

Chapter 8

Tracking Neotropical Monkeys in Santa Rosa: Lessons from a Regenerating Costa Rican Dry Forest

Linda M. Fedigan and Katharine M. Jack

Abstract The Santa Rosa primate project began in 1983 and we have studied the behavioral ecology of the resident primate species (*Cebus capucinus*, *Alouatta palliata* and *Ateles geoffroyi*) continuously since then. Most of our research has concentrated on the behavior, ecology, and life history of multiple groups of capuchins and on documenting the effects of forest protection and regeneration on the howler and capuchin populations. Our examination of capuchin life histories has shown that they lead complex and intriguing lives, many aspects of which are affected by the frequent movement of adult males between social groups throughout the course of their lives. Over the past 28 years, we have documented increases in both the capuchin and howler populations. However, the howler population apparently reached carrying capacity in 1999, whereas the capuchin population continues to grow, probably because of their ability to occupy early-regeneration habitats. Our long-term examination of the population structure and life history of these two species clearly demonstrate that many species-specific aspects of biology and behavioral ecology differentially influence patterns of primate population recovery. It is only after decades of research that we can begin to understand the underlying constraints and variability in the lives of these animals.

L.M. Fedigan (✉)

Department of Anthropology, University of Calgary, Calgary, Canada
e-mail: fedigan@ucalgary.ca

K.M. Jack

Department of Anthropology, Tulane University, New Orleans, LA, USA
e-mail: kjack@tulane.edu

8.1 History and Infrastructure of the Santa Rosa Monkey Project

In the early 1980s, I (L.M. Fedigan) began searching for a site to conduct long-term studies of primates. My wish list of ideal field site characteristics included the following: the site would be in a stable sociopolitical setting where I could safely bring students; the habitat would contain multiple primate species, at least one of which was relatively unstudied; the flora and fauna would be protected; the terrain would not be too formidable and the primates would be accessible for study and amenable to habituation. After a false start in one country where the monkeys were accessible and protected but the political situation was not stable, and in another where the government was stable but the primates were poorly protected, I made a trip to Costa Rica in 1982. After checking out many Costa Rican reserves and parks, I visited Santa Rosa National Park, home to white-faced capuchins (*Cebus capucinus*), mantled howlers (*Alouatta palliata*) and black-handed spider monkeys (*Ateles geoffroyi*). Not only was Santa Rosa an ideal location, but the three primate species, which all form multi-male, multi-female groups, display a range of dispersal patterns, dietary specializations, and social systems exhibited by polygynandrous primates, making them ideal for comparative studies. I knew immediately that I had found a place that met my criteria and where I could establish a stable long-term primate field site.

Santa Rosa National Park (SRNP) was created in 1971. The history of the park is a fascinating story in itself, far too long for this chapter, but well described in Evans (1999) and Allen (2001). SRNP was one of the first parks established by the fledgling Costa Rican National Park Service. It constitutes about 100 km² of tropical dry forest in Guanacaste Province and was chosen for early park designation mainly because its large central ranch house was the site of a famous 1857 battle in which a volunteer army of Costa Ricans repelled an invasion by American mercenaries. At the time of the park's establishment, the area was overrun with squatters, shacks, and roaming cattle owned by absentee landlords who planted African grasses that they burned annually to create pastureland. Soon after the park was established, the squatters were removed, hunting and logging were banned, a small complex of cement block buildings was constructed for park personnel, and the guards were given guns and horses (but no uniforms or vehicles!) to drive the poachers and the neighboring ranchers' cattle out of the park. Throughout the 1970s and 1980s, efforts were made on a shoestring budget to attract visitors and control the major forms of anthropogenic disturbance: poaching, logging, grass fires and grazing by cattle.

In the mid-1980s, Dan Janzen, a renowned tropical ecologist who first visited Santa Rosa before it became a park and who has made it his lifetime study site, convinced the park service and Costa Rican government to establish a large megapark, now called Área de Conservación Guanacaste (ACG; Janzen 1988, 2000, 2002, 2004). Dr. Janzen created a non-profit conservation organization (Guanacaste Dry Forest Conservation Fund) that initially raised funds to purchase the properties

surrounding Santa Rosa, in order to connect it to the small nearby parks and reserves. More recently, ACG has expanded further, as the Conservation Fund purchases cloud forest and Atlantic rainforest habitat on the eastern slopes of the mountains. Santa Rosa has now become a “sector” in the mega-park and is the core of a much larger protected zone (163,000 ha and counting) that covers nine Life Zones from the Atlantic rainforests of the east, to the volcanoes at the tops of the mountain range that runs along Guanacaste like a backbone, and into the Pacific Ocean on the west. ACG was declared a UNESCO World Heritage Site in 1999. The park now has ten sectors, most with their own buildings and staff. ACG also has a professionally-trained fire fighting team, locally-trained park researchers, police protection service, ecotourism office and outreach educational programs. Although far from wealthy and still dependent on donations from conservationists, the park has come a long way from the days when a small and poorly funded group of rangers tried to protect and maintain the land. Under Janzen’s visionary guidance, the goal of ACG is not only to protect the old growth rainforest and cloud forest that remain in the mountainous regions of Guanacaste Province, but also to engage the local populace in efforts to regenerate the severely endangered tropical dry forest that was the original habitat type of the western lowland areas. Over the past two decades, major fires have become a thing of the past in Santa Rosa, the introduced African grasses have mostly died out, and the pastures are transforming into newly regenerating dry forest (Janzen 2002, 2004).

When I first requested a research permit from the Costa Rican National Park Service in 1983, the administrators made it clear they wanted me to monitor how the monkey populations were faring in the park. No counts of the primate populations had occurred in Santa Rosa since Curtis Freese, a Peace Corps volunteer had censused the monkeys in 1972, 1 year after the area came under protection (Freese 1976). Therefore, along with my plans to study the life histories and behavioral ecology of the monkeys, I agreed to monitor the park-wide populations. Beginning in 1983, my students, field assistants and I conducted annual censuses in May/June of every year for 6 years, after which we switched to less frequent park-wide censuses with a goal of at least one census every 4 years.

In 1984, I also selected three groups of capuchins, four groups of howlers, and one community of spider monkeys to be habituated and closely tracked as our “study groups.” We found it difficult to distinguish individual howler monkeys and to track the rapidly-moving spider monkeys around their large home ranges. Therefore, with the help of Glander et al. (1991) we captured, marked, measured, and released many individuals in our howler study groups and several in our spider monkey community (Fedigan et al. 1988). In 1985, we started to systematically observe recognizable individuals in all three species in order to record births, deaths, disappearances, and dispersal, as well as foraging and social behaviors. The official “start” date for our life history data is June 1986, because it took us nearly a year to develop standardized and efficient methods for reliable data collection.

In the mid-1990s, I made the decision to concentrate my research on five groups of capuchins (Fig. 8.1), except for the park-wide censuses of monkey populations in



Fig. 8.1 A subadult female from one of our study groups carrying her infant sister (© Fernando Campos). Alloparenting, including extensive allonursing is very common in this species

May/June of designated census years. I maintained my focus on long-term life history data and started to direct and oversee many shorter-term (6–12 month) behavioral ecology projects carried out by graduate advisees.

Graduate students were actively involved in the Santa Rosa monkey project from the beginning. Dr. Colin Chapman was part of our original census team in 1983 and continued research in our park until 1989, focusing on the spider monkeys latterly (e.g., Chapman 1989, 1990; Chapman et al. 1988, 1989a, b). A young Costa Rican biologist, Rodrigo Morera Avila, worked as my local project manager for 10 years, until he completed his master's degree in wildlife management at the National University of Costa Rica and took up a post at the University of Costa Rica in Heredia. Since 1984, 30 graduate students from 12 universities and 6 countries have pursued and/or completed thesis projects on the monkeys of Santa Rosa (see partial list at <http://people.ucalgary.ca/~fedigan/fedigan.htm>). In 2000, Drs. Filippo Aureli and Colleen Schaffner initiated a long-term project on the spider monkeys of Santa Rosa. In 2004, I invited a former graduate advisee, Dr. Kathy Jack, now of Tulane University, to join me as co-director of the Santa Rosa capuchin project. Dr. Jack and her graduate students focus on capuchin behavioral ecology and life histories from the male perspective whereas my team addresses similar questions from the female perspective. We conduct many behavioral projects and all project data collection collaboratively.

Another major event in the history of our project was the creation of the Santa Rosa Database in June 2001 by Dr. John Addicott. This research tool is essential to our overall endeavor, although it will forever be a work-in-progress. It includes ~33 linked tables covering not only census and life history information, but also data on genetics (e.g., opsin genes, microsatellite DNA), climate (temperature, rainfall), phenology, food lists, dominance hierarchies, researcher names and other data

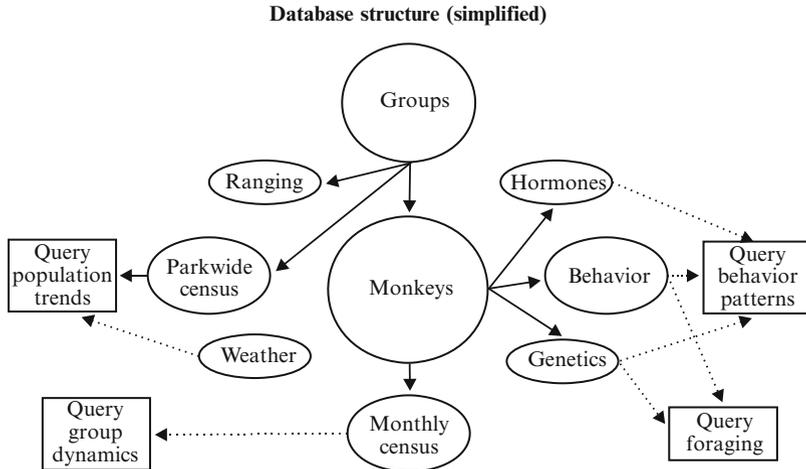


Fig. 8.2 Schematic diagram of selected linked tables that make up the Santa Rosa database. For additional information on the data included in each table, please contact the authors

(Fig. 8.2). We are putting this database on a server that will be remotely accessible by any user with appropriate permission.

Over the 28 years of this project, we have been variously housed: in tents, in an original 1971 park administration building, in a house outside of Santa Rosa that played a role in the “Iran-Contra” scandal, and in a more modern “dormitory” built in 1994. As of March 2011, we live in a designated “casa carablanca” that we built in the park with our own funds and grants from the Zemurray Foundation. This multi-roomed building is owned by the park but largely managed and maintained by our monkey research team.

8.2 Life History Parameters, Dispersal and Reproductive Success in the Santa Rosa Capuchins

Here we briefly review a few of the many aspects of capuchin life history, reproductive patterns, and socio-ecology that we could not have documented or understood without longitudinal data collection (see also Perry and Manson 2008; Perry et al. 2011). Table 8.1 summarizes capuchin reproductive and life history parameters at Santa Rosa. It did not take us long to discern that white-faced capuchins conformed to the *Cebus* pattern of male dispersal and female philopatry. However, only after many years could we determine the average age at which natal dispersal occurs, discover that males continue to change groups throughout their lives (Jack and Fedigan 2004b), and realize that adult females also disperse under some circumstances (Jack and Fedigan 2009). Although white-faced capuchins are best described as residing in multi-male/multi-female groups (current average

Table 8.1 Summary of life history parameters for white-faced capuchin monkeys in Santa Rosa National Park, Costa Rica between 1986 and 2010

		Value	Range	<i>N</i>
Gestation (days)		158 ± 8 ^a		6
Sex ratio at birth (proportion male)		0.605 ^b		119
Infant survival to age 1 (proportion)	All infants of known sex	0.823		119
	Females	0.914		47
	Males	0.763		72
	All infants (incl unknown sex)	0.680		144
Mean age at first birth (years)	Females	6.50	5.80–7.90	19
Mean interbirth interval (years)	First infant dies before age 1	1.05	0.67–1.75	22
	First infant survives to age 1	2.25	1.48–5.58	52
Mean age at 1st dispersal (years)	Females	≥7 ^c		5
	Males	4.5		30
Mean age at death (years) for individuals surviving to at least age 1	Females	9.41		18
	Males	2.96 ^d		14
Oldest age at death (years)	Females	27 ^e		
	Males	24.70 ^{d, e}		

^aSarah Carnegie unpublished data, based on ovarian hormone analyses

^bOf the 144 infants born in our study groups, 25 (17%) were not sexed prior to their neonatal death

^cAll five females that immigrated into our study groups were considered adults (all but one was parous)

^dFor males, death is not easily distinguished from dispersal

^eBirth dates of monkeys alive at the start of the study or immigrating into study groups are estimated

group size: 15.2, Table 8.2), their social structure varies and we have documented small uni-male/multi-female groups, and in one case, a group that had no resident adult, or even subadult, male for 10 months.

Even though the number of adult males per group varies across our five study groups and 48 census groups, all groups contain multiple, usually closely related, females and their immature offspring. Ovarian hormone analyses from fecal samples show that gestation length in our females is approximately 5.5 months, and that females typically experience only one or two cycles before they conceive (Carnegie 2011). Females appear to provide no visible cues to ovulation and often approach and direct proceptive signals to subordinate males when they are not fecund and even when they are pregnant (Carnegie et al. 2005). The occurrence of female-initiated, non-conceptive mating with subordinate males may explain why we see all resident adult males copulate, but genetic data show that the alpha males father most of the infants (Jack and Fedigan 2006).

Age at first birth for a female is usually around 6.5 years (Table 8.1), reflecting the slow life history of this species relative to its body size ($\sigma^7 = 3.7$ kg, $\text{♀} = 2.7$ kg; Ford and Davis 1992). In captivity, capuchins may live into their fifth decade (Fragaszy et al. 2004), but in the wild, mortality rates at our site are such that female

Table 8.2 Census data for (a) Capuchin monkeys and (b) Howler monkeys in Santa Rosa National Park, Costa Rica between 1972 and 2007

Year	# Monkeys counted	# Groups counted	Average group size	Estimated # groups	Estimated population size ^a
(a) Capuchins					
1972	? ^b	1	17.5	17	297
1983	226	20	11.5	28	318
1984	338	25	13.6	28	378
1985	175	13	14.8	28	397
1986	284	18	16.4	28	448
1987	173	10	16.7	28	474
1988	140	8	16.4	28	468
1990	314	18	17.7	28	491
1992	541	30	18.0	30	541
1999	521	31	16.8	35	588
2003	655	49	13.4	49	655
2007	594	39	15.2	48	716
(b) Howlers					
1972	65	8	8.1	10	85
1983	217	19	11.4	24	274
1984	295	23	12.8	25	321
1985	262	19	13.8	26	359
1986	315	19	16.6	28	464
1987	181	16	11.3	30	339
1988	212	12	17.7	31	548
1990	432	27	16.0	33	528
1992	563	35	16.1	34	547
1999	545	46	11.8	50	592
2003	529	44	12.0	49	589
2007	463	41	11.3	54	610

^aEstimated population size was computed as: # Monkeys Counted + ((Estimated # Groups – # Groups Counted) × Average Group Size))

^b Freese (1976) did not state how many capuchins he counted. Instead he estimated 15–20 groups of capuchins in Santa Rosa. The one group he tracked over time had on average 17.5 members

life expectancy at age one is only around 9 years whereas male life expectancy at age one is much lower, around 3 years (Table 8.1; Bronikowski et al. 2011). Santa Rosa has a large and intact predator community (cats, canids, mustelids, raptors, snakes; Janzen 1988) and we have seen capuchins killed by a *Boa constrictor* (Chapman 1986) and a puma (McCabe unpublished data), as well as observing predators stalking the monkeys. Other documented and inferred sources of mortality are intra-specific aggression, parasites, and contagious diseases (Fedigan 2003; Parr 2011). Obviously, some individuals live much longer than 3–9 years and we estimate that the oldest females in our study groups are about 27 years of age and the oldest males approximately 25 years. Estimating the life expectancy of capuchin males is problematic as it is often difficult to distinguish death from dispersal in this

sex. At Santa Rosa, males disperse from their natal groups at around 4.5 years of age (Jack et al. 2011, but see Perry et al. (2012) for an older average male age at natal dispersal, 7.6 years) and they continue change groups at approximately 4-year intervals throughout their lives (Jack and Fedigan 2004b).

Infant mortality in the first year of life is quite variable from year to year, but averages around 30%. If a female's infant dies, she is likely to produce another infant in about a year, whereas if her infant survives, her interbirth interval averages 2.25 years. We examined the factors that may affect length of interbirth interval and infant survival, using 21 years of data, 24 adult females, and 74 completed interbirth intervals (Fedigan et al. 2008). In brief, we found that the pace of a female's reproduction can be predicted by the number of matrilineal kin in her group (sources of supportive allomothers and coalitions) and by the availability of resources, as inferred from the amount of rainfall that occurred in the 12 months subsequent to each infant's birth (see justification for use of rainfall as a proxy for food availability in Murphy and Lugo 1986; Fedigan et al. 2008). But the strongest predictor of the length of interbirth intervals is whether or not the first infant in the interval survives. In turn, the survival of infants is best predicted by whether male membership in the group is stable at the time of birth or whether there is a take-over in the first year of the infant's life. Infant survival is also affected by sex – a higher proportion of female than male infants make it through their first year (Table 8.1). Somewhat surprisingly, the mother's dominance rank at the time of the infant's birth affects neither its survival nor the length of interbirth intervals. Thus, dominance rank does not influence female reproductive success, whereas we have found such a relationship for males (Jack and Fedigan 2006).

Santa Rosa is a highly seasonal tropical dry forest and white-faced capuchins prefer to drink water every day. Rainfall amounts vary greatly across the months of the year as well as across years (range: 818–4,012 mm per annum). The rainy season typically occurs between mid-May and mid-November, during which an average of 1,792 mm of rain falls. Between mid-November and mid-May, especially from January through April, virtually no rainfall occurs, most trees drop their leaves, all the streams dry up, and most sources of standing water disappear. In tropical dry forests, rainfall is a major influence on plant and insect productivity and thus available food energy (Murphy and Lugo 1986; Fedigan et al. 2008). Therefore, we have been interested in the extent of seasonality in capuchin conceptions and births. Analyses of 144 birthdates for capuchin infants in our study groups over many years show that births are significantly more likely to occur in the late dry/early wet season (Fig. 8.3; Fedigan 2003; Fedigan and Jack 2004). Given a 5.5-month gestation period, this indicates that conceptions are clustered in the second half of the wet and early part of the dry season (Carnegie et al. 2011). With 44% of infants born within the 3-month period of May through July (and therefore conceived within a 3-month period), the Santa Rosa white-faced capuchins display moderate breeding seasonality (see van Schaik et al. 1999 for classification overview). Although white-faced capuchins do not show strict birth seasonality, as has been demonstrated for the black capuchins (*Cebus nigrinus*) of Iguazu National Park, Argentina, studied by Di Bitetti and Janson (2000), (see also Janson and

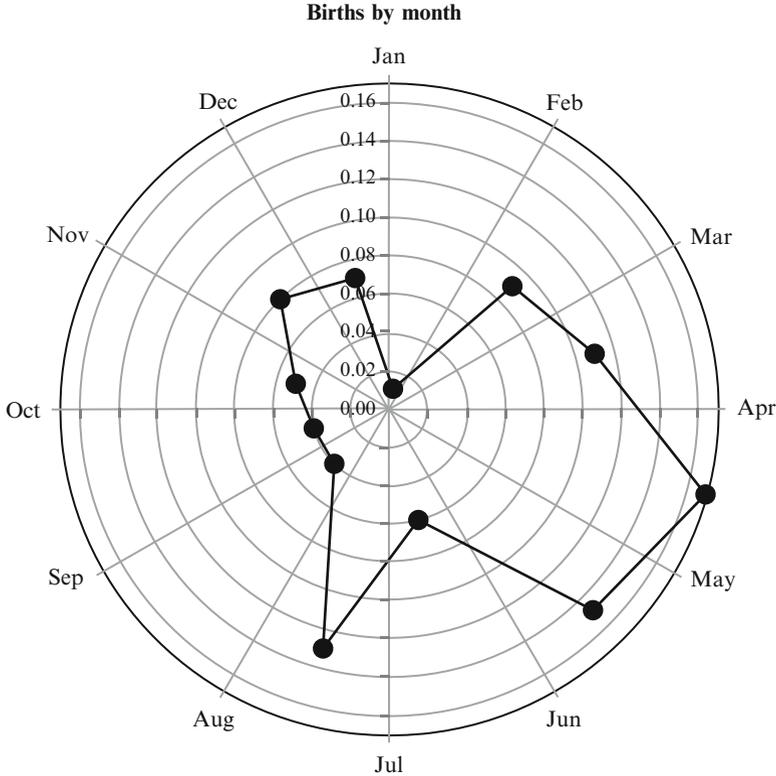


Fig. 8.3 The monthly pattern of births for 144 *Cebus capucinus* infants born in our study groups between 1986 and 2010. The dry season occurs from mid-December through mid-May

Verdolin 2005, Janson et al. 2012) they are similar to black capuchins and other more seasonal neotropical primates in that their birth peak coincides with, or slightly precedes, the seasonal peak in resource availability (Carnegie et al. 2011).

Interestingly, the white-faced capuchins studied at Lomas Barbudal (Perry et al. 2012) show even stronger reproductive seasonality than the Santa Rosa capuchins with 66.5% of all infants born between April and July. Lomas Barbudal and Santa Rosa are merely 55 km apart and are ecologically very similar so the reasons for this difference in birth seasonality are not easily explained. Variation in strength of reproductive seasonality may, perhaps, be tied to the fact that the capuchins at Lomas have year round access to fresh water, whereas the Santa Rosa capuchins drink from standing water holes, most of which have completely vanished by the end of the dry season. Indeed this single ecological difference may explain several of the demographic and life history differences that have been reported from these two nearby long-term study sites (e.g. group size, age at natal dispersal, and adult male tenure length). We plan to collaboratively address some of these inter-site differences with the Perry team of investigators over the next few years.

In some primate species, male dispersal is intimately linked to/timed with the breeding season (e.g. *Propithecus edwardsi*: Morelli et al. 2009; *Semnopithecus entellus*: Borries 2000), but the moderate seasonality displayed by our population of white-faced capuchins does not appear to directly influence male mobility. In our long-term analysis of natal and secondary dispersal, we did not find a significant relationship between the timing of male dispersal and the conception peaks (Fedigan and Jack 2004; Jack and Fedigan 2004a). Most dispersal events occur during the dry season months of January through April, a full 3–6 months prior to the conception peak. During the dry season, however, intergroup encounters are more likely to occur, usually around shared water holes, and males may use these encounters to appraise reproductive opportunities in neighboring groups and to assess the strengths of resident males in other groups. Assessment of the strength of groups targeted by would-be immigrants could be particularly important for dispersing adult males who typically fight their way into groups, although a few manage to peacefully join groups previously abandoned by resident males, a pattern we refer to as “waltz-ins”. Males usually disperse (77%, $N = 74$; Jack and Fedigan 2004a, b) in cohorts of two or more, and in almost all of the successful takeovers that we have observed to date ($N = 20$), coalitions of invading males outnumber those of resident males. This pattern of male dispersal leads to the complete replacement of resident males approximately every 4 years.

Over the years, we have observed 25 male replacement events in our five study groups and they are usually associated with the wounding, deaths, and disappearances of individuals from all age-sex classes (Fedigan 2003; Fedigan and Jack 2004; Jack and Fedigan 2009). Indeed male replacement events strongly influence many life history patterns. For example, the occurrence of a group takeover is the most significant factor explaining the highly variable age at which male natal dispersal occurs (Jack et al. 2010) and infant deaths are significantly more common, and females are more likely to disperse, during years with male replacements than during peaceful years (Fedigan 2003; Jack and Fedigan 2009). Given that white-faced capuchins show very high reproductive skew (Jack and Fedigan 2006; Muniz et al. 2010), with alpha males siring most infants, it is no surprise that males frequently change groups – likely in an attempt to maximize their reproductive opportunities (reviewed by Jack 2003). By changing groups, formerly subordinate males experience rank gains, which should also confer reproductive benefits (Jack and Fedigan 2004b). Even alpha males have been observed to abandon groups to join others, taking risks that seem counterintuitive at first. However, they target groups that proffer a more favorable sex ratio (i.e., more potential mates). While secondary/breeding dispersal by adult males is frequently suggested as a mechanism for the avoidance of breeding with maturing daughters (see Smith 1982), this does not appear to be the main proximate cause for the frequent dispersal of male white-faced capuchins (Jack and Fedigan 2004b). The average tenure length for an adult male in our study groups is 4 years (alphas and subordinates do not differ in this regard), which is well under the age that females first conceive and give birth (Table 8.1). Indeed in many primate species secondary dispersal by adult males is better explained by intrasexual mating competition

rather than inbreeding avoidance (reviewed by Jack 2003). Genetic studies of the Lomas Barbudal population of white-faced capuchins (Perry et al. 2012), where alpha males have much longer tenures (e.g. up to 18 years) than those in Santa Rosa, have shown that there are behavioral mechanisms in place to ensure inbreeding avoidance; namely, the daughters of alpha males reproduce with subordinate males rather than with their fathers (Muniz et al. 2006).

8.3 Population Recovery in a Regenerating Tropical Dry Forest

Our demographic research began in 1983 and 1984 with extensive attempts to count all the monkeys located throughout SRNP, and since that time we have conducted 11 park-wide censuses of capuchins and howlers (Table 8.2). Except for one census conducted in August–November of 1992, these have all been carried out in April through July and mainly in May and June. For the capuchin and howler groups, we use a modified quadrat (“complete count”) technique that has proven useful in fragmented forest patches (see Fedigan et al. 1996, 1998; Fedigan and Jack 2001 for details). However, unlike capuchins and howlers, spider monkeys have fission–fusion societies and individuals range over very large areas in “parties” of frequently changing composition. Therefore, we have had to assess spider monkey densities from transect studies, which have been conducted much less frequently than our censuses of capuchin and howler populations (see Chapman et al. 1988, 1989b; Sorensen and Fedigan 2000; DeGama-Blanchet and Fedigan 2006).

We choose one area of the park at a time (usually a large forest fragment) and walk all known trails and dry stream beds there to locate monkeys. We consider any individual monkey within 100–300 m of the group and consistently traveling in the same direction as the group (even if in a peripheral position) to be part of that group. We use unique markings, known individuals and distinctive age/sex compositions to identify the same group on successive days for repeat counts. Multiple observers repeatedly count a group until achieving a stable count and composition, and plot its location on a map. After establishing a stable count on one group, we locate its nearest neighbor group. Whenever possible, with the aid of two-way radios, we use simultaneous contact with neighboring groups by different observers to establish their independence. With many years of practice, it has become increasingly easy to relocate our census groups in successive years and to determine when new groups have appeared or former groups have become extinct.

Table 8.2 shows the number of monkeys and groups we counted and the estimated population sizes of capuchins and howlers in Santa Rosa between 1972 (Freese’s original count) and 2007, a 35-year period subsequent to the establishment of the park. Whether we begin with Freese’s 1972 census or our first census in 1983, the number of capuchins in SRNP has more than doubled (e.g., from 318 in 1983 to 716 in 2007) and it gives every indication of continuing to grow (Fig. 8.4).

Howler population dynamics are different. Freese concluded that there were only ten howler groups in Santa Rosa in 1972 with a total population of only

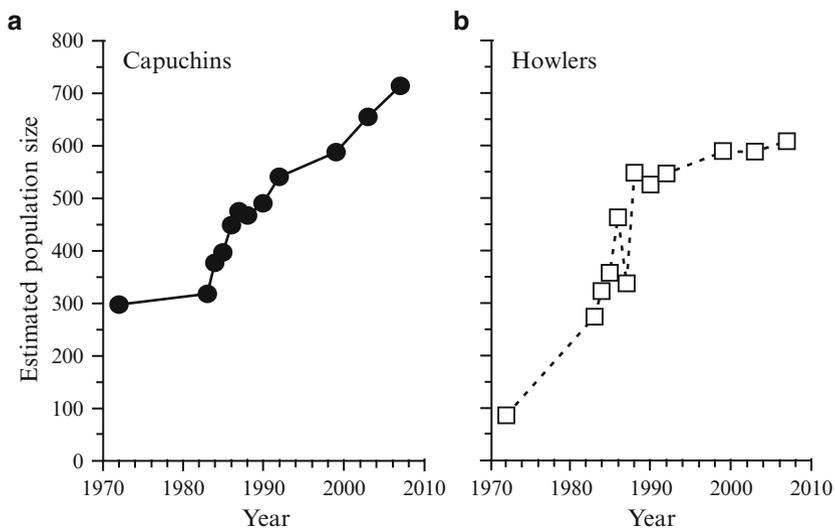


Fig. 8.4 Estimated population sizes of (a) capuchins and (b) howlers in Sector Santa Rosa, based on 12 park-wide censuses between 1972 and 2007

85 monkeys and he said that howlers were located only on the lower plateau, near the Pacific Ocean. The howler population apparently crashed shortly before the establishment of the park (see Fedigan et al. 1998; Fedigan and Jack 2001). However, at the time of our first census in 1983, we estimated there were 24 howler groups spread throughout the park, with a population of about 281 monkeys. That would indicate the howler population more than tripled in the 11-year time period between 1972 and 1983. Although howler females can first give birth at 3.5 years and can thereafter produce an infant every 20 months (Fedigan and Rose 1995), this would still be a remarkable rate of population growth. More conservatively, if we begin with our first census in 1983, the number of howlers more than doubled in a 14-year period (from 281 in 1983 to 620 in 2007). However, the Santa Rosa population of howlers began to level out in 1999 and since that time has experienced a near zero growth rate (Table 8.2).

Whether we begin our comparison of capuchins and howlers with Freese's 1972 census or our own first census in 1983, there were clearly more capuchins than howlers in Santa Rosa in the early days of the park's existence. The howler population then grew at a faster rate than the capuchins during the 1980s and 1990s, probably because howlers have a faster pace of reproduction and greater intrinsic rate of increase (earlier age at first birth, shorter interbirth intervals, Fedigan and Rose 1995). However, howlers are differentially found in the older (>60 years) evergreen forest that includes many large trees (DBH >63 cm, which is the smallest size tree in which Santa Rosa howlers rest and forage, probably to accommodate their larger body size and possibly also their folivorous diet). In the first two decades of our study, we observed several new groups of howlers colonize

strips of old growth riverine forest and small patches of secondary forest that were transitioning into primary forest. But the stabilization of their population size may indicate that, at least for now, howlers have run out of suitable habitat into which they can expand as the forest fragments of Santa Rosa slowly regenerate. The smaller bodied, omnivorous capuchins, in contrast, can occupy newly regenerating forests and, as of our most recent censuses in 2003 and 2007, they once again outnumber the howlers (Table 8.2).

Figure 8.5 shows important differences in how the two populations grew in the 1980s and 1990s versus the most recent decade. Between 1983 and 1999, the capuchin population grew mainly via increases in group size (average group size went from 11 to 17) while the number of groups in the park only increased from 28 to 35. In contrast, the average howler group size fluctuated between census years, but showed no steady increase, whereas the number of howler groups doubled from 24 to 50 between 1983 and 1999 (Fig. 8.5b). During that time period, we repeatedly saw lone howler males move into unoccupied forest fragments and howl until they were joined by females and thus we surmise that the howler population initially increased by budding off small new groups. This pattern of creating new groups is feasible for howlers because both males and females regularly disperse. In contrast, the mechanism of capuchin population growth was via an increase in group size (Fig. 8.4b). Unlike the lone howler males who moved into previously unoccupied forest fragments, entire groups of capuchins began to range into new areas and because we often saw them in young forest, we infer that they accommodated their

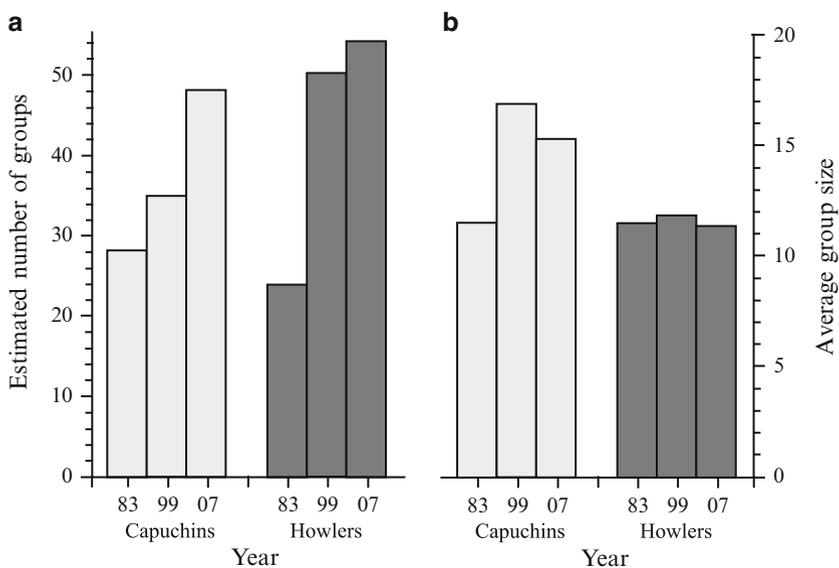


Fig. 8.5 (a) The estimated number of groups and (b) the mean group sizes of capuchin and howlers in Sector Santa Rosa in 1983, 1999 and 2007

increasing group size by expanding their home ranges into newly regenerating patches of forest.

However, beginning with our 2003 census, we started to see more new capuchin groups, their average group size stabilized and we ceased to locate new howler groups. The earlier species difference in population growth might have broken down because the howler population reached carrying capacity and because a large group size imposes reproductive costs on female capuchins – larger groups have lower female reproductive success (Fedigan and Jack 2011).

DeGama-Blanchet and Fedigan (2006) showed that the age of forest fragments significantly affects the densities of howlers and capuchins throughout ACG and that the availability of a dry season water source significantly predicts higher densities of capuchins. As pointed out by Altmann (1974) in his examination of baboon resources and home range sizes, water is the essential limiting resource for obligate drinkers living in arid regions. Sorensen and Fedigan (2000) found that capuchins can make use of forest patches as young as 25 years (Fig. 8.6), but whenever possible, they range in such a way as to have a source of dry season water within their home range from which they drink at least once daily. Capuchin densities follow a fairly linear pattern of increase from newly regenerating forest patches up to 180-year old (primary or evergreen) forest. Howlers do not usually appear in forest fragments under 60 years old and only become common in forests of 100–150 years old. Spider monkeys in Santa Rosa are only rarely seen in forest fragments less than 100–200 years old and they prefer larger patches, presumably to accommodate their trap-line pattern of foraging on fruit (Fig. 8.6). As described in Fedigan and Jack (2001), our long-term examination of the population dynamics of

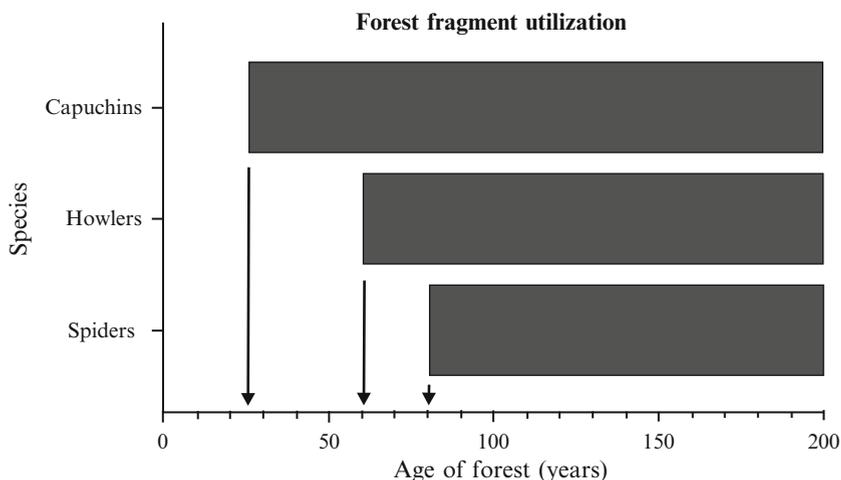


Fig. 8.6 The age of forest fragments that are utilized by capuchin, howler, and spider monkeys in Sector Santa Rosa. Capuchins can be found ranging, resting, and foraging in forest fragments ≥ 25 years of age, howlers in forest fragments ≥ 60 years and spider monkeys in forest fragments ≥ 80 years of age

these three species in a tropical dry forest habitat indicates that the fundamental requirement for capuchins is a year-round water source, whereas howlers (which seldom drink water) need large trees with leaves and fruit that have low levels of secondary compounds, and spider monkeys require large tracts of old growth forest to maintain their fission–fusion social system and frugivorous diet.

Another important difference in how the capuchin and howler populations have grown over the past 25 years concerns changes in age–sex compositions (Fig. 8.7). The age/sex composition of the howler population has fluctuated but not varied substantially between 1983 and 2007. However, adult males have accounted for an increasing proportion of the capuchin population. Furthermore, the ratio of adult males to females has gradually shifted from 0.47 in 1983 to 1.1 in 2007. Table 8.3 shows that while the numbers of infants, juveniles, and adult females doubled over the 25-year period, the number of adult males increased fivefold.

Why would there be a differential increase in the numbers of adult male capuchins? We offer three suggestions. First, the removal of hunters from the park has probably allowed more adult males to survive. Adult capuchin males assume a highly visible and audible protective role in their social groups and during encounters with humans they are always at the forefront of the group and are much more likely to be harmed or wounded than are other group members. Second, capuchins are a male-dispersal species and males are thus better able than are females to take advantage of protection in the park by immigrating into the more secure forests within the park boundaries. Finally, the infant sex ratios (Table 8.1) we recorded in our study groups between 1984 and 2000 were highly biased toward males in our groups and may reflect a population-wide bias toward male infants

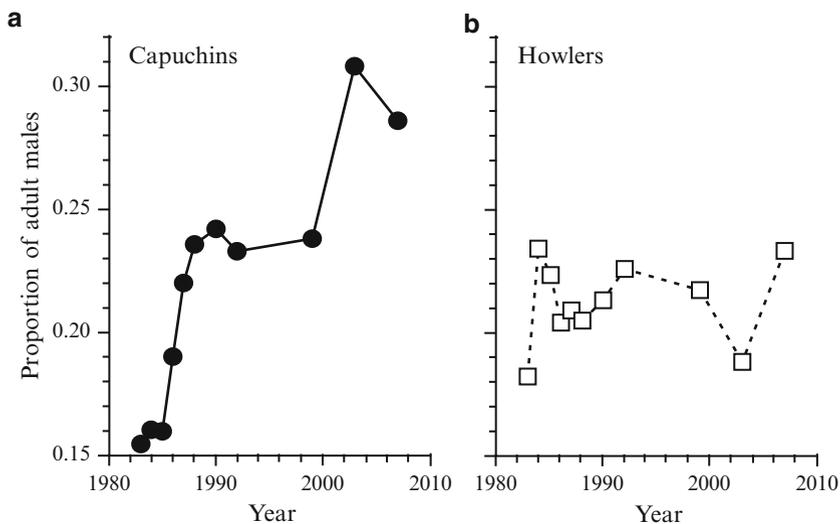


Fig. 8.7 Proportion of adult males for (a) capuchins and (b) howlers in the Santa Rosa population as counted during park-wide censuses between 1983 and 2007

Table 8.3 Age-sex composition of populations of (a) Capuchin monkeys and (b) Howler monkeys in Santa Rosa National Park, Costa Rica between 1983 and 2007

Year	# Counted	Prop. adult males	Prop. adult females	Prop. juveniles	Prop. infants	Prop. unknown	Adult males per adult female
(a) Capuchins							
1983	226	0.155	0.332	0.323	0.137	0.053	0.467
1984	338	0.160	0.337	0.349	0.109	0.044	0.474
1985	175	0.160	0.314	0.400	0.120	0.006	0.509
1986	284	0.190	0.313	0.345	0.109	0.042	0.607
1987	173	0.220	0.266	0.324	0.156	0.035	0.826
1988	123	0.236	0.276	0.382	0.098	0.008	0.853
1990	314	0.242	0.293	0.331	0.108	0.025	0.826
1992	541	0.233	0.298	0.237	0.176	0.057	0.783
1999	521	0.238	0.345	0.257	0.106	0.054	0.689
2003	655	0.308	0.276	0.342	0.072	0.002	1.116
2007	594	0.286	0.264	0.278	0.125	0.047	1.083
(b) Howlers							
1983	231	0.182	0.468	0.173	0.169	0.009	0.389
1984	299	0.234	0.425	0.217	0.124	0.000	0.551
1985	273	0.223	0.359	0.260	0.158	0.000	0.622
1986	313	0.204	0.403	0.201	0.176	0.016	0.508
1987	187	0.209	0.364	0.235	0.193	0.000	0.574
1988	220	0.205	0.382	0.205	0.209	0.000	0.536
1990	431	0.213	0.390	0.239	0.158	0.000	0.548
1992	579	0.226	0.408	0.185	0.169	0.012	0.555
1999	548	0.217	0.391	0.232	0.146	0.015	0.556
2003	538	0.188	0.411	0.227	0.169	0.006	0.457
2007	463	0.233	0.443	0.173	0.145	0.006	0.527

during this time period. If the infant sex ratios we observed in our study groups during this time period are reflective of the capuchin population as a whole, then the current population-wide male-biased adult sex ratio is not unexpected. Interestingly, the infant sex ratios in our study groups has changed to a nearly 1:1 ratio over the past decade and we are interested to see how this change will be reflected in the population-wide adult sex ratios in the years to come. Subsequent to the Trivers–Willard hypothesis (Trivers and Willard 1973), much has been published on factors affecting primate sex ratios at birth (see review and meta-analyses in Brown and Silk 2002). However, we agree with Strier (2009) that the sample sizes common in studies such as our own are too small to test whether the observed changes over time are truly adaptive or are random deviations from what will eventually prove to be a 50:50 ratio between sons and daughters at birth. Only the continuation of our already long-term study will tell.

8.4 Conclusions

Under the protection of the ACG park service, the typical tree species of a neotropical dry forest are slowly re-establishing themselves in former pasture land, creating arboreal corridors between fragments and growing into secondary forests that can be exploited by capuchins. Also, the forest fragments of Santa Rosa that were not cleared for agriculture but were selectively logged and subjected to other forms of human exploitation are now protected. Our long-term research has clearly demonstrated that monkey populations increase under these conditions. However, we can also draw the wider lesson that because the life history pattern and interaction of each species with its environment is unique, the successful restoration of primate populations is more complicated than simply removing the disturbances that humans introduced in the first place (hunters, loggers, cattle, non-native plants, anthropogenic fires).

It is essential to understand the species-specific aspects of vulnerability and potential for recovery. As pointed out by Chapman et al. (2010), a complex set of interactions govern changes in habitat composition and structure and the associated changes in animal populations. Chapman and colleagues found from repeated transect censuses in Kibale National Park between 1970 and 2006, that two of five primate species (mangabeys, black-and-white colobus) had increased in density over the study period, two (redtails, red colobus) were stable, and one (blue monkeys) had declined. In contrast, our long-term research indicates that population sizes of all three monkey species we study have increased since 1971, but differentially so. We attribute their differential patterns of population recovery to the many species-specific aspects of their biology and behavioral ecology (e.g., differences in body size, diet, life history pace, social organization and behavioral flexibility in response to change). It is encouraging that the monkey populations in the protected forests of Santa Rosa have grown substantially in the 40 years since the park was established. Although it requires great energy, optimism, and patience

to work toward the regeneration of a forest, our research shows that humans have successfully created the conditions to re-grow the monkey populations of Santa Rosa.

It also takes effort, diligence and a long view to maintain a field study over a nearly 30-year period. But without a multi-year study, there is much vital information about these monkeys we could not know. We hope that this brief overview of some of the findings from our Santa Rosa project demonstrate that the rewards are well worth the effort.

Acknowledgments We thank the Costa Rican National Park Service for permission to work in SRNP from 1983 to 1989 and the administrators of the Area de Conservación Guanacaste (especially Roger Blanco Segura) for allowing us to continue research in the park through the present day. Many people contributed to the census and life history database on the Santa Rosa monkeys and we are grateful to all of them. John Addicott developed the database and helped with the figures. Greg Bridgett maintains the database and helped with editorial matters. Research protocols reported in this paper complied with all institutional and government regulations regarding ethical treatment of our study subjects. L.M. Fedigan's research is supported by NSERC and the Canada Research Chairs Program. K.M. Jack's research is supported by grants from Tulane University's Research Enhancement Fund and Committee on Research. We also thank the Zemurray Foundation for support of our project.

References

- Allen W (2001) *Green phoenix: restoring the tropical forests of Guanacaste*. Oxford University Press, New York
- Altmann SA (1974) Baboons, space, time, and energy. *Am Zool* 14:221–248
- Borries C (2000) Male dispersal and mating season influxes in Hanuman langurs living in multi-male groups. In: Kappeler PM (ed) *Primate males: causes and consequences of variation in group composition*. Cambridge University Press, Cambridge, pp 146–158
- Bronikowski AM, Altmann J, Brockman DK, Cords M, Fedigan LM, Pusey AE, Stoinski T, Morris WF, Strier KB, Alberts SC (2011) Aging in the natural world: comparative data reveal similar mortality patterns across primates. *Science* 331:1325–1328
- Brown GR, Silk JB (2002) Reconsidering the null hypothesis: is maternal rank associated with birth sex ratios in primate groups? *Proc Natl Acad Sci USA* 99:11252–11255
- Carnegie SD (2011) *Reproductive behaviour and endocrinology of female white-faced capuchins (Cebus capucinus)*. PhD Dissertation, University of Calgary
- Carnegie SD, Fedigan LM, Ziegler TE (2005) Behavioral indicators of ovarian phase in white-faced capuchins (*Cebus capucinus*). *Am J Primatol* 67:51–68
- Carnegie SD, Fedigan LM, Melin AD (2011) Reproductive seasonality in female capuchins (*Cebus capucinus*) in Santa Rosa (Area de Conservación Guanacaste), Costa Rica. *Int J Primatol*. doi:10.1007/s10764-011-9523-x
- Chapman CA (1986) *Boa constrictor* predation and group response in white-faced cebus monkeys. *Biotropica* 18:171–171
- Chapman CA (1989) Spider monkey sleeping sites: use and availability. *Am J Primatol* 18:53–60
- Chapman CA (1990) Ecological constraints on group size in three species of neotropical primates. *Folia Primatol* 55:1–9
- Chapman CA, Fedigan LM, Fedigan L (1988) A comparison of transect methods of estimating population densities of Costa Rican primates. *Brenesia* 30:67–80

- Chapman CA, Fedigan LM, Fedigan L, Chapman LJ (1989a) Post-weaning resource competition and sex ratios in spider monkeys. *Oikos* 54:315–319
- Chapman CA, Chapman L, Glander KE (1989b) Primate populations in northwestern Costa Rica: potential for recovery. *Primate Conserv* 10:37–44
- Chapman CA, Struhsaker TT, Skorupa JP, Snaith TV, Rothman JM (2010) Understanding long-term primate community dynamics: implications of forest change. *Ecol Appl* 20:179–191
- DeGama-Blanchet HN, Fedigan LM (2006) The effects of forest fragment age, isolation, size, habitat type, and water availability on monkey density in a tropical dry forest. In: Estrada A, Garber PA, Pavelka MSM, Luecke L (eds) *New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation*. Springer, New York, pp 165–188
- Di Bitetti MS, Janson CH (2000) When will the stork arrive? Patterns of birth seasonality in neotropical primates. *Am J Primatol* 50:109–130
- Evans S (1999) *The green republic: a conservation history of Costa Rica*. University of Texas Press, Austin
- Fedigan LM (2003) Impact of male takeovers on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. *Int J Primatol* 24:723–741
- Fedigan LM, Jack KM (2001) Neotropical primates in a regenerating Costa Rican dry forest: a comparison of howler and capuchin population patterns. *Int J Primatol* 22:689–713
- Fedigan LM, Jack KM (2004) The demographic and reproductive context of male replacements in *Cebus capucinus*. *Behaviour* 141:755–775
- Fedigan LM, Jack KM (2011) Two girls for every boy: the effects of group size and composition on the reproductive success of male and female white-faced capuchins. *Am J Phys Anthropol* 144:317–326
- Fedigan LM, Rose LM (1995) Interbirth interval variation in three sympatric species of neotropical monkey. *Am J Primatol* 37:9–24
- Fedigan LM, Fedigan L, Chapman CA, Glander KE (1988) Spider monkey home ranges: a comparison of radio telemetry and direct observation. *Am J Primatol* 16:19–29
- Fedigan LM, Rose LM, Morera Avila R (1996) See how they grow: tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In: Norconk MA, Rosenberger AL, Garber PA (eds) *Adaptive radiations of neotropical primates*. Plenum Press, New York, pp 289–307
- Fedigan LM, Rose LM, Morera Avila R (1998) Growth of mantled howler groups in a regenerating Costa Rican dry forest. *Int J Primatol* 19:405–432
- Fedigan LM, Carnegie SD, Jack KM (2008) Predictors of reproductive success in female white-faced capuchins (*Cebus capucinus*). *Am J Phys Anthropol* 137:82–90
- Ford SM, Davis LC (1992) Systematics and body size: implications for feeding adaptations in New World monkeys. *Am J Phys Anthropol* 88:415–468
- Fragaszy DM, Visalberghi E, Fedigan LM (2004) *The complete capuchin: the biology of the genus Cebus*. Cambridge University Press, Cambridge
- Freese CH (1976) Censusing *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus* in the Costa Rican dry forest. In: Thorington RW, Heltne PG (eds) *Neotropical primates: field studies and conservation*. National Academy of Science, Washington, DC, pp 4–9
- Glander KE, Fedigan LM, Fedigan L, Chapman CA (1991) Field methods for capture and measurement of three monkey species in Costa Rica. *Folia Primatol* 57:70–82
- Jack KM (2003) Males on the move: evolutionary significance of secondary dispersal in male primates. *Primate Rep* 67:61–83
- Jack KM, Fedigan LM (2004a) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: patterns and causes of natal emigration. *Anim Behav* 67:761–769
- Jack KM, Fedigan LM (2004b) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: patterns and causes of secondary dispersal. *Anim Behav* 67:771–782
- Jack KM, Fedigan LM (2006) Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In: Estrada A, Garber PA, Pavelka MSM, Luecke L (eds) *New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation*. Springer, New York, pp 367–386

- Jack KM, Fedigan LM (2009) Female dispersal in a female-philopatric species, *Cebus capucinus*. *Behaviour* 146:471–497
- Jack KM, Sheller C, Fedigan L (2010) Predicting natal dispersal in male white-faced capuchins (*Cebus capucinus*). *Am J Phys Anthropol* 141(suppl S50):133
- Jack KM, Sheller C, Fedigan LM (2011) Social factors influencing natal dispersal in male white-faced capuchins (*Cebus capucinus*). *Am J Primatol* 73: 1–7
- Janson CH, Verdolin JL (2005) Seasonality of primate births in relation to climate. In: Brockman DK, van Schaik CP (eds) *Seasonality in primates: studies of living and extinct human and non-human primates*. Cambridge University Press, Cambridge, pp 307–350
- Janson C, Baldovino MC, Di Bitetti M (2012) The Group Life Cycle and Demography of Brown Capuchin Monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina. In: Kappeler PM (ed) *Long-term field studies of primates*. Springer, Heidelberg
- Janzen DH (1988) Guanacaste National Park: tropical ecological and biocultural restoration. In: Cairns J Jr (ed) *Rehabilitating damaged ecosystems*. CRC Press, Baton Rouge/FL, pp 143–192
- Janzen DH (2000) Costa Rica's Area de Conservación Guanacaste: a long march to survival through non-damaging biodevelopment. *Biodiversity* 1:7–20
- Janzen DH (2002) Tropical dry forest: Area de Conservación Guanacaste, northwestern Costa Rica. In: Perrow MR, Davy AJ (eds) *Handbook of ecological restoration, vol 2, Restoration in practice*. Cambridge University Press, Cambridge, pp 559–583
- Janzen DH (2004) Ecology of dry forest wildland insects in the Area de Conservación Guanacaste. In: Frankie GW, Mata A, Vinson SB (eds) *Biodiversity in Costa Rica: learning the lessons in a seasonal dry forest*. University of California Press, Berkeley, pp 80–96
- Morelli TL, King SJ, Pochron ST, Wright PC (2009) The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. *Behaviour* 146:499–523
- Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2006) Father-daughter inbreeding avoidance in a wild primate population. *Curr Biol* 16:R156–R157
- Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2010) Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. *Am J Primatol* 72:1118–1130
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annu Rev Ecol Syst* 17:67–88
- Parr N (2011) Predictors of parasitism in wild white-faced capuchins. MA thesis, University of Calgary
- Perry S, Manson JH (2008) *Manipulative monkeys: the capuchins of Lomas Barbudal*. Harvard University Press, Cambridge, MA
- Perry S, Godoy I, Lammers W (2012) The Lomas Barbudal Monkey Project: Two Decades of Research on *Cebus capucinus*. In: Kappeler PM (ed) *Long-term field studies of primates*. Springer, Heidelberg
- Smith DG (1982) Inbreeding in three captive groups of rhesus monkeys. *Am J Phys Anthropol* 58:447–451
- Sorensen TC, Fedigan LM (2000) Distribution of three monkey species along a gradient of regenerating tropical dry forest. *Biol Conserv* 92:227–240
- Strier KB (2009) Seeing the forest through the seeds: mechanisms of primate behavioral diversity from individuals to populations and beyond. *Curr Anthropol* 50:213–228
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92
- van Schaik CP, van Noordwijk MA, Nunn CL (1999) Sex and social evolution in primates. In: Lee PC (ed) *Comparative primate socioecology*. Cambridge University Press, Cambridge, pp 204–240