexual, and affiliative bonds between adult males are reported to be weaker (Table 9.1). Grooming relationships and spatial proximity, however, are strong between adult and subadult males, and adult males appear to cooperate during intergroup encounters (Di Fiore & Campbell 2007). Female woolly monkeys solicit copulations, copulate outside their ovulatory period, and adult males are highly tolerant of within-group copulations by other resident males (Peres 1996).

Alouatta is characterized by bisexual dispersal, and therefore adult group members are generally unrelated (Table 9.1). Although in red howlers (*Alouatta seniculus*) related males may disperse together into the same group and females are more tolerant of adult daughters than unrelated females (Pope 2000), this does not appear to be the case for other species. In *Alouatta palliata*, the overwhelming majority of females and males disperse from their natal group (Clarke & Glander 2001), and stable bisexual groups with as many as 8–12 adult males have been reported (Chapman 1990). Wang and Milton (2003) identified an alpha male in an *A. palliata* group with 6 males and 12 females in Panama, but could not discern any hierarchy among the other resident males of the group. In addition, these authors observed several males copulating with the same female during her estrous period in full view of other males, including the alpha male, without eliciting an aggressive response.

Although *A. palliata* is unusual in living in groups that can exceed 20 individuals, other howler species are known to form smaller bisexual groups composed of one or a small number of adult males (Brockett *et al.* 2001; Crockett & Janson 2000; Kowalewski & Zunino 2004). In *Alouatta caraya*, groups may contain up to four adult males (Kowalewski 2007), within-group agonism is rare, and adult males spend as much as 5.2% of their activity budget engaged in affiliative behavior including grooming and embracing. In addition, females may mate with most or all resident male group members during both fertile and non-fertile periods, and in full view of other male group members (Table 9.1). Unrelated resident adult male *A. caraya* act cooperatively to defend the group from incursions by extra-group males throughout the year (Table 9.2).

Overall, we feel that atelids offer an instructive model for understanding the basis of male cooperation in the pitheciines. Depending on patterns of natal and secondary migration, adult sex ratio and group stability, we expect partner reliability and competence, kinship and the mutual benefits of cooperative mate defense to be primary factors in the evolution of male social tolerance (Table 9.2). Given long-term residence in the same social group, opportunities for cooperative reciprocity among males are expected to be greater in male philopatric species than in species in which males migrate (unless male relatives migrate in pairs: Garber *et al.* 1993; Jack 2007). In addition, mutualistic behaviors among either related or unrelated males are likely to be very common given their immediate return and low cost to all participants (Dugatkin 1997). Moreover, if the presence of several adult males offers advantages to females in terms of enhanced infant survivorship or greater genetic diversity for their offspring (Garber 1997; Altmann 1990; Mitani *et al.* 1996; Nunn 2000), then females may prefer groups composed of cooperative adult males. Female promiscuity and sexual receptivity during non-fertile periods would serve to promote male–female bonds and reduce the potential for infanticide.

In conclusion, present evidence indicates high levels of social tolerance among resident male pitheciines. The basis of male–male cooperation in the pitheciines requires additional long-term behavioral and genetic investigation. We view intrasexual social cooperation as an important component of a male reproductive strategy, and have tried to identify factors that are likely to influence the costs and benefits of male cooperation. Based on comparisons with the atelids, low-cost forms of mutualism appear to best explain male cooperation in *Pithecia*. In *Chiropotes* and *Cacajao*, we anticipate that mutual and immediate benefits of cooperation are common, but where males reside in the same group over long periods of time, low-cost forms of reciprocity also are expected (Table 9.2). Male–male tolerance, affiliation and cooperation are found in many platyrrhine taxa (e.g. Boinski 1994; Di Fiore & Campbell 2007; Digby *et al.* 2007). It is likely that long-term familiarity, partner competence and the mutual and reciprocal benefits of male collective action represent the primary adaptive basis of male–male cooperation in many primate species (Chapais 2006; Dugatkin 1997).

Acknowledgments

PAG wishes to acknowledge the nonhuman primates of Central and South America for allowing me to observe the intimate details of their lives for over 30 years. PAG thanks Sara and Jenni for teaching me about the virtues of tolerance and cooperation, and Chrissie McKenney for her love and kindness. MK thanks all his friends and especially dedicates this chapter to Polo – Ramon Romero – for years of cooperation, friendship, assistance and collaboration. We thank Mark Bowler for allowing us to cite his unpublished data on *Cacajao calvus*, and for his sharing his insights on pitheciine social behavior.

References

Altmann, J. (1990). Primate males go where the females are. *Animal Behaviour*, **39**, 193–195.

Ayres, J.M. (1989). Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *Journal of Human Evolution*, **18**, 697–716.

Axelrod, R. & Hamilton, W.D. (1981). The evolution of cooperation. *Science*, **211**, 1390–1396.

Barnett, A.A. (2005). *Cacajao melanocephalus. Mammalian Species*, **776**, 1–6.

Barnett, A.A. & Brandon-Jones, D. (1997). The ecology, biogeography and conservation of the uakaris, *Cacajao* (Pitheciinae). *Folia Primatologica*, **68**, 223–235.

Boesch, C., Boesch, H. & Vigilant, L. (2006). Cooperative hunting in chimpanzees: kinship or mutualism In *Cooperation in Primates and Humans: Mechanisms and Evolution*, ed. P.M. Kappele r & C.P. van Schaik. Berlin: Springer Verlag, pp. 139–150.

Boinski, S. (1994). Affiliation patterns among male Costa Rican squirrel monkeys. *Behaviour*, **130**, 191–209.

Bonvicino, C.R., Boubli, J.P., Otazu, I.B., *et al.* (2003). Morphologic, karyotypic, and molecular evidence of a new form of *Chiropotes* (Primates, Pitheciinae). *American Journal of Primatology*, **61**, 123–133.

Boubli, J.P. (1999). Feeding ecology of black-headed uacaris (*Cacajao melanocephalus melanocephalus*) in Pico do Neblina National Park, Brazil. *International Journal of Primatology*, **20**, 719–749.

Bowler, M. (2007). The ecology and conservation of the red uakari monkey on the Yavarí River, Peru. Unpublished PhD thesis, University of Kent.

Brockett, R.C., Horwich, R.H. & Jones, C.B. (2001). Reproductive seasonality in the Belizean black howling monkey (*Alouatta pigra*). *Neotropical Primates*, **8**, 136–138.

Buchanan, D.B., Mittermeier, R.A. & van Roosmalen, M.G.M. (1981). The saki monkeys, genus *Pithecia*. In *Ecology and Behavior of Neotropical Primates*, Vol. 1., ed. A.F. Coimbra-Filho & R.A. Mittermeier. Rio de Janeiro: Academia Brasileira de Ciências, pp. 391–417.

Chapais, B. (2006). Kinship, copetence and cooperation in primates. In *Cooperation in Primates and Humans: Mechanisms and Evolution*, ed. P.M. Kappeler & C.P. van Schaik, Berlin: Springer Verlag, pp. 47–64.

Chapman, C.A. (1990). Ecological constraints on group size in three species of Neotropical primates. *Folia Primatologica*, **55**, 1–9.

Chapman, C.A. & Chapman, L.J. (2000). Determinants of group size in primates: the importance of travel costs. In *On the Move: How and Why Animals Travel in Groups*, ed. S. Boinski & P.A. Garber. Chicago, IL: University of Chicago Press, pp. 24–42.

Clarke, M.R. & Glander, K.E. (2001). Presence of mother and juvenile dispersal in free-ranging howling monkeys (*Alouatta palliata*) in the tropical dry forest of Costa Rica. *American Journal of Physical Anthropology*, Suppl **32**, 50.

Crockett, C.M. & Janson, C. (2000). Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In *Infanticide by Males and its Implications*, ed. C.P. van Schaik & C. Janson. Cambridge: Cambridge University Press, pp. 75–98.

Defler, T.R. (1999). Fission–fusion in the black-headed uacari (*Cacajao melanocephalus*) in eastern Colombia. *Neotropical Primates*, **7**, 5–8.

Defler, T.R. (2001). *Cacajao melanocephalus ouakary* densities on the lower Apaporis River, Colombian Amazon. *Neotropical Primates*, **9**, 31–36.

Di Fiore, A. & Campbell, C.J. (2007). The atelines: variation in ecology, behavior, and social organization. In *Primates in Perspective*, ed. C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger & S.K. Bearder. New York, NY: Oxford University Press, pp. 155–185.

Digby, L.J., Ferrari, S.F. & Saltzman, W. (2007). Callitrichines: the role of competition in coopertatively breeding species. In *Primates in Perspective*, ed. C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger & S.K. Bearder. New York, NY: Oxford University Press, pp. 85–106.

Dugatkin, L.A. (1997). *Cooperation among Animals: An Evolutionary Perspective*. New York, NY: Oxford University Press.

Ford, S.M. (1994). Evolution of sexual dimorphism in body weight in platyrrhines. *American Journal of Primatology*, **34**, 221–244.

Garber, P.A. (1997). One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. *Evolutionary Anthropology*, **5**, 187–199.

Garber, P.A., Encarnación, FF., Moya, L., *et al.* (1993). Demographic and reproductive patterns of mating in moustached tamarin monkeys (*Saguinus mystax*): implications for reconstructing platyrrhine mating systems. *American Journal of Primatology*, **29**, 235–254.

Goldberg, T.L. & Wrangham, R.W. (1997). Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA. *Animal Behaviour*, **54**, 559–570.

Hamilton, W.D. (1964). The genetical evolution of social behavior. I and II. *Journal of Theoretical Biology*, **7**, 17–52.

Harcourt, A.H., Purvis, A. & Liles, L. (1995). Sperm competition: mating system, not breeding season, affects testes size of primates. *Functional Ecology*, **9**, 468–476.

Jack, K.M. (2007). The cebines: toward an explanation of variable social structure. In *Primates in Perspective*, ed. C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger & S.K. Bearder. New York, NY: Oxford Univesity Press, pp. 107–122.

Janson, C. (2000). Primate socio-ecology: the end of a golden age. *Evolutionary Anthropology*, **9**, 73–86.

Janson, C. & Goldsmith, M.L. (1995). Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology and Sociobiology*, **6**, 326–336.

Kappeler, P.M. & van Schaik, C.P. (2002). Evolution of primate social systems. *International Journal of Primatology*, **23**, 707–740.

Kay, R.F., Plavcan, J.M., Glander, K.E., *et al.* (1988). Sexual selection and canine dimorphism in New World monkeys. *American Journal of Primatology*, **77**, 385–397.

Koenig, A., Beise, J., Chalise, M.K., *et al.* (1998). When females should contest for food: testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology*, **42**, 225–237.

Kowalewski, M.M. (2007). Patterns of affiliation and co-operation in howler monkeys: an alternative model to explain social organization in non-human primates. PhD thesis, University of Illinois.

Kowalewski, M.M. & Garber, P.A. (2010). Mating promiscuity and reproductive tactics in female black and gold howler monkeys (*Alouatta caraya*) inhabiting an island on the Parana River, Argentina. *American Journal of Primatology*, **72**, 734–748.

Kowalewski, M.M. & Zunino, G.E. (2004). Birth seasonality in *Alouatta caraya* in Northern Argentina. *International Journal of Primatology*, **25**, 383–400.

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

Masterson, T.J. & Hartwig, W.C. (1998). Degrees of sexual dimorphism in *Cebus* and other New World monkeys. *American Journal of Physical Anthropology*, **107**, 243–256.

Mitani, J.C. (2006). Reciprocal exchange in chimpanzees and other primates. In *Cooperation in Primates and Humans: Mechanisms and Evolution*, ed. P.M. Kappeler & C.P. van Schaik. Berlin: Springer Verlag, pp. 107–120.

Mitani, J.C., Gross-Louis, J. & Manson, J.H. (1996). Number of males in primate groups: comparative tests of competing hypotheses. *American Journal of Primatology*, **38**, 315–332.

Moynihan, M. (1976). *The New World Primates*. Princeton, NJ: Princeton University Press.

Noe, R. (2001). Biological markets: partner choice as the driving force behind the evolution of mutualisms. In *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*, ed. R. Noe, J.A.R. A.M. van Hoof & P. Hammerstein. Cambridge: Cambridge University Press, pp. 93–118.

Norconk, M.A. (2006). Long-term study of group dynamics and female reproduction in Venezuelan *Pithecia pithecia*. *International Journal of Primatology*, **27**, 653–674.

Norconk, M.A. (2011). Sakis, uakaris, and titi monkeys: behavioral diversity in a radiation of primate seed predators In *Primates in Perspective* (2nd end), ed. C.J. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder & R.M. Stumpf. New York, NY: Oxford University Press, pp. 122–139.

Norconk, M.A. & Conklin-Brittain, N.L. (2004). Variation on frugivory: the diet of Venezuelan white-faced sakis. *International Journal of Primatology*, **25**, 1–26.

Nunn, C.L. (2000). Collective benefits, free-riders, and male extra-group conflict. In *Primate Males: Causes and Consequence of Variation in Group Composition*, ed. P.M. Kappeler. Cambridge: Cambridge University Press, pp. 192–204.

Peetz, A. (2001). Ecology and social organisation of the bearded saki, *Chiropotes satanas chiropotes* (Primates: Pitheciinae) in Venezuela. *Ecotropical Monographs*, **1**, 1–170.

Pereira, M.E., Clutton-Brock, T.H. & Kappeler, P.M. (2000). Understanding primate males. In: *Primate Males: Causes and Consequence of Variation in Group Composition*, ed. P.M. Kappeler. Cambridge: Cambridge University Press, pp. 271–277.

Peres, C.A. (1993). Notes on the ecology of buffy saki monkeys (*Pithecia albicans*, Gray 1860): a canopy seed predator. *American Journal of Primatology*, **31**, 129–140.

Peres, C.A. (1996). Use of space, spatial group structure, and foraging groups size of gray woolly monkeys (*Lagothrix lagotricha cana*) at Urucu, Brazil: a review of the Atelinae. In *Adaptive Radiations of Neotropical Primates*, ed. M.A. Norconk, A.L. Rosenberger & P.A. Garber. New York, NY: Plenum Press, pp. 467–488.

Pope, T.R. (2000). Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behavioral Ecology and Sociobiology*, **48**, 253–267.

Schneider, H. & Rosenberger, A.L. (1996). Molecules, morphology, and platyrrhine systematics. In *Adaptive Radiation of Neotropical Primates*, ed. M.A. Norconk, A.L. Rosenberger & P.A. Garber. New York, NY: Plenum Press, pp. 3–20.

Smuts, B.B. (1997). Social relationships and life histories of primates. In *The Evolving Female: A Life-History Perspective*, ed. M.E. Morbeck, A. Galloway & A.L. Zihlman. Princeton, NJ: Princeton University Press, pp. 60–68.

Snaith, T.V. & Chapman, C.A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, **59**, 185–190.

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

Steenbeek, R. & van Schaik, C.P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and Sociobiology*, **49**, 100–110.

Sterck, E.H.M., Watts, D.P. & van Schaik, C.P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, **41**, 291–309.

Strier, K.B. (1992). Causes and consequences of nonaggression in the woolly spider monkey, or muriqui (*Brachyteles arachnoides*). In *Aggression and Peacefulness in Humans and Other Primates*, ed. J. Silverberg & J.P. Gray. New York, NY: Oxford University Press, pp. 100–116.

Strier, K.B. (1999). Why is female kin bonding so rare? Comparative sociality of neotropical primates. In *Comparative Primate Socioecology*, ed. P.C. Lee. Cambridge: Cambridge University Press, pp. 300–319.

Strier, K.B. (2000). From binding brotherhoods to short-term sovereignty: the dilemma of male Cebidae. In *Primate Males: Causes and Consequence of Variation in Group Composition*, ed. P.M. Kappeler. Cambridge: Cambridge University Press, pp. 72–83.

Sussman, R.W. & Garber, P.A. (2007). Cooperation and competition in primate social interactions. In *Primates in Perspective*, ed. C.J. Campbell, A. Fuentes, K.C. MacKinnon, M. Panger & S.K. Bearder. New York, NY: Oxford University Press, pp. 636–651.

Symington, M.M. (1990). Fission–fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology*, **11**, 47–61.

Trivers, R. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 25–57.

van Roosmalen, M.G.M., Mittermeier, R.A. & Milton, K. (1981). The bearded sakis, genus *Chiropotes*. In *Ecology and Behavior of Neotropical Primates, Volume 1*, ed. A.F. Coimbra-Filho & R.A. Mittermeier. Rio de Janeiro: Academia Brasileira de Ciências, pp. 419–442.

van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour*, **87**, 120–144.

van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. In *Comparative Socioecology. The Behavioural Ecology of Humans and Other Mammals*, ed. V. Standen & R.A. Foley. Oxford: Blackwell Scientific, pp. 195–218.

van Schaik, C.P. & Kappeler, P.M. (2006). Cooperation in primates and humans: closing the gap. In: *Cooperation in Primates and Humans: Mechanisms and Evolution*, ed. P.M. Kappeler & C.P. van Schaik. Berlin: Springer Verlag, pp. 3–21.

van Schaik, C.P., van Noordwijk, M.A. & Nunn, C.L. (1999). Sex and social evolution in primates. In *Comparative Primate Socioecology*, ed. P.C. Lee. Cambridge: Cambridge University Press, pp. 204–231.

Veiga, L.M. & Ferrari, S.F. (2006). Predation of arthropods by southern bearded sakis (*Chiropotes satanas*) in Eastern Brazilian Amazonia. *American Journal of Primatology*, **68**, 209–215.

Veiga, L.M. & Silva, S.S.B. (2005). Relatives or just good friends? Affiliative relationships among male southern bearded sakis (*Chiropotes satanas*). *Livro de Resumos, XI Congresso Brasileiro de Primatologia*, Porto Alegre: Sociedade Brasileira de Primatologia, p. 174.

Veiga, L.M., Pinto, L.P. & Ferrari, S.F. (2006). Fission–fusion sociality in bearded sakis (*Chiropotes albinasus* and *Chiropotes satanas*) in Brazilian Amazonia. *International Journal of Primatology*, **27**(Suppl 1), 224.

Wang, E. & Milton, K. (2003). Intragroup social relationships of male *Alouatta palliata* on Barro Colorado Island, Republic of Panana. *International Journal of Primatology*, **24**, 1227–1244.