

Neotropical Primates in a Regenerating Costa Rican Dry Forest: A Comparison of Howler and Capuchin Population Patterns

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*Few data exist on how primate populations return to regenerating tropical forests. We compare the ways that two populations of neotropical monkeys, *Alouatta palliata* and *Cebus capucinus*, expanded over a 28-year period after the establishment of Santa Rosa National Park on reclaimed ranchlands in Costa Rica. We found that both howler and capuchin populations increased substantially in size subsequent to protection, but the howler population grew faster. This is likely due to their faster-paced life-history pattern than that of capuchins. The howler population increased mainly via the establishment of many new groups, whereas the capuchins expanded mainly by increasing the size of existing groups. We related this finding to the fact that capuchins are limited largely by their need to drink from water holes during the dry seasons whereas howlers are limited principally by their preference for larger-sized trees that occur in older forests. Proportions of adult male capuchins increased significantly during our study, likely due to skewed sex ratio at birth or male-biased immigration into the protected park or both factors. Our main finding is that, in as short a time period as 28 years, we can substantially enhance the size of monkey populations by allowing the regeneration of tropical forest. Furthermore, we provide a preliminary interpretation of how extrinsic factors—deforestation, hunting, crop-spraying, destruction of the watershed—and intrinsic variables, e.g., pace of reproduction; diet, differentially affect not only each species' vulnerability to extinction but also its capacity to recover when human disturbances are minimized.*

KEY WORDS: neotropical; primates; howlers; capuchins; conservation.

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INTRODUCTION

Humans have been burning, logging, and clear-cutting forests at least since the beginnings of agriculture 10,000 years ago, but the rate of forest destruction is ever-increasing with the expansion of the human population. Although monkeys have co-existed in tropical habitats with humans as far back as we can trace the fossil record, the accelerating pace at which tropical forests are being converted to agricultural lands in recent decades is threatening the extinction of many species. Not surprisingly, numerous primatologists have turned their attention to monitoring the catastrophic decline of primate populations that are being forced to live in forest fragments of ever diminishing size (Bearder, 1991; Dobson and Lyles, 1989; Estrada and Estrada, 1988, 1996; Ferrari and Diego, 1995; Ganzhorn, 1995; Harcourt, 1998; Johns and Skorupa, 1987; Marsh *et al.*, 1987; Mitani *et al.*, 2000; Mittermeier and Cheney, 1987; Oates, 1994; Robinson and Ramirez, 1982; Robinson and Redford, 1986). For example, neotropical dry forest once covered most of Central America, but by the 1980s <2% of it was in an undisturbed state and only 0.09% of it was protected (Janzen, 1986a). The protection of remaining forest fragments in concert with the reclamation of agricultural lands and the restoration of natural patterns of forest succession is thus an essential tool in tropical conservation biology. Around the world, conservation groups are working toward the expansion of habitat refuges and the establishment of protected areas. However, only a small body of literature exists on how and when mammalian populations return to protected and regenerating forests (Chapman *et al.*, 1989a; Johns, 1992; Johns and Johns, 1995; Majer, 1989; Oluput *et al.*, 1994; Patten, 1997; Sorensen and Fedigan, 2000).

We documented and compared the ways that two populations of neotropical monkeys, mantled howlers (*Alouatta palliata*) and white-faced capuchins (*Cebus capucinus*) have expanded over a 28-year period subsequent to the establishment of a national park on reclaimed ranchlands in Costa Rica. Caro (1998) argued that conservation biologists greatly need long-term demographic information of the type collected by behavioral ecologists, but such data are seldom available because quick management decisions must be made before long-term studies can be conducted. He also pointed out that behavioral ecologists prefer to study animals in relatively undisturbed habitats even though data on behavioral and demographic parameters in disturbed habitats have much to teach us about animal responses to human influences. By presenting our findings on the growth of howler and capuchin populations in a regenerating tropical dry forest, we hope to shed some light on the potential for recovery of neotropical primates in reclaimed habitats. Furthermore, we provide a preliminary interpretation of

how extrinsic factors, e.g., deforestation, hunting, crop-spraying, destruction of the watershed, and intrinsic variables, e.g., pace of reproduction, diet, differentially affect not only each species' vulnerability to extinction but also its capacity to recover when human disturbances are removed. As Harcourt (1998) and Pearl (1992) have noted, conservation biologists need a better knowledge of both extrinsic and intrinsic indicators of risk. We suggest that at least some of these same factors can also be used as predictors of recovery.

METHODS

(1) Study Site

Established in 1971, Santa Rosa National Park (SRNP) is located near the Nicaraguan border, 35 km northwest of Liberia in Guanacaste Province, Costa Rica. SRNP comprises 108 km² of tropical dry forest covering an upper and lower plateau and ranging from the foothills of volcanic mountains down to the Pacific coastal plain (300–0 m elevation). In 1986, a project was begun to purchase the ranchlands surrounding SRNP, using a debt for nature swap (Honey, 1999; Janzen, 1986b; Liebow, 1993; Wallace, 1992), and the result is a much enlarged megapark—Area de Conservacion Guanacaste (ACG)—that is the site of an experiment in tropical forest restoration. The core of ACG remains SRNP (Sector Santa Rosa), and the original SRNP park boundaries form the borders of our census research, which began in 1983 and continues presently.

The original forests of SRNP consisted mainly of semi-evergreen trees (Janzen, 1983a,b, 1986a,b), but over the past 400 years, much of the upper plateau was cleared for cattle pasture and planted with African jaragua grass, (*Hyparrhenia rufa*) while a large beef, hide and mule-producing ranch was in operation. In addition, the forests of Santa Rosa were selectively logged, primarily for mahogany, *Swietenia macrophylla*, and subject to frequent fires resulting from runaway grass fires set by humans. Since the establishment of the park in 1971, cattle and hunters/poachers have been removed, fires blowing in from neighboring ranchlands have been increasingly controlled, and trees have begun to grow again in abandoned pastures (Gebhardt, 1994; Janzen, 1988). This history of differential disturbance and subsequent protection has resulted in a mosaic landscape with various stages of forest regeneration. There are fragments of evergreen and riparian forest, and early secondary forest succeeding in former pastures, usually dominated by wind-dispersed species. *Cochlospermum vitifolium*, *Tabebuia rosea*, *Luehea speciosa*. There are also fragments of oak and mangrove forest that are sometimes used by

the monkeys. However, the majority of the forest cover is best described as dry deciduous forest in various stages of succession.

SRNP receives 800–2600 mm of rainfall annually (mean = 1473 mm) and mean high temperatures range from 21.6°C (September) to 34.4°C (April; Janzen and Hallwachs, 1995). The province of Guanacaste typically experiences a severe dry season lasting from approximately mid-December to mid-May, during which virtually no rain falls and deciduous trees lose their leaves (Janzen, 1986b). Although there are several seasonal streams that cross SRNP, they only flow at the height of the rainy season. During the dry season, streams, creeks and waterholes gradually dry up. Only a few spring-fed water sources last throughout the year. Riparian strips of forest and patches of semi-evergreen forest are more likely to retain their leaves throughout the dry season than other types of forest cover, and they are important sources of food and shade for primates.

There are three species of monkeys in SRNP, mantled howlers (*Alouatta palliata*), white-faced capuchins (*Cebus capucinus*) and black-handed spider monkeys (*Ateles geoffroyi*). Members of our research team have studied all of them since 1983. Many aspects of the behavioral ecology of primates in Santa Rosa have now been described, including diet, home ranges, group compositions, locomotor and social patterns and associations with particular ages and types of forest (howlers: Bergeson, 1996; Chapman, 1988; Gebo, 1992; LaRose, 1996; capuchins: Chapman, 1986; Chapman and Fedigan, 1990; Fedigan, 1990, 1993; Hall and Fedigan, 1997; Rose and Fedigan, 1995; Rose, 1994a,b; spider monkeys: Chapman, 1989; Chapman and Chapman, 1991; Chapman *et al.*, 1989b; Fedigan *et al.*, 1988; Glander *et al.*, 1991).

(2) Subjects and Census Techniques

Freese (1976) first attempted to count the number of monkeys in SRNP in 1972. Our long-term research on the monkeys of Santa Rosa started with a brief demographic survey of primates in 1982, followed by more intensive censuses in 1983 and 1984 (Fedigan, 1986; Fedigan *et al.*, 1985; Chapman *et al.*, 1988). In 1984, we selected a few study groups of each species for intensive research and began to discriminate and to habituate individuals in them. In 1985, we began to record births, deaths and migrations (Fedigan and Rose, 1995), as well as details of foraging and social behavior on a regular biweekly basis, a practice that continues. To facilitate reliable discrimination of individuals, we captured and marked most adult members of the howler study groups and a few members of the capuchin groups and spider monkey community (Glander *et al.*, 1991). Although we have added and lost (through

attrition) many individuals and several study groups in the 17-year history of this project, the intensive biweekly data obtained from the study groups provide a detailed sample or microcosm of typical demographic events in the larger population and help us to validate the broader survey data obtained from our intermittent park-wide population censuses.

Between 1983 and 1999, we conducted 9 censuses of howlers and capuchins throughout SRNP. We did not include spider monkeys in this census project because of the fission-fusion nature of their social system and their ability to travel great distances rapidly (Fedigan *et al.*, 1988). We use a modified quadrat technique that has proven useful in areas of fragmented patches of forest (Fedigan *et al.*, 1996, 1998). The censuses were almost always carried out in May and June, during which time we located and counted as many of the howler and capuchin groups as possible and marked their home ranges on a map.

We chose one area at a time, usually a patch of forest, and walked either transects or all known trails and dry stream beds in the area to locate monkeys. The loud howling vocalizations of *Alouatta* and noisier calls of *Cebus* were particularly useful to locate groups, which we followed for the day. We considered any monkey within 100–300 m of the group that travels consistently in the same direction of the group, even if in a peripheral position, to be part of the group. We used unique markings and distinctive age/sex compositions to identify the same group on successive days for repeat counts. Multiple observers repeatedly counted a group until achieving a stable count and composition, and plotted their location on a map. After establishing a stable count on one group, we located its nearest neighboring group. Whenever possible, with the aid of two-way radios, we used 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. This method of censusing does not account for single individuals that may be transferring between groups. Solitary monkeys are difficult to spot in the forests of Santa Rosa unless they are vocalizing, primarily because they are secretive and do little to attract attention (Glander, 1992). When we have observed solitaires near our study groups, they did not remain alone or in the same area for any length of time; they either attempted to join a group as a peripheral individual or traveled on. Because lone individuals can range over large distances, we did not count them, as it would be possible to count solitaires twice in widely separated places on different days of the census. We see very few solitaires during a census, so the number of migrating individuals that could be found and counted in any given census is small.

We assigned each individual in each group to one of four age/sex classes: adult male, adult female, juvenile and infant per Fedigan *et al.* (1996, 1998). The sexes of adult howlers and adult capuchins are easily noted and the age classes of infants, juveniles and adults are easily distinguished by size. The sexes of immature howlers and capuchins are more difficult to identify, and we did so reliably only for the members of our well-known study groups.

(3) Data Analysis

Although our first census took place in 1983, there were a few areas of the park that we did not search adequately until 1984. They are probably more representative of the population sizes at the beginning of our study. Furthermore, the 9 censuses were differentially complete due to variable amounts of time and resources to conduct the surveys in different years. Because we know the location of each established group we know which ones we have failed to find and to count on any given year. Our most thorough censuses took place in 1984, 1992, and 1999.

We compared the demographic parameters of the howler and capuchin populations between 1984 and 1999, which were our earliest and latest complete census years. Further, we compared long-term changes in population structure and growth rates among 1972, 1984, 1992 and 1999. We could not always use the use of Freese's 1972 census data because the survey was conducted with somewhat different methods than those used later. Accordingly, several inter year comparisons exclude the 1972 data. For group composition analyses and ratios, we used only groups for which we have complete counts and age/sex identification of individuals. We used t-tests (unpaired, two-tailed) to compare group size and composition between census years. All statistical analyses employed SPSS-PC; significance is at $p \leq 0.05$.

RESULTS

(1) Population Growth Rate

Between 1972 and 1999, the estimated number of howlers in the park increased from 85 to 606 (Table 1), and the estimated number of capuchins went from 300 to 585. Thus, the howler population has increased more than seven-fold over the past 28 years, whereas the capuchin population has not quite doubled. Between 1984 and 1992, the howler population grew at an average rate of 6.2% per annum, whereas the capuchin population grew on average 3.7% per year. Thus, over this 8-year period, the howler population grew at nearly twice the rate of the capuchin population.

Table 1. Demographic trends in Santa Rosa howlers and capuchins from 1972 to 1999

Year	Howlers					Capuchins				
	No. of monkeys counted	No. of groups counted	Average group size	Estimated no. of groups	Estimated pop size	No. of monkeys counted	No. of groups counted	Average group size	Estimated no. of groups	Estimated pop size
1972	65	8	8.10	10	85	?	1	17.5	17	300
1983	223	19	11.7	24	281	229	20	11.5	28	321
1984	342	25	13.6	25	342	393	28	13.6	28	393
1985	264	16	16.5	26	437	193	13	14.8	28	415
1986	314	20	15.7	28	440	311	19	16.4	28	458
1987	164	15	10.9	30	322	217	13	16.7	28	467
1988	211	12	17.6	31	546	164	10	16.4	28	459
1990	439	28	15.7	33	510	318	18	17.7	28	495
1992	554	34	16.3	34	554	526	29	18.1	29	526
1999	537	45	12.1	50	606	534	31	17.2	34	585

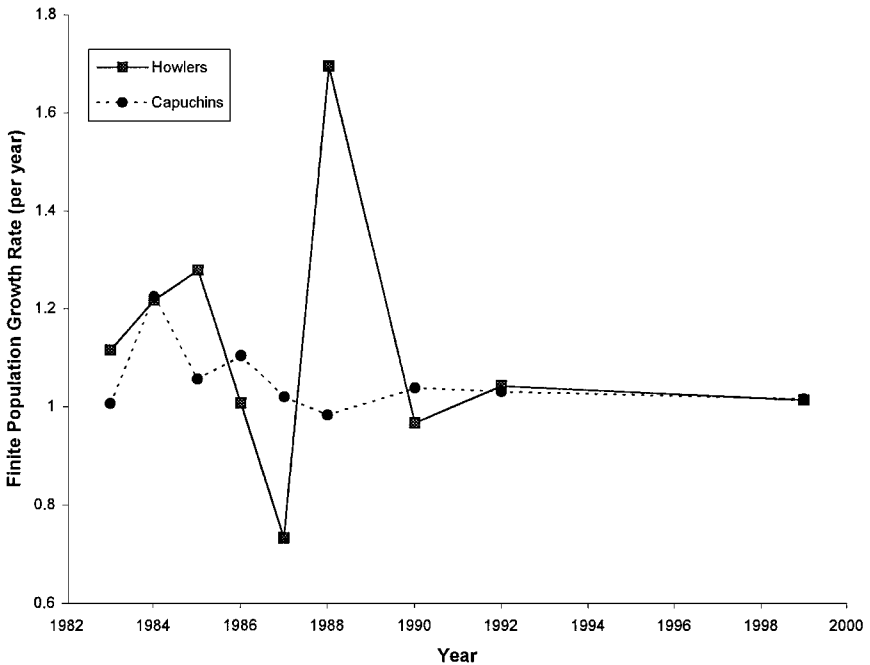


Fig. 1. Finite population growth rates (per year) in SRNP howlers and capuchins between 1983 and 1999.

However, Fig. 1 shows that the growth rate per year of the howler population was actually fluctuating more than that of the capuchin population. Between 1992 and 1999—a 7-yr interval—both the howler and the capuchin populations grew at an average rate of 1.2% per annum, that is, the growth rates of both monkey populations slowed down in the 1990s versus the earlier years of our study. (Fig. 1).

(2) Age Structure of the Population

One indicator of the health of a primate population and a measure of its reproductive rate is its age structure, which we represent as the ratio of infants to adult females, and the ratio of juveniles to adult females. Figure 2 shows the ratios of infants and juveniles to adult females in howlers (a) and capuchins (b) at four times since the creation of Santa Rosa National Park and the protection of the flora and fauna therein. These four time periods are 1972 (6 mo after the park was established), 1984 (when we conducted our first complete census and 13 years post-protection), 1992

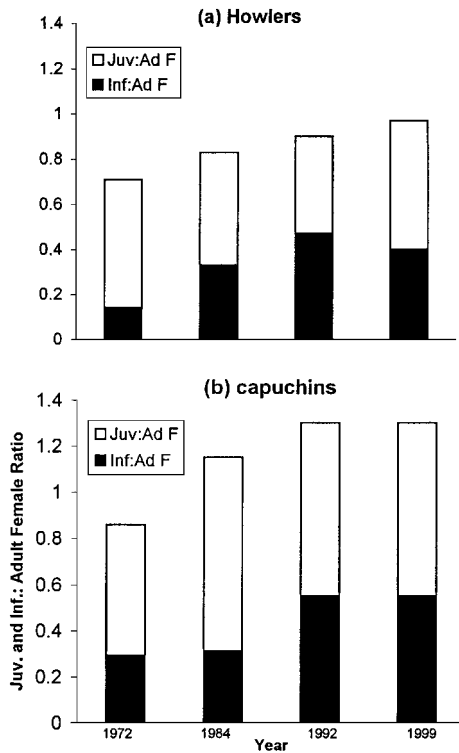


Fig. 2. Age structure, based on ratios of infants:adult females and juveniles:adult females in SRNP howlers and capuchins between 1972 and 1999.

(21 years post-protection) and 1999 (28 years post-protection). The proportions of infants to adult females were at their lowest values immediately post-protection (howlers: 0.14; capuchins 0.29) and climbed steadily for both species until 1992, by which time there was approximately 1 infant to every two adult females in both howlers (0.47) and capuchins (0.55). Concomitant with the plateau in population growth (Fig. 1), the increasing ratio of infants to adult females leveled off between 1992 and 1999 (and decreased slightly in the howlers). However, there has still been a trend of increasing ratios of infants to adult females since the park was established, and the infant: adult female ratios most recently recorded in 1999 are significantly greater than those that were recorded by Freese in 1972 (howlers: 1972 versus 1999; $t = -3.118$; $df = 51$; $p = 0.003$; capuchins: 1972 versus 1999; $t = 3.640$; $df = 27$; $p = 0.001$).

The pattern for the juvenile:adult female ratio is less clear over the years since the park was established than that of infants to adult females. The ratios of howler juveniles remained almost constant over this period, from 0.57 in 1972 to 0.56 in 1999 ($t = 0.033$; $df = 51$; $p = 0.974$). In contrast, there was a significant increase in the capuchin juvenile:adult female ratio, from 0.57 in 1972 to 0.93 in 1999 ($t = 3.268$; $df = 27$; $p = 0.003$). Moreover, the overall ratios of immatures—(infants and juveniles)—to adult females, shows that the age structure of both monkey populations has been shifting to a greater component of immature individuals over the years since the park was established, but only significantly so in the capuchins. The howler population showed a non-significant trend to increasing immature: adult female ratios (0.79 in 1972 versus 0.97 in 1999, $t = -1.421$; $df = 61$; $p = 0.161$), driven no doubt by the increasing proportions of infants. The capuchins showed a significant increase in immature: adult female ratios (0.86 in 1972 versus 1.44 in 1999, $t = 4.463$; $df = 27$; $p = 0.000$).

(3) Number of Groups and Group Size

Between 1984 and 1999, the estimated number of howler groups doubled (from 25 groups in 1984 to 50 in 1999), whereas the number of capuchin groups increased <20% (from 28 to 34, Table I). When we include the earlier data from Freese for (1972), we find that over a 28-year period, the estimated number of howler groups in the park went from 10 to 50 (a five-fold increase), whereas the estimated number of capuchin groups only doubled (17 groups in 1972 to 34 groups in 1999).

The average size of howler groups has fluctuated over the census years, ranging from a low of 8.1 monkeys per group to a high of 17.6 (Fig. 3). There is no significant difference between average howler group sizes in 1984 and 1999 ($t = 0.50$; $df = 68$; $p = 0.621$). In contrast, the average group size of capuchins has increased relatively steadily from a low of 11.5 in 1983 to a high of 18.1 in 1992 (Fig. 3). Even though the average group size of capuchins decreased slightly in our 1999 census to 17.2 monkeys per group, the 1999 average size is still significantly larger than the average of 13.8 group members in 1984 ($t = -2.19$; $df = 56$; $p = 0.033$).

Figure 4 is a comparison of howlers to capuchins for three demographic variables: population size, number of groups, and number per group. The howler population was far smaller than the capuchin population (85 versus 300) when Freese first censused them in 1972, 6 months after the establishment of the park. When we carried out our first complete census in 1984 the howler population was still smaller than the capuchin population (342 versus 393). However, by 1999 there were slightly more howlers than capuchins in Santa Rosa (606 versus 585).

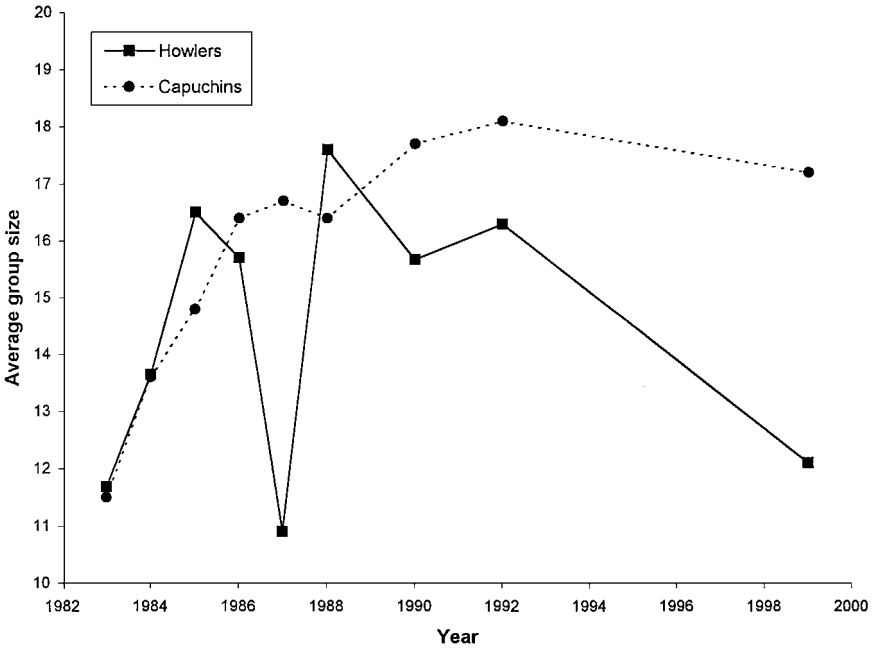


Fig. 3. Variation in mean howler and capuchin group sizes at SRNP from 1983 to 1999.

Thus, the growth of the two populations was accomplished in different ways (Fig. 4). Whereas the howler population expanded via the establishment of new groups, the capuchin population expanded mainly by increasing the size of their groups rather than the number of them.

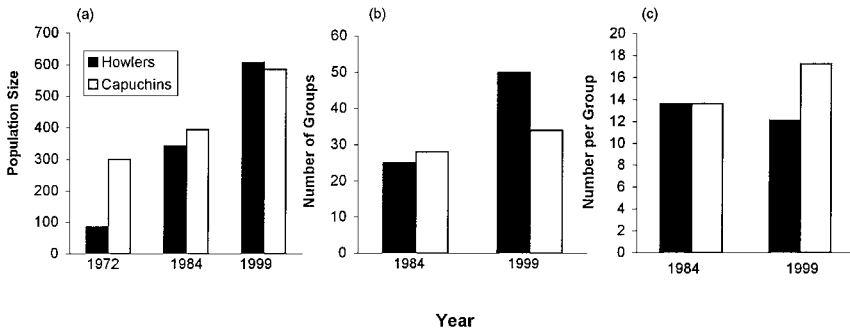


Fig. 4. Demographic changes in howler and capuchin SRNP populations: (a) population size; (b) number of groups; and (c) number of monkeys per group.

Table II. Group composition of Santa Rosa howlers and capuchins (1983–1999)

Year	\bar{x} Proportion in Age/Sex Class ¹							
	Howlers				Capuchins			
	Adult male	Adult female	Juvenile	Infant	Adult male	Adult female	Juvenile	Infant
1983	0.19	0.52	0.13	0.16	0.17	0.34	0.34	0.15
1984	0.22	0.44	0.20	0.14	0.17	0.37	0.36	0.10
1985	0.22	0.37	0.25	0.16	0.19	0.33	0.36	0.12
1986	0.20	0.41	0.21	0.18	0.20	0.29	0.41	0.10
1987	0.20	0.39	0.20	0.19	0.23	0.27	0.36	0.14
1988	0.21	0.43	0.18	0.18	0.23	0.27	0.37	0.12
1990	0.24	0.41	0.19	0.16	0.25	0.30	0.32	0.13
1992	0.24	0.41	0.16	0.19	0.22	0.31	0.29	0.18
1999	0.22	0.39	0.23	0.16	0.25	0.31	0.27	0.17
\bar{x} =	0.22	0.42	0.19	0.17	0.21	0.31	0.34	0.13

¹Group sizes and proportions are means across all groups counted in each year.

(4) Group Composition: Age/Sex Classes and Sex Ratios

In Table II, we present group composition data for howlers and capuchins, calculated as the average proportions of individuals in each age/sex class across all groups in a given year. Averaged over all the years of our study (1983–99) adult howler females make up 42% of the group, and adult males constitute about 22% of the group's membership. Juveniles constitute on average about 19% of the group's membership and infants make up 17%. These proportions have been remarkably consistent over time, even as average group sizes and overall population size have changed. There is no difference in group composition between 1984 and 1999 except in the proportion of adult females in groups, which decreased modestly from 44% to 39% ($t = 2.53$; $df = 68$; $p = 0.014$).

In the majority of howler groups censused, the adult sex ratio is biased toward females. Over all years of the study, the adult sex ratio averaged 0.54, or 1 male per 1.85 females (Fig. 5). The adult sex ratio did not differ significantly between 1984 (M:F = 0.5) and 1999 (M:F = 0.62; $t = -0.75$; $df = 68$; $p = 0.456$) and shows no consistent trend over time. We conclude that the howler groups generally have about twice as many adult females as adult males.

On average, adult female and juvenile capuchins each make up approximately one-third of the group (31% and 34% respectively) while males constitute about 21% and infants comprise 13% (Table 2). In contrast with the howlers, the age/sex composition of capuchin groups has changed

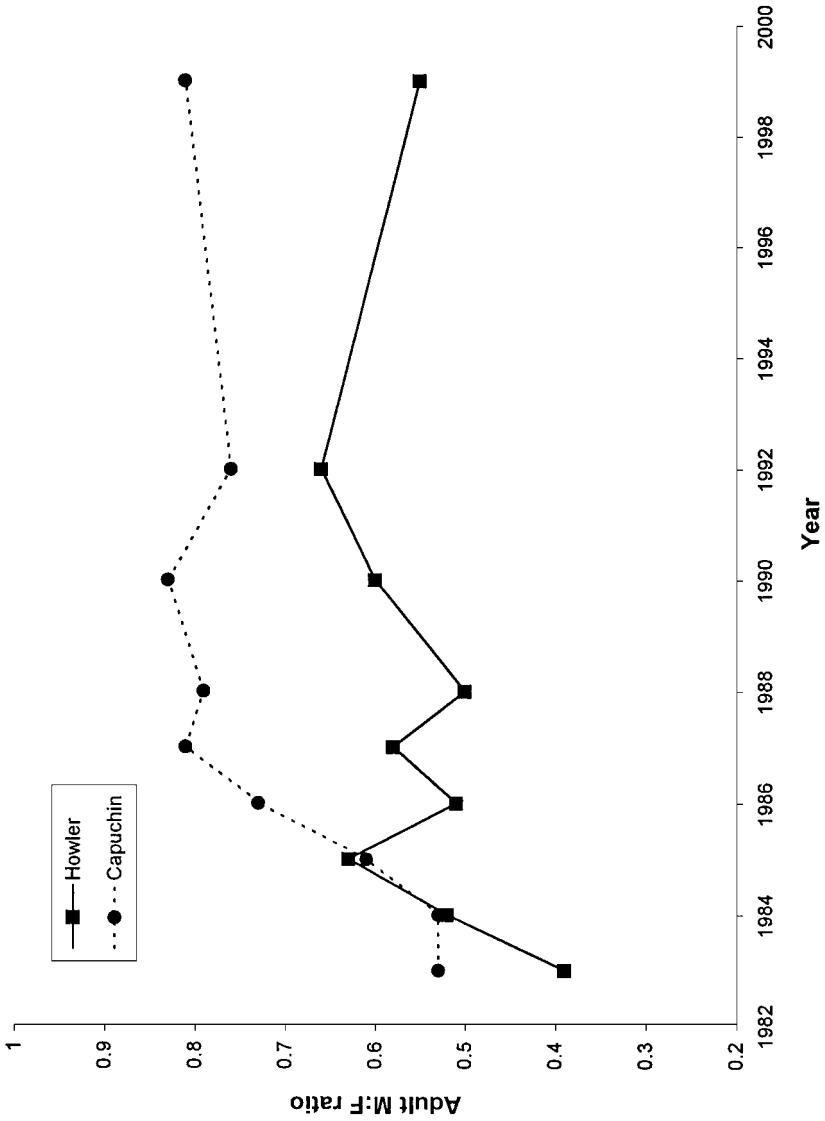


Fig. 5. Comparative changes in adult sex ratios in SRNP howlers and capuchins between 1983 and 1999.

significantly over the years. For example, between 1984 and 1999 the proportions of males increased from 17% to 25% ($t = -4.32$; $df = 53$; $p = 0.000$). The proportions of juveniles decreased from 36% to 27% ($t = 2.88$; $df = 53$; $p = 0.006$), and the proportions of infants increased from 10% to 17% ($t = -2.58$; $df = 53$; $p = 0.013$). Only the proportion of adult females in the groups fail to show a significant difference when it decreased 37% to 31% ($t = 2.88$; $df = 53$; $p = 0.055$).

The adult sex ratio in capuchins has become increasingly biased in favor of males since 1983 (Fig. 5), from an average of 0.55 in 1984 to 0.86 in 1999 ($t = -3.10$; $df = 53$; $p = 0.003$). Thus, by 1999, we counted nearly equal proportions of adult males and adult females in the capuchin groups, a marked contrast to the adult female-biased howler groups.

In summary, the howler groups have, on average, proportions of adult males similar to those of the capuchin groups, but higher proportions of adult females, and lower proportions of juveniles than the capuchin groups. The proportions of infants in groups of both species are relatively similar, with howler groups having slightly more infants. In terms of change over time, the age/sex composition of the howler groups has remained rather consistent, whereas there has been considerable shifting in the age/sex compositions of capuchin groups, marked especially by increasing proportions of adult males.

DISCUSSION

Both Populations have Increased in Size

In the 28 years since SRNP was first established, the populations of both howlers and capuchins have increased substantially—the capuchin population doubled and the howlers grew more than sevenfold. Furthermore, the ratios of infants and immatures to adult females increased steadily from 1972 (immediately postprotection) until the early 1990s. Both of these findings indicate that by creating zones of land protected from hunting, as well as from further forest destruction and other forms of human disturbance, humans can facilitate the growth of neotropical monkey populations in such areas. In particular, the dramatically increased infant to adult female ratios in SRNP over the past 28 years suggests that adult female monkeys in protected areas give birth to more infants or experience greater infant survivorship or both.

Before 1972, the Santa Rosa monkeys experienced the constraints of (1) hunting, (2) forest destruction by logging, anthropogenic fires, and clear-cutting, and (3) the disturbing proximity of ranchers, agricultural crops, and

cattle. During the 1970s and 1980s, after being released from these pressures, the monkey populations, particularly that of howlers, grew rapidly. In the 1990s, both the howler and the capuchin populational growth rates slowed down. This may indicate that they have saturated the current forest in the park and that further population growth will depend not only on protection but also on forest regeneration. The objective of the newer megapark, Area de Conservacion Guanacaste, that now surrounds SRNP is to not only protect existing forest but also to regrow the tropical dry forest that once covered the area. The regeneration project is carried out mainly through purchase of buffer zone neighboring ranches, control of anthropogenic fires and by prevention of human activities that adversely affect natural patterns of forest succession.

Satellite images from Landsat Thematic Mapper Scenes comparing forest cover between 1986 and 1997 established that forest cover is increasing in Area de Conservacion Guanacaste (Sanchez-Azofeifa et al., unpubl. ms.) They confirm on-the-ground observations that small abandoned pastures can revert to woody vegetation in as little as 20 years by invasion of wind and animal dispersed plants from surrounding forest (Janzen, 1988, pers.obs. and pers. comm. from park botanists). Clearly, it takes longer (50–200 years) to regenerate larger deforested patches and it will take many hundred years to restore the area to something like a pristine dry forest (Janzen, 1986b). Although the history and ages (=years since cessation of human disturbance) of various patches of forest in SRNP are generally known, the overall changes in forest cover of different types—secondary growth, evergreen, mixed deciduous—since the park was established have not yet been adequately quantified. Accurate estimates of changing primate densities depend on detailed knowledge of the increasing amounts of habitat that have become available to the monkeys over time as pastures revert to forest; the monkey density estimates must await analyses of aerial and satellite data on changes in forest cover. In the meantime, we have established that tree species diversity, canopy height, and fruit biomass are highest in older forests and that capuchin and howler densities are positively associated with forest age (Sorensen and Fedigan, 2000).

The Howler Population has Increased Faster

In Freese's 1972 census of the park and in our initial two census years, we counted fewer howlers than capuchins in SRNP. Why was the howler population lower than that of the capuchins when the park was first established? Although sufficient data do not exist to definitively answer the question,

Fedigan *et al.* (1998) presented several possible reasons: (1) Howlers experience cycles of yellow fever (Milton, 1982), and the SRNP howlers may have experienced a population crash immediately before 1972 from which they only began to recover in the 1980s. (2) Howlers only feed and rest in trees that are sufficiently large to support their weight, a minimum DBH (diameter at breast height) of 20 centimeters at our site, and a preferred DBH of 63 cm (Chapman, 1988; LaRose, 1996). In contrast, capuchins use secondary forest and smaller trees to a much greater extent. It is likely that the agricultural disturbances of the Santa Rosa area before 1972 had changed the balance of the remaining forest cover to favor capuchin habitat preferences. (3) Autopsies of howlers from the Santa Rosa area in the late 1960s showed that they were loaded with pesticides which were being sprayed from crop-dusters onto local cotton fields. Since howlers are facultative folivores, they may be more susceptible to pesticides that accumulate on the surface of leaves than omnivorous capuchins are. Whatever the reason or combination of reasons, it is clear that the howler population was very low at the time that the park was first established. According to Freese (1976), there were very few howlers on the upper plateau of the park, whereas in 1999, there were 22 groups of howlers in this area.

A related question is, having started out behind, how did the howler population catch up and surpass that of the capuchins? As with the earlier question, there are several possible answers, all of which may pertain. First, the mantled howler species has the capacity to reproduce somewhat faster than white-faced capuchins can, due to a greater maximum intrinsic rate of natural population increase ($r_m = 0.18$ in *Alouatta palliata* versus 0.17 in *Cebus capucinus*, Ross, 1991). Our findings on the life-history patterns of the species in Santa Rosa demonstrate (Fedigan and Rose, 1995, also unpubl. data and see also Glander, 1980) that mantled howlers first give birth at half the age of white-faced capuchins (3.5 versus 7 years). Compared to capuchins, howler females also reach menarche earlier, wean their infants earlier, and exhibit shorter interbirth intervals (Fig. 6). Since SRNP howler females give birth on average every 19 months versus 26 months in capuchins, howlers have the potential to produce more infants over their lifetimes. However, in captivity, howler females only live to 27 years of age whereas capuchins have been reported to live to 54 years. The mean ages at last birth and at death in the wild is not known for either species. Santa Rosa howlers also experience lower infant survival rates than those of capuchins (49% versus 69% survival in the first year of life).

Thus, there are reproductive constraints on the howler's faster-paced life-history pattern—shorter maternal life span and lower infant survivorship—but the extent to which this counteracts the potential for

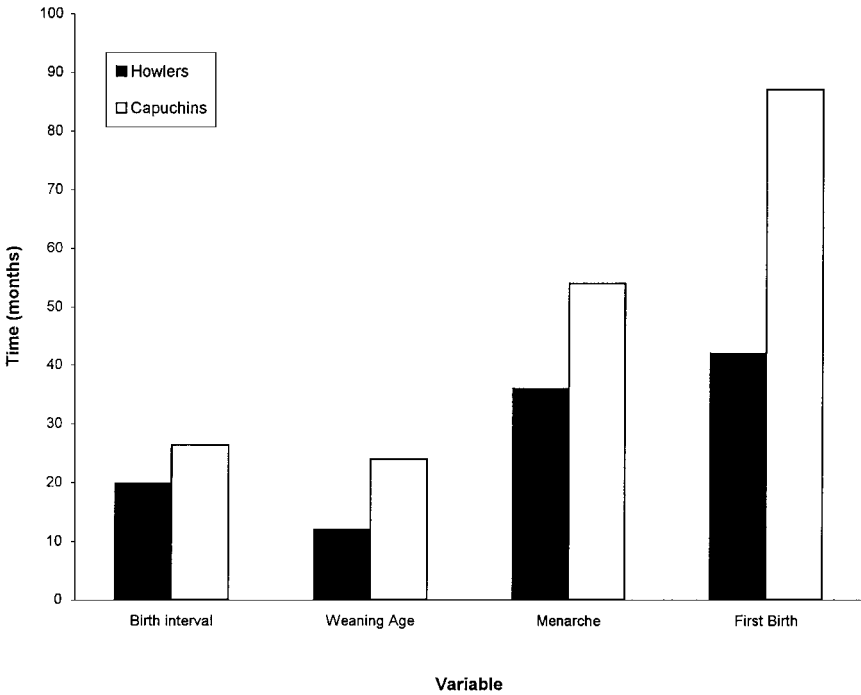


Fig. 6. Comparative pace of reproduction in *Alouatta palliata* and *Cebus capucinus*, based on data from Fedigan and Rose (1995), Fedigan(unpubl) and Glander (1980).

howlers to outproduce the capuchins is unknown. Nonetheless, the greater intrinsic capacity of howlers to reproduce is likely to have been a factor that allowed them to rapidly fill the extant forests with young howlers and new howler groups when the pressures of human disturbance were removed. During the 1980s, the howler population of SRNP was growing at twice the rate of the capuchin population.

Secondly, SNRP howlers have consistently had a higher proportion of adult females in the population ($\bar{x} = 42\%$) than that of capuchins ($\bar{x} = 31\%$), and it is the proportion of reproducing females that ultimately determines the rate of population growth. One reason why we find greater proportions of adult female howlers may be that it takes female capuchins (7 years) longer than female howlers (3.5 years) to mature. Howler groups are even more adult female-biased at the nearby site of La Pacifica (Clarke *et al.*, 1986; Clarke and Zucker, 1994) and on Barro Colorado Island, Panama (Milton, 1996), so large proportions of adult females in the population seem to be a common pattern in mantled howlers.

Thirdly, the major constraint on howler occupation of tropical dry forest is the size of its trees, whereas the major constraint on white-faced capuchins is the availability of water during the dry season (Fedigan *et al.*, 1996, 1998). In the 28 years, since SRNP was established, the forest patches have been getting older and the trees have been getting bigger, but the availability of water during the dry season has not improved and may have deteriorated. Fleming (1986) argued that there is a long-term (50 yr) drying trend in Guanacaste Province. Whether this is correct or not, it is the case that at least two of the spring-fed, formerly year-round water sources in the park have dried up since 1983. Thus, the types of habitat improvement that have occurred since the park was founded may have favored the needs of howlers, i.e., larger trees, over those of capuchins: access to water.

Howlers and Capuchins have Grown Differently in Group Structure of the Populations

Although change in habitat quality in SRNP has been to the advantage of howlers, it is also true that capuchins can make more use of secondary forest than howlers can, especially in the early stages of regeneration. And it is capuchins and not howlers that venture out onto the many newly regenerating fields of SRNP that were clear-cut pastures in 1971 (Sorensen and Fedigan, 2000). Over the years of our study, the capuchin groups have increasingly exploited the regenerating pastures by expanding their home ranges to encompass areas of recent secondary growth. But, we have never seen a new capuchin group with an entirely new range establish itself in a patch of recently regenerating forest. We argued that this is because each capuchin group tries to maintain access to the limited number of water sources that persist through most or all of the dry season, and to at least a few large fruiting trees, especially figs that can fruit during the dry season. (Fedigan *et al.*, 1996). This explains our finding that the capuchin population has increased mainly through an expansion in group size rather than via the formation of new groups. Groups that increase in size can maintain access to water and still exploit newly regenerated forest by expanding their home ranges, but newly formed groups might be cut off from a water supply and large fruit trees. A substantial proportion of white-faced capuchin agonistic intergroup encounters occur near permanent water sources in the dry season, during which time they become central-place foragers around water holes (Rose and Fedigan, 1995). Robinson (1988) found that a wedge-capped capuchin population in a dry forest in Venezuela also expanded mainly via an increase in group size.

Howlers, which are not restricted by the need to drink water daily, can more easily foster small subgroups or lone individuals, which establish new groups. Howlers prefer evergreen and riparian forests, though they also exploit the older deciduous forest patches of SRNP. They usually range along riparian strips and will recolonize adjacent deciduous forests only when trees of sufficient DBH have survived the earlier deforestation or grown to adequate size since the park was established.

Our direct observations of new howler groups being formed clarify some of our quantitative findings about the structure of the howler population. First of all, larger howler groups in SRNP (>25 members) seem to be unstable and typically fission repeatedly into temporary subgroups that eventually become permanent. Secondly, almost all howlers, both males and females, emigrate from their natal groups. Glander (1992) reported that at La Pacifica, 79% of male and 96% of female howlers disperse from their natal groups. Thirdly, there are at least two mechanisms by which new groups are formed: via small groups budding from larger established groups, or by solitaries joining together. Typically, a single vocalizing male attracts ≥ 1 females to his range.

Both females and males may also attempt to join established groups, but they encounter resistance from group members of like sex. All of these factors—constraints on group size, ubiquitous dispersal by both sexes, and availability of various mechanisms for the formation of new groups—may explain our finding that the howler population has expanded mainly via an increase in the number of groups rather than number per group. Clarke and Zucker (1994) also found at the nearby site of La Pacifica that the howler population increased in the number of groups over time rather than the size of groups.

Howler and Capuchin Populations have Grown Differently in Age/Sex Composition

Another way in which the populations of these two sympatric species have grown differently is that the proportions of the age/sex classes have remained quite consistent in the howler census groups, whereas the proportions of adult male capuchins has increased steadily and significantly over the course of the study. Why would there be increasing proportions of adult male capuchins in the census groups? One possibility is that with the removal of hunters from the park, more adult males survive. Capuchins may have been extensively hunted in Costa Rica outside of protected areas, not so much for their size and meat as to counteract their proclivity to crop-raid

(Gonzales-Kirchner and Sainz de al Maza, 1998). Adult male capuchins are the ultimate in-your-face defenders of their groups and are easily picked off by hunters. When we census unhabituated groups, it is almost inevitably an adult male that moves towards us and breaks branches over our heads while the rest of the group fades into the distance. One of the alpha males of a study group brought a line of large tourist buses to a standstill by displaying in the road while his group crossed behind him. Such behavior must lead to low survival rates in adult males outside of protected areas.

A second possibility, related to the fact that the park is a protected island, is that more adult male than female capuchins may be moving into the safety of the park. In capuchins, females rarely disperse from their natal group and home range, whereas male capuchins inevitably disperse from their natal groups, and males change groups many times throughout their adult lives. Fedigan *et al.* (1996) raised the possibility that protected areas may differentially attract the dispersing sex. To test this hypothesis on the 1999 census data, we compared the size and composition of capuchin groups near the boundaries of the park (<0.5 km from SRNP borders) to those in the interior but we found no trend for boundary groups to contain greater proportions of adult males than those of interior groups. It is still possible that more and more adult males are entering the SRNP area and travelling further into the interior of the park before joining a group, but this would be difficult to document. Emigration of capuchin males into the study groups may occur peacefully or may take place in the context of aggressive invasions during which infants are killed, resident males are driven out, and females are wounded. Groups with higher proportions of adult males are better able to resist these violent invasions. Thus, many confounding variables may determine the proportions of adult males in any particular group, whether it is located at the boundaries of the park or in the interior.

A third reason why there are increasing numbers of adult males in our censuses since 1983 is that the sex ratio of immature capuchins in the park appears to be skewed in favor of males. We do not have sex-ratio data on immatures from all census groups, since it is very difficult to detect the sex of nonadult capuchins. However, we have sex-ratio information on the immatures of our intensively-studied focal groups. Of 67 infants born to known females, 38 (57%) have been positively identified as males, 8 (12%) as females, and 21 (31%) died before we were able to conclusively determine their sex. We have considered the possibility that female births are being underestimated, since it is harder to conclusively detect the sex of a female infant and that many of the unsexed infants may have been females. However, the skewed sex ratio also occurs in the juveniles ($n = 70$), where we are certain of the sexes of all individuals in the study groups: 66% of them

are males and 33% are females. This bias towards immature male capuchins may have introduced more males than females into our adult population (Fedigan *et al.*, 1996).

Regenerating a Tropical Forest: If We Regrow It, Will They Come?

In a study comparing the age of forest patches and densities of monkeys within Santa Rosa, Sorensen and Fedigan (2000), documented that more monkeys live in the older forest patches. More specifically, they returned to former pastures that are regenerating into forest in the following pattern: capuchins first return when the forest is 14–25 years old and howlers not until the forest is at least 30–60 years old. Only undisturbed patches of forest >150–180 years contained maximum densities of monkeys. Accordingly, capuchins return before howlers to areas of former habitat destruction and current forest regeneration.

However, one of our major findings is that howlers can (re)colonize a protected area more rapidly than capuchin can via population increase. We argue that this ability is largely due to their intrinsic maximum rate of increase and their fast-paced life-history pattern. Howlers have also colonized the park differently from capuchins over the years of our study. Capuchins expanded group sizes and ranges to take advantage of new secondary growth areas, whereas howlers produced more small groups that have set up new ranges in successional forests when the forest patches reached sufficient age and tree size. Another difference is that many demographic parameters of the howler population, e.g., population size, group size, sex ratios, have shown a tendency to fluctuate over the 28 years since the park was established, whereas the same variables for the capuchin population have increased steadily. Milton (1982, 1996) found a similar fluctuating pattern in demographic parameters for howlers on Barro Colorado Island.

Nonetheless, both monkey populations have grown/expanded at rates that are quite high for nonprovisioned primate populations (Richard, 1985). Thus, from a conservational perspective, our most important and encouraging finding is that we can enhance neotropical monkey populations in reclaimed ranchland by allowing and encouraging the regeneration of tropical forest. Even though it takes enormous effort, patience, and optimism to attempt to regrow a tropical forest, we can see results, even in long-lived anthropoid primates, in the form of significant growth of their populations in as few as 28 years.

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