Chapter 3 The Behavior, Ecology, and Social Evolution of New World Monkeys

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RESEARCH ON the behavior and ecology of New World primates (infraorder Platyrrhini) began in the 1930s with C. R. Carpenter's pioneering work on mantled howler monkeys (*Alouatta paliatta*) and Geoffroy's spider monkeys (*Ateles geoffroyi*) in Panama (Strier 1994a, for a brief review). It was not until the late 1970s and 1980s, however, that significant work on the ecology and behavior of wild populations of platyrrhines developed (Coimbra-Filho & Mittermeier 1981; Mittermeier et al. 1981). For a long time, research on neotropical primates tended to focus more on aspects of the natural history and diversity of New World taxa than on the theoretical issues being debated by researchers focused on Old World monkeys and apes. Thus, by the mid-1980s, insufficient information was available from long-term studies of platyrrhines to contribute significantly to the canon of primate socioecological theory, or to test most hypotheses and predictions stemming from studies of Old World primates. Even by the late 1990s, most field data on New World primates had been gathered from a few genera (*Alouatta*, *Ateles*, *Cebus*, *Leontopithecus*, *Saimiri*) studied at a few research sites, or from studies of one or two social groups at a single location. In the 25 years since the publication of *Primate Societies* (Smuts et al. 1987), neotropical primatology has grown impressively. In this chapter we provide an overview of our current understanding of the behavior, ecology, and social evolution of platyrrhines.

Diversity and Biogeography

Platyrrhines occur exclusively in the tropical and subtropical Americas, from northern Mexico to northern Argentina. They represent a radiation of primates with a long evolutionary history independent from those of catarrhines and strepsirrhines. Based on several molecular studies conducted over the past decade (Schneider et al. 1993, 1996, 2001; von Dornum & Ruvolo 1999; Singer et al. 2003; Ray et al. 2005; Opazo et al. 2006; Poux et al. 2006), we now have a far better appreciation of the evolutionary relationships among the platyrrhines than we did 25 years ago. Molecular data strongly confirm that extant taxa can be divided into three major monophyletic groups: the atelids (muriquis, spider monkeys, woolly monkeys, and howlers), the pitheciids (titis, sakis, bearded sakis, and uakaris), and the cebids (marmosets and tamarins, squirrel monkeys, capuchins, and owl monkeys). The branching order among these three major groups remained unclear for many years, even after molecular data had shed light on the evolutionary relationships among genera within each of them. More recently, data from various molecular markers have provided support for the position of the pitheciids as basal within the platyrrhine radiation (Herke et al. 2007; Hodgson et al. 2009). It has also become clear that the three extant families diverged rapidly; the internode between the last common ancestor of all extant platyrrhines and the last common ancestor of the pitheciids and the atelid-cebid clade was very short, on the order of only a few million years, thus contributing to the difficulty of resolving the relationships among the major groups (Opazo et al. 2006; Hodgson et al. 2009).

Among the atelids, four genera are proposed (table 3.1). A fifth genus (*Oreonax*, Groves 2001) has been suggested, but the promotion of this taxon to a new genus has been questioned (Rosenberger & Matthews 2008). The pitheciids include four genera. The number of species is still debated, and for titi monkeys in particular the estimates vary considerably and are a topic of much debate (table 3.1 follows the classification of Rylands & Mittermeier 2009; for alternative classifications see Hershkovitz 1990; van Roosmalen et al. 2002). The third family consists of three quite distinct subfamilies: the Cebinae (including capuchins and squirrel monkeys), the Aotinae, and the Callitrichinae. This lastsubfamily traditionally included five genera (table 3.1), but some authors have proposed dividing the genus *Callithrix* (marmosets) and adding two genera, *Mico* (Amazonia marmosets, Rylands & Mittermeier 2009) and *Callibella* (black-crowned dwarf marmoset, van Roosmalen & van Roosmalen 2003). The position of *Aotus* was for a long time unclear, but it is now established within the Cebidae, even though its exact position within the family is still controversial (Opazo et al. 2006; Hodgson et al. 2009; Babb et al. 2011).

Even when the evolutionary relationships among clades are apparently resolved, the geographic and temporal origins of the platyrrhines remain topics of debate among contemporary primatologists. Phylogenetic analyses of both fossil and molecular data strongly support the position that platyrrhines are a monophyletic group that originated from migrants moving from Africa to South America (Bandoni de Oliveira et al. 2009). Additionally, coalescence analyses constrained by well-regarded fossil dates indicate that the separation of neotropical monkeys from African anthropoids occurred approximately 40 million years ago (Goodman et al. 1998; Schrago & Russo 2003). Nonetheless, there is still discussion regarding *how* stem platyrrhines moved from Africa to South America and *when* they did so. The existing evidence does not support the idea of a land bridge connecting Africa and South America, but instead indicates an oceanic dispersal sometime between 50 and 30 million years ago as the most likely explanation of the distribution of fossil and present day taxa (Bandoni de Oliveira et al. 2009).

Molecular estimates of divergence dates among the various lineages suggest a relatively rapid radiation, at least among extant taxa. The last common ancestor of living platyrrhines, for example, dates to the early Miocene, only 20 million years ago (Poux et al. 2006; Hodgson et al. 2009). The oldest fossil New World monkeys, dating to approximately 26 million years ago, are the Bolivian *Branisella boliviana* and *Szalatavus attricuspis* (Fleagle & Tejedor 2002). According to some researchers, several fossil taxa from the middle Miocene show affinities to a range of modern forms. This has led to the formulation of the "Long Lineage Hypothesis," which proposes that a preponderance of long-lived generic lineages, characterized by morphological stasis, may be a defining feature of the platyrrhine radiation during the past 15 to 20 million years (Rosenberger et al. 2009). Still others believe these fossils to belong to extinct lineages, and thus view successive radiations as crucial characteristics of the group, with a rapid radiation of the crown group of extant platyrrhines starting approximately 20 million years ago (Hodgson et al. 2009).

Ecology and Life History

A full understanding of the New World primate radiation requires knowledge of ecological conditions at the time of the colonization of South America. The first ancestors arriving on the continent would not have encountered the conditions that characterize contemporary tropical Amazonia, as the Amazon basin only began to take on its present character approximately 15 million years ago and changed profoundly during the Cenozoic (Bigarella & Ferreira 1985; Campbell et al. 2006; Hoorn et al. 2010). Due to the Andean uplift, for example, the original drainage system was reversed: the western parts of today's Amazonia harbored large areas of wetlands, shallow lakes, and swamps, changing later to fluvial systems dominated by grasses (Hoorn et al. 2010).

There is substantial evidence indicating that the radiation of New World primates occurred within a narrower range of ecological variation than the one cercopithecoids may have experienced. For example, no members of the radiation, fossil or extant, evolved to fill several comparable ecological niches occupied by fossil or extant primates in the Old World (see below). This relatively narrow ecological range available to New World monkeys is highlighted in an analysis of the ecological niche space of modern primate communities worldwide. Fleagle and Reed (1996) used a suite of variables (e.g., body size, activity pattern, locomotor pattern, diet) to characterize the members of eight well-studied primate communities, two from each of the major biogeographic regions where extant primates are found (the New World, Africa, Asia, and Madagascar). Using principal components analysis, they reduced those variables to two dimensions that maximally captured the variation in niche space across primate taxa, and examined the total "ecological space" thus covered by different primate communities.

Table 3.1. Taxonomy, number of species, body mass, diet, and brain mass of the 18 platyrrhine genera

Family[a]	Subfamily[a] / tribe	Genus	Common name	Number of species[a]	Adult female body mass (kg)[b]	Adult male body mass (kg)[b]	Diet#	Brain mass [g]/ body mass [g][c]
Atelidae	Alouattini	*Alouatta*	Howler monkey	14	4.3–6.6	6.3–11.4	F, L, I	55.1/6550[d]
								50.0/5085[e]
								50.8/6400[f]
	Atelini	*Ateles*	Spider monkey	7	7.3–9.3	7.8–9.4	L, F, I	110.9/6000[d]
								104.7/8000[f]
		Lagothrix[g]	Woolly monkey	5	4.5–7.7	7.1–9.4	L, F, I	96.4/6300[d]
								92.7/7650[e]
								98.9/5200[f]
		Brachyteles	Muriqui	2	8.3–8.5	9.4–10.2	L, F, I	115.5/8380[e]
Pitheciidae	Callicebinae	*Callicebus*	Titi monkey	29	0.81–1.4	0.85–1.3	F, S, L, I	18.6/900[f]
	Pithecinae	*Pithecia*	Saki	5	1.6–2.1	1.9–3.0	S, F, L, I	34.1/1500[f]
		Chiropotes	Bearded saki	5	2.5–3.0	2.9–3.2	S, F, L, I	n.a.
		Cacajao	Uakari	3	2.7–2.9	3.2–3.5	S, F, L, I	n.a.
Cebidae	Cebinae	*Cebus*	Capuchin	12	2.3–2.5	3.2–3.7	F, I, V	62.6/2377[e]
								69.3/3100[f]
	Saimirinae	*Saimiri*	Squirrel monkey	5	0.65–0.80	0.78–1.0	I, F, V	24.4/665[d]
								23.4/660[f]
	Aotinae	*Aotus*	Owl/night monkey	10	0.7–1.2	0.7–1.2	F, L, I	18.2/960[d]
								16.8/830[f]
	Callitrichinae	*Callimico*	Goeldi's monkey	1	0.36	0.37	Fu, F, I, V, Ex	10.9/480[f]
		Callithrix	Atlantic marmoset	6	0.3–0.43	0.32–0.43	Ex, F, I, V, Fu	7.9/300[d]
								7.5/280[f]
		Callibella	Black-crowned dwarf marmoset	1	0.17	0.13	Ex, F, I, V	n.a.
		Mico	Amazonian marmoset	13	0.33–0.4	0.32–0.37	Ex, F, I, V	n.a.
		Cebuella	Pygmy marmoset	1	0.12	0.11	Ex, F, I, V	4.5/140[f]
		Saguinus	Tamarin	15	0.36–0.54	0.34–0.59	F, I, V, Ex	9.0/500[d]
								9.9/360[f]
		Leontopithecus	Lion tamarin	4	0.54–0.60	0.58–0.62	F, I, V, Ex	13.0/600[e]

#: F = fruit, flowers, or nectar; Fu = fungi; S = seeds; Ex = exudates (tree gums and saps); L = leaves; I = insects; V = vertebrates.

[a] Number of species and subfamilies follows Rylands & Mittermeier (2009), except for the inclusion of *Oreonax/Lagothrix flavicauda* into *Lagothrix*; refer to the relevant chapters in Campbell et al. (2007) for other estimates of species numbers. Family designations follow Opazo et al. 2006.

[b] Body mass gives the range of the averages provided by Smith and Jungers (1997), except for *Callibella* (van Roosmalen and van Roosmalen 2003), *Callimico* (Encarnación and Heymann 1998), and *Lagothrix* and *Brachyteles* (Di Fiore et al. 2010).

[c] Values are available for only one or a few species. Body mass and brain values are reported for the same species.

[d] Schillaci (2006): Values for brain masses are average values for males and females, without stating explicitly whether wild or captive.

[e] Barrickman (2008): Values are for wild female body masses and female brain masses; for *Cebus* the means of three species' ratios were used.

[f] Pérez-Barbería (2007): Not explicitly stated whether samples are from males or females, or from wild or captive animals.

[g] Includes the contested genus *Oreonax*.

Their analysis suggested that the range of "ecological space" occupied by New World monkeys is considerably smaller than that occupied by primate communities in other major biogeographic regions. In other words, extant New World monkeys show less adaptive diversity in ecological patterns than is seen in other parts of the world and in other major primate radiations (Fleagle & Reed 1996). In contrast, the adaptive radiation of platyrrhines was accompanied by the evolution of several unique morphological and behavioral features (e.g., prehensile tails), as well as substantial variability in social systems not seen outside of the clade (see below).

Body Size and Unique Morphological Traits

The smallest New World monkeys are the pygmy marmosets (*Cebuella pygmaea*), with a body mass slightly over 100 g. The largest members, found among the atelids, can weigh more than 10 kg (table 3.1). Marmosets and tamarins apparently reduced their body size during the course of their evolution ("phyletic dwarfism," Martin 1992). The callitrichines also secondarily evolved claw-like nails (tegulae) on most digits, which enable them to use smooth vertical trunks as substrates for locomotion or feeding.

Another unique trait among some platyrrhines, prehensility in the tail (fig. 3.1), evolved not once but twice: in stem atelids and in stem capuchins (Rosenberger 1983). Again, it is not obvious what selective pressures may have led to the parallel evolution of prehensile tails in these two groups, but the tail is used in both groups to provide support and balance in a variety of suspensory postures and during locomotion, even though in *Cebus* the tail is not fully prehensile (Garber & Rehg 1999; Cant et al. 2003; Schmitt et al. 2005). In this context, it is intriguing to note that prehensile tails evolved in a variety of neotropical taxa, distributed among six mammalian, one amphibian, and two reptilian families. In contrast, their evolution has been much rarer in the paleotropics. One possible explanation is that the forest structure of the neo- and paleotropics may differ in the relative number of lianas and palm trees (Emmons & Gentry 1983).

Fig. 3.1. A white-bellied spider monkey (*Ateles belzebuth*) in Amazonian Ecuador hangs by its prehensile tail. Photo courtesy of Dylan Schwindt.

Brain Size

There have been numerous attempts to examine the relationships that might exist between brain size and various life history traits and cognitive abilities among primates (van Schaik et al. 2006; Deaner et al. 2007; Barrickman et al. 2008; chapter 10, this volume). In both New and Old World monkeys, brain mass does not simply increase allometrically with body mass; there seems to be a clearer relationship with energy supply, suggesting an important role for basal metabolic rate (Armstrong 1985). Tradeoffs between investment in brain tissue and in growth or reproduction are examined in more detail in chapter 10. Generally, studies investigating those relationships have used different measures and methods that have hindered comparative analyses (Barrickman et al. 2008). Table 3.1 presents the ratio of brain mass to body mass for representatives of most genera (see also chapter 10, this volume). These values, however, should be considered with caution for several reasons. First, data are usually only available for one species within a genus, even when there may be considerable intrageneric variability in both of these measures. Second, the data are heterogeneous. Some are from captive individuals, who are typically larger in body mass, whereas other data are from wild animals. Some data are only from females and others are from members of both sexes. For these reasons, we include in table 3.1 the body mass of the species for which brain mass is reported. Third, although some authors maintain that total brain mass explains cognitive abilities better than brain/body ratios (van Schaik et al.

2006; Deaner et al. 2007), others prefer to use specific parts of the brain (e.g., see Rilling & Insel 1999) or ratios of specific parts (de Winter & Oxnard 2001; Walker et al. 2006) to analyze potential patterns within primates. These caveats aside, there seem to be no clear patterns across taxa in the relationships among brain variables, life history traits, and cognitive abilities and, in contrast to strepsirrhines (chapter 2, this volume), no fundamental difference between catarrhines and platyrrhines (de Winter & Oxnard 2001; Oxnard 2004; Rosa & Tweedale 2005; Walker et al. 2006).

Diet

All New World monkeys have rather catholic diets (table 3.1), even if some taxa show specializations for particular kinds of food items. For example, some of the idiosyncratic structures of the callitrichines (claws and marmoset dentition) allow them to exploit food resources such as gums, saps, and embedded insect prey that are not available to many other arboreal mammals besides rodents (Garber 1992). Still, some marmosets, like the buffy-tufted-ear marmoset (*Callithrix aurita*), may devote as much as 11% of their diet to fruits and 39% to animal prey (Martins & Setz 2000). At one site in Bolivia, Goeldi's monkeys (*Callimico goeldii*) commonly consume fungi, a food source very rarely used by other primates (Porter 2001b). There are no New World primates committed to folivory, either behaviorally or morphologically, as are some other primates like Malagasy lemurs (e.g., *Propithecus*, *Lepilemur*, *Indri*, *Hapalemur*, *Prolemur*), most colobines, geladas (*Theropithecus gelada*), or mountain gorillas (*Gorilla gorilla*). Still, a significant commitment to folivory evolved twice, independently in howlers (*Alouatta* spp.) and in muriquis (*Brachyteles* spp); these taxa have evolved dental and behavioral adaptations for folivory, instead of the digestive specializations displayed by other primates (Milton 1993, 1998; Lambert 1998).

Predation

Both large and small neotropical primates are preyed upon by several animals. Predators include constricting and venomous snakes (Chapman 1986; Heymann 1987; Corrêa & Coutinho 1997; Cisneros-Heredia et al. 2005), tayras (*Eira barbara*, a mustelid species, Bezerra et al. 2009), felids (Peetz et al. 1992; Miranda et al. 2005; Bianchi & Mendes 2007; Ludwig et al. 2007) domestic animals (Oliveira et al. 2008; Raguet-Schofield 2008), raptors (Sherman 1991; Julliot 1994; Oversluijs Vásquez & Heymann 2001; Martins et al. 2005; De Luna et al. 2010), and even other monkeys (Sampaio & Ferrari 2005). Observations of unsuccessful predator attacks provide convincing evidence that New World monkeys derive benefits in terms of avoiding predation via group life and group defense (Eason 1989; Shahuano Tello et al. 2002; chapter 8, this volume).

It is plausible that the kinds of predators that platyrrhines encounter, and the antipredator strategies they might employ could differ qualitatively from those present in other primate groups. For example, some evidence suggests that platyrrhines may have radiated initially in the absence of venomous snakes, since the latter arrived in South America after the platyrrhines (Isbell 2006). Among the platyrrhines, the small-bodied tamarins, titis, and squirrel monkeys are also likely to be at risk from a somewhat different set of predators than the larger-bodied taxa. Unfortunately, our knowledge on how the risk of predation from any particular kind of predator varies with body mass, group size, or other major life-history trait is still quite limited (chapter 8, this volume). Sociality, or living in relatively larger groups, has usually been considered to decrease the risk of being preyed upon by some predators. On the other hand, it is plausible that in taxa that rely on crypsis to avoid predators, sociality may increase the risks. How animals integrate the risk posed by different predators into their decisions about whether to live with conspecifics requires additional research (chapter 8, this volume).

Locomotion and Activity Patterns

All extant neotropical primates radiated into nearly exclusively arboreal niches. While the Malagasy strepsirrhines, the cercopithecoids, and the hominoids all have various terrestrial representatives, there are no habitually terrestrial taxa among platyrrhines. Some species come to the ground occasionally to drink water or visit mineral licks (Izawa 1993; Campbell et al. 2005; Mourthé et al. 2007; Link et al. 2011), to forage for insects (Nadjafzadeh & Heymann 2008), to cross natural gaps between patches of forest (Fernandez-Duque 2009), to play (Mourthé et al. 2007), or to escape from predators (Martins et al. 2005; De Luna et al. 2010). There are in fact vast expanses of savannahs and open habitats in South America (Rosenberger et al. 2009), so a lack of open habitat cannot be the reason why none of the modern platyrrhines is habitually terrestrial.

Platyrrhines are predominantly diurnal with only one genus regularly displaying nocturnal activity: the night or owl monkeys (*Aotus*, Fernandez-Duque 2007; Erkert 2008). Owl monkeys concentrate their activities during the dark portion of the 24-hour cycle, with peaks of activity at dawn and dusk. Interestingly, our understanding of the evolution of nocturnality in the genus is further challenged by the existence of at least one owl monkey species that shows some remarkable temporal plasticity in its activity patterns. Azara's owl monkey (*Aotus azarae*) of Argentina and Paraguay is active during both day and night, like some lemurs (Wright 1989; Fernandez-Duque 2003; Fernandez-Duque & Erkert 2006; Fernandez-Duque et al. 2010). Why this species has shifted secondarily to part-daytime activity is still not completely understood. Lack of predation pressure, harsh climatic conditions, and a seasonal environment are all hypotheses that have been considered but will require further examination (Wright 1989; Engqvist & Richard 1991; Ganzhorn & Wright 1994; Overdorff & Rasmussen 1995).

Life History

Like other major primate groups, New World monkeys also have relatively slow life histories compared with other mammals. For example, age at first reproduction is considerably older than for other mammals of similar size (table 3.2). The small callitrichines (110–620 g) do not reproduce in the wild before approximately two years of age (and usually later), and the larger woolly monkeys (*Lagothrix* spp.) and muriquis may not do so until they are nine years old (Martins & Strier 2004). These estimates should be considered with caution, since for some species there are few data available from wild individuals, and estimates of age at first reproduction tend to be younger for well-nourished captive animals. For example, golden lion tamarin (*Leontopithecus rosalia*) females in captivity mature when they are between 12 and 17 months old (review in Digby et al. 2007), whereas the average age of first reproduction for females in the wild is 3.6 years (Bales et al. 2001; table 3.2).

Gestation length ranges between four and eight months and is roughly correlated with maternal size (Hartwig 1996). Still, some of the callitrichines have quite long gestation periods given their body size, which is due to a lag phase prior to the onset of embryonic development (Oerke et al. 2002). Squirrel monkeys (*Saimiri* spp.) also have long gestation periods for their body size, resulting in relatively

Table 3.2. Social organization, mating systems, dispersals, and various life history traits. Values are typically derived from wild populations; they often come from one or a few species within the genus, and sometimes from only a single population. Mating systems refer to modal patterns.

Genus & references	Social organization[a]	Social mating system[b]	Dispersal[c]	Age at females' first reproduction in the wild (in years)	Gestation length (in days)	Interbirth interval (in months)	Allomaternal care[d]
Alouatta[1,2]	H, M(M)FF	PG	B	4–7	152–194	20	
Ateles[2]	MMFF	P	F	7	226–232	35	
Lagothrix[2,3]	MMFF	P	F, (B)	6–9	210–225	n.a.	
Brachyteles[3]	MMFF	P	F	7–9	215–219	n.a.	
Callicebus[4,5,6]	P	M	B	Average in captivity: 3.7	124–135	In captivity: 12	Yes
Pithecia[6,7]	P, MMFF (?)	M?	B	5	153	21.5	
Chiropotes[6,8,9,10]	MMFF	P?	(F?)[e]	Sex maturity (in captivity, 3)	~135–165?	24	
Cacajao[8,11]	MMFF	P?	F or B?	n.a.	n.a.	n.a.	
Cebus[12,13]	MMFF, MmFF	P, PG	M	5–7	154–162	22–26	(Yes)
Saimiri[13,14,15,16]	MMFF	P, PG	M, F, B	2.5	153–155	12–24	(Yes)
Aotus[17,18]	P	M	B	5	133–141	12	Yes
Callimico[19,20]	F(F)M(M)	PA, PG	B	Sex maturity (in captivity, 1)	147–157	6	Yes
Callithrix[20,21]	F(F),M(M)	M, PG, PA	B	Sex maturity (in captivity, 1–1.3)	143–144	6	Yes
Callibella[22]	MMFF	PG?	n.a.	n.a.	n.a.	n.a.	Yes
Mico[20]	F(F)M(M)	M?, PA, PG?	B	n.a.	n.a.	6	Yes
Cebuella[20,23,24]	F(F)M(M)	M, (PA?)	B	Sex maturity (in captivity, 1.3–1.5)	131–142	6	Yes
Saguinus[20,24,25]	F(F)MM	PA	B	Sex maturity (in captivity, 1–1.5)	140–184	(6–)12	Yes
Leontopithecus[20,26,27]	F(F)M(M)	PA,PG	B	Wild: 3.6 Sex maturity (in captivity, 1–1.5)	125	(6–)12	Yes

[a] H: harem (single male, multifemale). M(M)FF: single male or sometimes few males, multifemale. MMFF: multimale, multifemale. MmFF: multimale, multifemale, with one male clearly dominant. P: pair (with offspring of up to several generations). F(F)MM: single or few females, multimale. F(F)M(M): one to several females and one to several males.

[b] M: monogamy (extrapair copulations may occur). P: promiscuity/polygynandry. PG: polygamy (including effectively polygamous societies in which one alpha male essentially monopolizes access to group females). PA: polyandry.

[c] M: male-biased. F: female-biased. B: with dispersal by both sexes.

[d] Yes: alloparental care crucial for infant survival. (Yes): alloparental care sometimes substantial, but apparently not obligate and crucial for infant survival. No entry: no regular and intensive direct care (carrying, food provisioning) given by group members other than the mother.

[e] Based on strong male-male bonds, from which male philopatry and thus female dispersal can be suspected.

Sources: [1]Pope 1992; [2]Di Fiore et al 2010; [3]Martins and Strier 2004; [4]Anzenberger 1988; [5]Valeggia et al.1999; [6]Norconk 2007; [7]Di Fiore et al.2007; [8]Kinzey 1997; [9]Peetz 2001; [10]Silva and Ferrari 2009; [11]Bowler and Bodmer 2009 ; [12]Fragaszy et al.2004 ; [13]Jack 2007 ; [14]Boinski 1987 ; [15]Williams et al.1994 ; [16]Boinski et al.2005 ; [17]Fernandez-Duque 2002 ; [18]Fernandez-Duque 2007 ; [19]Porter 2001a ; [20]Digby et al. 2007 ; [21]Yamamoto et al.2009 ; [22]van Roosmalen and van Roosmalen 2003 ; [23]Soini 1987; [24]Hartwig 1995; [25]Löttker et al.2004a; [26]Baker et al.1993; [27]Dietz and Baker 1993.

heavy neonates with large brains (see also above, Hartwig 1996). Unfortunately, gestation length is not known for many taxa, particularly for the larger and more recently described species.

Most callitrichines routinely give birth to twins, and occasionally litters of three or more, in a single reproductive event. This is an unusual characteristic among haplorrhine primates, and although there is no consensus regarding the evolutionary origins of twinning, it is consistently associated with small body size, male involvement in offspring care, and use of high-quality food sources (Leutenegger 1979; Goldizen 1990; Garber 1994; Ah-King & Tullberg 2000).

Interbirth intervals can be as short as half a year for some callitrichines (Soini 1987; Porter 2001a; French et al. 2002; but see Löttker et al. 2004b), and as long as three years among the atelines (table 3.2). The development of infants is usually related to maternal body mass; development occurs faster in smaller taxa than in larger ones (cf. chapter 11, this volume). There are still some notable exceptions. Capuchins (*Cebus* spp.), a medium-sized taxon, have very altricial young which are unable to completely maintain their body temperature after birth (review in Fragaszy et al. 2004).

Evolution of Social Systems

Below, we furnish a brief overview of the social organization, mating systems, and some features of the social structures in the three families of extant platyrrhines. We then focus our attention on several unique features of New World monkey social systems that have no comparable analogs among other extant primates: intensive paternal care, cooperative breeding, and cooperative mate defense.

Social Organization

A striking feature of the New World primates is the impressive range of variation in social systems, particularly in view of the comparatively narrow ecological range available to them (Fleagle & Reed 1996). Perhaps even more remarkable is the dramatic intrageneric and intraspecific variation in some taxa. In addition to the unimale-multifemale and multimale-multifemale systems that characterize many catarrhines, several platyrrhine taxa live in small monogamous and polyandrous groups. The smallest groups are found in the socially monogamous titis and owl monkeys and among the callitrichines; females who range alone only with their young, without regular contact with males, have not been described in any neotropical taxon. Even among spider monkeys, where females and their dependent offspring often travel independently of males and one another, contact between the sexes is regular and mixed-sex parties are quite common. The lack of solitary species among the platyrrhines may be linked to the paucity of nocturnal taxa, the exception being the owl monkeys. Additionally, independent and relatively persistent bachelor groups, such as those reported for many colobines and cercopithecines, are not as common, although squirrel monkeys may live for several years in all male bands before joining mixed-sex groups (Mitchell 1990, 1994), and small extragroup associations or coalitions of males have been reported for some other taxa in connection with parallel emigration or relatively brief group fissions (white-faced capuchins, *Cebus capucinus*, Jack & Fedigan 2004a; Jack & Fedigan 2004b; Lynch Alfaro 2007; Poeppig's woolly monkeys, *Lagothrix poeppigii*, Di Fiore & Fleischer 2005).

Atelids

The atelid primates (howler monkeys, woolly monkeys, spider monkeys, and muriquis) live in either unimale or multimale social groups like many Old World species. Most species of howler monkeys live in cohesive groups with fewer than 10 to 15 animals, commonly including only one adult male per group and seldom more than three. In mantled howler monkeys (*Alouatta palliata*), groups are sometimes larger (40 or more individuals) and typically contain three or more adult males and nine or more adult females (Fedigan 1986; Chapman 1988; Neville et al. 1988). Among the remaining atelids, groups are generally large, and typically contain multiple reproductive-age animals of both sexes. Woolly monkey groups, for example, may have as many as 45 individuals (Ramirez 1980, 1988; Nishimura 1990; Peres 1994; Stevenson et al. 1994; Defler 1995, 1996; Di Fiore 1997), whereas some groups of spider monkeys (*Ateles* spp.) and muriquis may contain almost twice as many (Di Fiore et al. 2010). Among woolly monkeys and northern muriquis (*Brachyteles hypoxanthus*), group members may be spread over large areas (Peres 1996). They occasionally split into separate, independently traveling subgroups (Defler 1996; Di Fiore 1997), and the spatial associations among these subgroups can be quite flexible. Nonetheless, groups tend to remain socially cohesive and to divide into discrete subgroups only infrequently (Di Fiore & Strier 2004). Spider monkeys, by contrast, typically live in "fission-fusion" societies, in which the individual members of a large community associate on a daily basis in small, flexible parties that change size and membership frequently (Klein 1972; Cant 1977; van Roosmalen 1985; McFarland 1986; Chapman 1990; Symington 1990; Di Fiore et al. 2010). In this respect they are very similar to chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*; Klein & Klein 1977; Symington 1990;

chapter 6, this volume). Southern muriquis (*Brachyteles arachnoides*) have also been reported to live in the same type of fission-fusion societies as spider monkeys (Torres de Assumpção 1983; Milton 1984; Coles et al. 2008).

The most significant contrast between the atelids and most Old World primate taxa living in unimale or multimale societies involves their dispersal patterns. Both natal and secondary dispersal are strongly male-biased among cercopithecoids, whereas dispersal by females and male philopatry are common in all the atelids (Di Fiore 2009; Di Fiore et al. 2009, 2010). As a result, atelid social groups are not often organized matrilineally around a core of related females like many cercopithecine groups (chapter 5, this volume). In *Ateles* and *Brachyteles*, for example, dispersal is largely or solely by females, and males become breeding adults in their natal communities when they grow up (Strier 1987, 1990, 1991; Symington 1987, 1988, 1990). In woolly monkeys, observed transfers of individuals among groups also suggest that dispersal is predominantly by females (Nishimura 1990, 2003; Stevenson et al. 1994, 2002), and genetic studies confirm that the level of female transfer is substantial (Di Fiore 2002, 2009; Di Fiore & Fleischer 2005; Di Fiore et al. 2009). Nonetheless, solitary males, including adults, have been seen in at least *Lagothrix poeppigii* (Di Fiore 2009; Di Fiore et al. 2009), suggesting some degree of male transfer as well.

The dispersal pattern of the ursine howler monkey (*Alouatta arctoidea*) population studied by Pope (1989; 1992) in Venezuela (formerly the red howler monkey, *Alouatta seniculus*) is less easily described. While only males took over established groups (male dispersal), a high proportion of females dispersed further on average than males did. Females did not enter established groups, but formed new ones. Founding females were rarely related to each other, and subsequently only the offspring of one female would stay in a group and form matrilines (female philopatry, Pope 1992). In mantled howlers, dispersal by both sexes has likewise been reported (Glander 1992).

Pitheciids

The range of variation in social systems is larger among the pitheciids (titi monkeys, sakis, bearded sakis, and uacaris) than it is among the atelids. Throughout their geographic range, titi monkeys (*Callicebus* spp.), the basal member of the clade, live in small groups, each consisting of an adult pair and two to four young (Kinzey 1981; Robinson et al. 1987; Defler 2004; Norconk 2007; Schmitt et al. 2007). The two adults in a group often coordinate their activities during feeding, resting, and travel (Mason 1966; Robinson 1979, 1981; Kinzey & Wright 1982; Wright 1985; Mendoza & Mason 1986a; Price & Piedade 2001). As might be expected for species living in small groups, both sexes disperse (Bossuyt 2002).

The social organization of sakis is not as well understood, since there have only been a few studies of groups including identified and habituated individuals in undisturbed habitats (Setz & Gaspar 1997; Norconk 2006; Di Fiore et al. 2007). Like titis, sakis (*Pithecia* spp.) have also been reported to live in small social groups that typically include a single mating pair and a few young. Although there have also been studies reporting larger groups (Norconk 2007), many of those groups were found in island habitats that limit the dispersal possibilities of individuals (Setz & Gaspar 1997; Vié et al. 2001; Norconk 2006). Large groups have also been reported during censuses of nonhabituated individuals where the identity of groups has not always been known (Lehman et al. 2001). Preliminary data on white-faced sakis (*Pithecia pithecia)* suggest that, as in titi monkeys, both males and females disperse (M. A. Norconk pers. obs., cited in Norconk 2007).

The bearded sakis (*Chiropotes* spp.) and uacaris (*Cacajao* spp.) are the least studied and understood genera of all platyrrhines. They live in large, loosely structured multimale troops, sometimes containing more than 100 individuals, that regularly fission into smaller groups for traveling and foraging (Ayres 1986, 1989; Boubli 1994; Kinzey & Cunningham 1994; Norconk & Kinzey 1994; Barnett & Brandon Jones 1997; Defler 1999; Gregory & Norconk 2006; Boubli & Tokuda 2008; Bowler & Bodmer 2009; Silva & Ferrari 2009). These social aggregations may, in fact, represent temporary associations of smaller core social units plus peripheralized adult and subadult males (Bowler & Bodmer 2009). Genetic data regarding group structure and information on dispersal patterns are not yet available. A recent study of uacaris indicates that males affiliate more than females, and this observation has been used to suggest that the latter disperse (Bowler & Bodmer 2009). On the other hand, observations of male bachelor units at the periphery of larger groups, and of a few solitary males, suggest that males might occasionally disperse as well (Bowler & Bodmer 2009), in a pattern similar to that observed in *Lagothrix* (Martins & Strier 2004; Di Fiore et al. 2010). In black bearded sakis (*Chiropotes satanas*), observations conducted on an island that limited the possibilities for dispersal suggested that it is probably female-biased (Peetz 2001).

Cebids

The Cebids (capuchins, squirrel monkeys, owl monkeys, marmosets, and tamarins) also show significant diversity in social systems, group size, mating behavior, and dispersal patterns. Capuchins (*Cebus* spp.) usually live in multimale-multifemale social groups that range in size from 3 to 30 individuals (Janson 1984; Perry 1996, 1997, 1998; Di Bitetti 1997; Di Bitetti & Janson 2001; Jack & Fedigan 2004a, b, 2009; Jack 2007). Dispersal is predominantly by males, which would tend to reduce the opportunity for kin-based male cooperation, but parallel dispersal by pairs of males from the same social group is not uncommon (Jack & Fedigan 2004a). Female dispersal may occasionally occur, however, in the otherwise female philopatric white-faced capuchins (Jack & Fedigan 2009).

Squirrel monkeys (*Saimiri* spp.) tend to live in large groups ranging in size from 25 to 50 animals (Mitchell 1990; Boinski 1999; Jack & Fedigan 2004a; Stone 2007). Dispersal patterns vary across squirrel monkey populations and species. Females in *S. boliviensis* are philopatric, both sexes disperse in common squirrel monkeys (*S. sciureus*), and dispersal is reported to be female-biased among Central American squirrel monkeys (*S. oerstedii*, Mitchell et al. 1991; Boinski 2005; Boinski et al. 2005a, b), although a recent genetic study of *Saimiri oerstedii* found no evidence of female-biased dispersal and concluded that both males and females disperse, with males likely traveling farther than females (Blair & Melnick 2012).

Owl monkeys (*Aotus* spp.), the only nocturnal monkeys, are consistently described as socially monogamous. They live in small groups, each containing a single adult male-female pair and a few young, and defend territories. The primarily nocturnal habits of all owl monkey species have hindered the study of their social organization. However, studies of a cathemeral Azara's owl monkey population in northern Argentina have shown that both sexes disperse. Male and female dispersers may travel widely and live as solitary "floater" animals from a few weeks to several months before disappearing or successfully becoming members of adult pairs in an established group (Fernandez-Duque 2009; Huck et al. 2011).

The relatively small marmosets and tamarins (callitrichines) show highly flexible patterns of social organization and mating (Terborgh & Goldizen 1985; Heymann 2000; Baker et al. 2002; Digby et al. 2007; Porter & Garber 2009; Yamamoto et al. 2009). Most callitrichines live in small, territorial groups of 3 to 12 individuals that typically include one to three adult individuals of each sex. Animals of both sexes usually disperse, though females in some species might do so earlier or farther (Faulkes et al. 2003; Huck et al. 2007; but see Nievergelt et al. 2000). Adult-sized males commonly outnumber adult-sized females within groups of most callitrichine species (Heymann 2000).

Mating Systems

The mating systems of New World monkeys are remarkably varied. Among the atelids, spider monkeys, woolly monkeys, and muriquis mate promiscuously (table 3.2). Within social groups of these species, females mate multiple males and males mate multiple females with little overt aggression among males in the mating context (Di Fiore et al. 2010). Indeed, a recent genetic study revealed no significant reproductive skew among the multiple adult males in one group of northern muriquis (*Brachyteles hypoxanthus*, Strier et al. 2011). Among howler monkeys, dominance-based polygynous mating occurs in some species whereas female promiscuity, including mating with resident and nonresident males, is displayed by others (Pope 1992; Agoramoorthy & Hsu 2000; Kowalewski & Garber 2010).

Some of the pitheciids apparently fission into small, unimale-multifemale breeding groups or small groups of females defended by coalitions of affiliative males (for uacaris, see Bowler & Bodmer 2009). Sakis are assumed to be monogamous, since they have been most frequently described as living in pairs, but there are also some preliminary reports indicating the possibility of other mating systems in the genus (Norconk 2007). Little is known about the mating system of bearded sakis. Observations of large groups and of single females mating with multiple males suggest that it may be similar to that of the atelids (Peetz 2001; Norconk 2007). In contrast to the other members of the pitheciid clade, titi monkeys are socially monogamous (Kinzey 1981; Robinson et al. 1987; Defler 2004; Norconk 2007; Schmitt et al. 2007). Genetic data are not yet available to confirm whether mating is restricted to socially monogamous pairs and whether extrapair copulations occur. However, except for a few behavioral observations of extrapair copulations in Orabassu titi monkeys (*Callicebus moloch,* Mason, 1966), there are no data suggesting a high potential impact of extrapair copulations.

Mating in capuchins is promiscuous, but the degree to which dominant males monopolize matings varies across species (Fragaszy et al. 2004; Muniz et al. 2010). In white-faced and white-fronted (*Cebus albifrons*) capuchins, females sometimes copulate with lower-ranking males (Janson 1986; Fedigan 1993; Perry 1997), whereas in wedge-capped (*Cebus olivaceus*) and brown (*Cebus apella*) capuchins they apparently mate only or predominantly with alpha males (Janson 1984; Fragaszy et al. 2004). In squirrel monkeys, females usually mate promiscuously, although in Bolivean (*Saimiri boliviensis*) and Central American squirrel monkeys one male or a few may be able to monopolize the majority of matings (Boinski 1987, 2005; Boinski et al. 2005b; Jack 2007). Another curious feature of squirrel monkeys' mating system is the "fattening" of males during the mating season, a period when they may increase their body mass between 12 and 20% (Dumond & Hutchins 1967; Boinski 1987). This change seems to make them more attractive to females, who prefer to mate with the "fattest" male (Boinski 1987). Owl monkeys historically have been described as mating monogamously. The situation is actually more complex, because in Azara's owl monkey adults of either sex frequently replace same-sex residents (Fernandez-Duque 2007; Fernandez-Duque et al. 2008), resulting in serial monogamy. It is not known whether extrapair copulations occur in this species.

Callitrichines are quite unusual, even among platyrrhines, as they display an array of derived social organizational features not commonly observed in other primates and mammals. First, mating patterns within the clade are unusually variable. Monogamous, polygynous, polyandrous, and polygynandrous matings have all been reported in the different genera, sometimes within the same genus and even within the same population (Digby et al. 2007). Polyandry (fig. 3.2) is particularly noteworthy as it has only been reported outside of the callitrichines among a handful of hylobatids during relatively short study periods (Sommer & Reichard 2000; Lappan 2008; chapter 6, this volume). Second, female reproductive competition is a prominent feature of callitrichine reproductive biology. The reproductive success of females is strongly skewed within groups; breeding is typically monopolized by a single dominant female and the reproduction of subordinate females is often either physiologically or behaviorally suppressed (French et al. 1984; Abbott 1993; Snowdon et al. 1993). Continuing controversy exists over whether physiological suppression represents a by-product of captivity or exists as a general mechanism (Löttker et al. 2004b; Yamamoto et al. 2009). Except for a few callithrichine species, relatively little is known about how the social mating system translates into genetic relationships. For example, despite the clear polyandrous social mating system of moustached tamarins (*Saguinus mystax*), paternities tend to be monopolized by one male in the group over several years, even though multiple paternities between and among litters can occur (Huck et al. 2005).

Fig. 3.2: Polyandry is a common mating system among callitrichines, such as these grooming saddle-back tamarins. Photo courtesy of Petra Löttker.

Social Structure

As with other aspects of behavior, there is also variability in the social relationships of platyrrhines. However, our understanding of how kinship influences social relationships among platyrrhines remains limited compared with our understanding of this issue in other primates. Still, some qualitative patterns distinguish the social relationships and social structure of New World monkeys from those of catarrhines and strepsirrhines.

Dominance and agonistic interactions

Clear, stable linear dominance hierarchies among either males or females have proven difficult to discern in most platyrrhines living in large multimale-multifemale social groups (e.g., *Brachyteles*, Strier 1992; *Lagothrix*, Di Fiore 1997; *Alouatta*, Wang & Milton 2003). This may be due in part to the observational challenges of distinguishing among individuals in large social groups of arboreal primates, but it is also almost certainly due to the fact that overt intrasexual competition is rare among group-living platyrrhines. Agonistic interactions, particularly severe ones with physical contact, are comparatively infrequent (Goldizen 1989; Caine 1993; Boinski 1994; Heymann 1996; Fragaszy et al. 2004). However, escalated encounters between or within groups, some leading to fatalities, have been witnessed in some taxa (Mitchell 1994; Campbell 2006; Talebi et al. 2009).

With the exception of the titi monkeys, which live in pairs and do not exhibit intrasexual dominance relationships, pitheciids have not been studied well enough to draw conclusions about the nature of dominance relationships and hierarchies within groups. In addition, low rates of aggression make it difficult to characterize dominance relationships. For instance, wild bald-headed uacaris (*Cacajao calvus*) spend about 2% of their time engaged in agonistic and display behavior, but only a small proportion of that behavior involves actual fighting with physical contact (Bowler & Bodmer 2009). Similarly, in one group of black-bearded sakis studied for more than a year, very little aggression between females or between the two males, one of which was much younger than the other, was observed (Peetz 2001).

Among cebids, patterns of within-group dominance relationships have been better documented. In some capuchins it is possible to discern a clear dominance hierarchy (e.g., brown capuchins, Janson 1985). In other populations there is a single, clear alpha male that is socially central and tends to monopolize matings; a linear hierarchy below this position, however, cannot always be determined (Izawa 1980; Robinson 1988; O'Brien 1991; Fedigan 1993; Perry 1997, 1998). Among white-faced capuchins, females can be ranked in a dominance hierarchy (Perry 1996). Male relationships in the male philopatric Central American squirrel monkeys are very peaceful, making it difficult to define their dominance relationships (Boinski 1987, 1994). By contrast, in the male-dispersing Bolivian squirrel monkeys, males may have intense aggressive interactions, with clear hierarchies forming as a consequence (Mitchell 1994). The same pattern is found among female squirrel monkeys. In species exhibiting female philopatry (Bolivian squirrel monkeys), linear dominance hierarchies have been reported. Alternatively, in species where female dispersal is common (Central American squirrel monkeys), relationships between females are more egalitarian (Mitchell et al. 1991). In callitrichines, one female usually monopolizes reproduction and is clearly dominant toward others, but even though certain males may monopolize paternity, agonistic interactions may be too infrequent to determine rank relationships (Goldizen 1989; Caine 1993; Huck et al. 2004a).

Grooming and other affiliative interactions

Allogrooming is extremely rare or nonexistent in some of the best-studied group-living platyrrhines, while in other taxa individuals may spend hours each day grooming and engaging in other sociopositive interactions. Among the atelids, female-biased dispersal and the possibility for male philopatry may limit the potential for nepotism and affiliative grooming interactions among females while setting up a unique opportunity for the kind of kin-based male bonding that among primates is elsewhere seen only in chimpanzees and bonobos (chapter 6, this volume). Among the three atelins (spider monkeys, woolly monkeys, and muriquis), males tend to be tolerant of, and in some species even affiliative with, each other and to cooperate in intergroup encounters against males from other groups (Di Fiore et al. 2010). In most species of howler monkeys, grooming is a regular activity (2 to 3% of the total activity budget), with females being much more active groomers than males (Chiarello 1995; Sánchez-Villagra et al. 1998). Mantled howler monkeys appear to be an exception in this regard, with grooming rates that are ten times lower than those for other howlers (review in Sánchez-Villagra et al. 1998). The species difference has been attributed to differences in female-female relationships; in contrast to other howler monkeys, female mantled howlers seldom form cooperative alliances or matrilines (Sánchez-Villagra et al. 1998).

Recent field studies of black-bearded sakis (Silva & Ferrari 2009) and bald-headed uacaris (*Cacajao calvus*, Bowler & Bodmer 2009) have commented on high rates of affiliative interactions among males and females (Peetz 2001). Grooming was observed regularly (3 to 5% of the activity budget) among black bearded sakis, where adult females groomed disproportionately more than males or younger individuals (Peetz 2001). Established pairs of monogamous sakis do not groom each other frequently, but newly formed pairs are much more interactive (7% of the male's activity), suggesting that grooming plays a role in establishing rather than maintaining pair bonds (Di Fiore et al. 2007). The pair mates of titi monkeys exhibit a high degree of intimacy, coordination, interdependence, and distress following separation, and the existence of a strong and specific mutual attachment or "bond" is regularly inferred (Mason 1975; Mendoza & Mason 1986b; Anzenberger 1988; Fernandez-Duque et al. 1997). Pair mates groom each other frequently (approximately10% of daily activity), and it has been suggested that this helps to maintain social bonds (Kinzey & Wright 1982).

Among cebids, low levels of allogrooming have been reported in socially monogamous owl monkeys (Wolovich & Evans 2007); these monkeys appear to be extremely similar to titi monkeys in several aspects of their social system. Their grooming tends to be associated with sexual behavior between adults (Wolovich & Evans 2007). Among capuchins, which converge with Old World cercopithecines in many aspects of social organization (chapter 5, this volume), grooming interactions and other forms of within-group affiliation are common (e.g., 4.6% of observation time in brown capuchins, recalculated from Di Bitetti 1997). Females spend more time grooming each other than do males, and there is clear indication that grooming serves an important social function (O'Brien 1993; Perry 1996, 1998; Di Bitetti 1997). The nature of affiliative interactions in squirrel monkeys follows the reverse pattern of the aggressive interactions between same-sex partners described for them before. In the male-bonded, female-dispersing Central American squirrel monkeys, males show remarkably close associations, while females do not (Boinski 1994). In contrast, the opposite is true for female-philopatric Bolivian squirrel monkeys (Mitchell et al. 1991).

Among callitrichines, grooming is a prominent behavior observed among all combinations of individuals; it can sometimes occupy as much as 14% of the daily time budget of individual monkeys (Goldizen 1989; Heymann 1996; Lazaro-Perea et al. 2004; Löttker et al. 2007; Porter & Garber 2009). For moustached tamarins, grooming has been suggested to be a mechanism used by females to develop associations with breeding males and to induce cer-

Fig. 3.3. An owl monkey infant (*Aotus azarai*) rides dorsally on the back of his father. Photo courtesy of Victor Dávalso.

tain individuals to stay in the group and help with infant care (Löttker et al. 2007).

Paternal Care and cooperative breeding

In contrast to other primate radiations, for many platyrrhine taxa in two of the three extant families, most reproduction within groups is concentrated in a single female. This is true for titi monkeys and sakis among the pitheciids, and for owl monkeys and the callitrichines among the cebids. Associated with this pattern of female reproduction are unusual patterns of infant care. Intensive care of offspring in the form of carrying (fig. 3.3) and food sharing by the group male (i.e., the putative father) occurs in most of the taxa mentioned above. Cooperative breeding, which involves additional alloparental care, is the norm in the callitrichines.

Among titi monkeys and owl monkeys, paternal care of offspring is intensive and apparently obligate (Fernandez-Duque et al. 2009; Huck & Fernandez-Duque, in press). Both of these monkeys live in small groups that typically consist of an adult pair and two to four young (Fernandez-Duque 2007; Norconk 2007). Females give birth to a single infant each year and the male assumes the role of primary carrier for the infant soon after birth (Moynihan 1964; Wright 1981, 1994; Robinson et al. 1987; Aquino & Encarnación 1994; Kinzey 1997; Fernandez-Duque 2007). Dependent infants, carried as much as 90% of the time by their putative fathers, frequently transfer from the males' backs to their mothers for brief periods, usually for nursing (Dixson & Fleming 1981; Fragaszy et al. 1982; Wright 1984; Mendoza & Mason 1986b; Fernandez-Duque et al., in press; Huck & Fernandez-Duque, in press). In both titis and owl monkeys, males regularly play with, groom, and share food with infants (Wolovich et al. 2008; Fernandez-Duque et al. 2009). In captive titi monkeys, infants develop a preference for their fathers over their mothers, as assayed by a stronger pituitary-adrenal stress response when they are separated from their fathers rather than from their mothers (Hoffman et al. 1995). Siblings rarely help to carry titi or owl monkey infants (Fernandez-Duque et al. 2008). This contrasts to the pattern displayed by cooperatively breeding callitrichines.

Among callitrichines, parents, other relatives (e.g., older siblings), and even group members unrelated to offspring may share in the care of the offspring that are born up to twice per year. Unrelated group members may even contribute more to offspring care than the parents themselves (Tardif & Garber 1994; Bales et al. 2000; Ziegler 2000; Tardif et al. 2002; Huck et al. 2004b; Zahed et al. 2007). Dependent infants appear to be highly attractive to other group members, who often compete for the opportunity to carry them. In callitrichines, this peculiar social arrangement is associated with their habit of twinning. The combined weight of twins may require a considerable amount of care that cannot be provided by the mother alone (Tardif 1997). Outside of the callitrichines, cooperative breeding has not been reported for any other primate except humans (Gray & Anderson 2010; chapter 20, this volume) and it is relatively rare among mammals (see reviews in Solomon & French 1997).

The high level of care provided by nonmothers in titi monkeys, owl monkeys, and callitrichines is quite conspicuous and appears to be obligate. The involvement of nonmothers in the care of capuchin and squirrel monkey infants is also striking. Young capuchins and squirrel monkeys may be carried by various group members. These include males (reviews in Williams et al. 1994; Fragaszy et al. 2004), older sisters, and even unrelated females, who may nurse infants (see, e.g., O'Brien 1988; O'Brien & Robinson 1991; Williams et al. 1994; Perry 1996).

Cooperative Mate Defense

Cooperative mate defense, with quite flexible association patterns and limited overt intrasexual competition among males of the same social group, characterizes some atelids, some cebids, and perhaps even some pitheciids. Cooperative mate defense is rare among primates, occurring only in platyrrhines and chimpanzees (chapter 6, this volume). Both atelids and cebids are notable in the extent to which male group members cooperate with one another when interacting aggressively with males from other groups. Males cooperate most likely to obtain access to females and, by extension, personal reproductive opportunities (Mitchell 1994; Strier 1994b; Perry 1998). At the same time, interactions between males of the same group tend to be more tolerant or affiliative and less aggressive (see above) than is common for most Old World monkey species, like yellow baboons (*Papio cynocephalus*), where some males may form strategic coalitions with one another over consortship opportunities or in the context of intragroup conflicts with higher-ranking males, or Hanuman langurs (*Semnopithecus entellus*), which might cooperate to take over other groups but show high intrasexual competition over females within groups (Nöe 1990; Packer 1977; Hrdy 1977; Sommer et al. 2002; Alberts et al. 2003, 2006; chapters 4 and 5, this volume). In atelids, cooperative mate defense is presumably related to the prevalence of female-biased dispersal and a greater degree of male philopatry (Strier 2008; Di Fiore et al. 2010), although males do not have to be close relatives for this system to be advantageous (Link et al. 2009). In ursine howler monkeys, coalitions of males cooperate to take over small groups of females or defend access to them from other males. Furthermore, coalitions of ursine howler monkeys composed of related males persist for longer periods of time than coalitions formed by nonrelatives, suggesting a role for kin selection in the cooperative social interactions of males (Pope 1990, 1992). Among the atelins, male-male cooperation in the context of intergroup encounters has been reported for all genera (Strier 1994b, 2004; Di Fiore & Fleischer 2005; Strier 2008; Di Fiore et al. 2011), and in at least some atelin groups, adult male group members are close relatives, though this is by no means a universal pattern (Di Fiore et al. 2009). Among the cebids (e.g., white-faced capuchins), close cooperation among males may be facilitated by the high incidence of parallel dispersal, which may translate into inclusive fitness benefits as well as increased survivorship (Jack & Fedigan 2004a). In Bolivian squirrel monkeys, males emigrate together in migration alliances; alliance members support each other as they compete with males in other groups and seek entrance into new groups during immigration events (Mitchell 1994).

Summary and Conclusions

Compared with other primates, New World monkeys display relatively limited ecological variability. New World monkey anatomy and social systems, however, are extremely diverse. Several unique morphological features (e.g., claws, prehensile tails) and uncommon patterns of social organization (e.g., paternal care, cooperative breeding, female dispersal) have evolved in some platyrrhine species. Social organization and mating patterns include typical harem-like structures where mating is largely polygynous, and large multimale, multifemale groups with promiscuous mating and fission-fusion societies. In addition, some species are socially monogamous and polyandrous. Even closely related species may exhibit strikingly different social organizations, as the example of the squirrel monkeys demonstrates (Mitchell et al. 1991; Boinski et al. 2005b).

New World monkey behavior varies within species as well as between them. While the behavior of many species is known from only one study site, intriguing patterns of intraspecific variation are beginning to emerge from observations of populations that sometimes live in close proximity. For example, spider monkeys are often described as showing sex-segregated ranging behavior. Several studies show that males range farther, travel faster, and use larger areas than females, who tend to restrict their habitual ranging to smaller core areas within a group's large territory (Symington 1988; Chapman 1990; Shimooka 2005). In at least one well-studied population in Yasuní National Park, Ecuador, however, males and females both travel over the entire community home range, and different females within the community show little evidence of occupying distinct core areas (Spehar et al. 2010). Similarly, in most well-studied populations of spider monkeys, females disperse and the resident males within a group are presumed to be close relatives—a suggestion corroborated by genetic data for one local population of spider monkeys in Yasuní. Still, in a different local population, males are not closely related to one another, an unexpected pattern if significant male philopatry were common (Di Fiore 2009; Di Fiore et al. 2009). While the causes of this local variation in group genetic structure are not clear, it may be significant that the groups examined likely had different histories of contact with humans. For long-lived animals who occupy relatively small social groups, the loss of even a handful of individuals to hunting, or to any other demographic disturbance, can have a dramatic impact on a group's genetic structure. Intragroup social relationships, in turn, are likely to be influenced by patterns of intragroup relatedness and by the relative availability of social partners of different age or sex class (chapter 21, this volume). Thus, historical and demographic contingencies are likely to create conditions where considerable local, intrapopulation variation in social systems exists.

Slight changes in ecological conditions may also contribute to variation in the behavior of individuals living in a single population over time. For example, some authors have hypothesized that howler monkey populations may undergo dramatic fluctuations in size and composition in response to several ecological factors, including resource abundance, parasite and predation pressure, and climate (Milton 1982; Crockett & Eisenberg 1986; Crockett 1996; Milton 1996; Rudran & Fernandez-Duque 2003). This variability, not only among populations, but also within populations across time highlights the need for long-term studies.

In sum, our understanding of the behavior of New World monkeys has increased dramatically over the past 25 years. This understanding highlights how their behavior varies within populations over time and among populations or species across space. As our knowledge of platyrrhine behavior continues to unfold and is enriched via additional long-term studies, a central challenge will be to explain how these variations arise. It will be important to entertain adaptive explanations while acknowledging that some differences may emerge via stochastic changes in demography (Struhsaker 2008) or nongenetic, relatively short-term, nonadaptive responses to sudden ecological change.

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