ARTICLES

Neotropical Region

Primate Populations in Northwestern Costa Rica: Potential for Recovery

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Tropical dry forest was once widespread throughout Central America. Today, however, with less than 2% of its original 550,000 km² cover remaining in a relatively undisturbed state (Janzen, 1986), it represents one of the most threatened habitats. The critical need for the conservation of this type of forest is particularly evident when the accelerating rate of deforestation is considered. Only two decades ago, dry forest covered 20% of its original area (Janzen, 1986).

Three species of primates inhabit the dry forest of Costa Rica: spider monkeys (*Ateles geoffroyi*), howlers (*Alouatta palliata*), and white-faced capuchin monkeys (*Cebus capucinus*). The conservation of primate populations in dry forest has received little attention, and few quantitative studies have been conducted to provide the data necessary for the effective formulation of conservation plans. The howler and spider monkeys are presently considered endangered by the U.S. Endangered Species Act (USDI, 1977), while capuchins are not listed. The IUCN lists the spider monkey as vulnerable, but does not list either of the other two species (Thornback and Jenkins, 1982). Wolfheim (1983) considers all three species threatened.

Within Costa Rica, *Ateles* is probably the most threatened of the three species; it is now absent in large sections of the country where it was recently found. Vaughan (1983) and Wolfheim (1983) have suggested that spider monkeys are more restricted to moist forests and are not as adaptable to altered environments as are the other two species. In addition, Vaughan (1983) reports that spider monkeys are often the first species to be exterminated following human settlement. Relative to other New World primates, the spider monkey has a slow reproductive rate.

Fig. 1. White-faced capuchin monkeys (*Cebus capucinus*) (photo by R.A. Mittermeier)

Fig. 2. The Panamanian spider monkey (*Ateles geoffroyi panamensis*) is one of three subspecies of *Ateles geoffroyi* found in Costa Rica (photo by R.A. Mittermeier)

Females do not mature until approximately seven years of age and only give birth approximately once every three years (Chapman and Chapman, in press; Glander, 1980). This slow potential for increase, in addition to high infant mortality, may contribute to the relatively high vulnerability of *Ateles* to human interference.

Presently, northwestern Costa Rica is the site of two major conservation projects. The Guanacaste National Park (GNP) project has focused on the ecological restoration of tropical dry forest. This ongoing project involves the purchase and protection of large sectors of ranch land surrounding the existing Santa Rosa National Park and volcano forests (Janzen, 1986). The second project has focused on the establishment and protection of Lomas Barbudal National Park. This area was designated a national park in 1986, and prior to this time the forest was largely undisturbed. Primate hunting occurred in both areas; however, the relative impact of hunting in the different areas is difficult to evaluate. Today, primates are rarely hunted in this part of Costa Rica.

Here we report the results of a census of Lomas Barbudal and GNP which was conducted to compare primate abundances in areas with different histories of human interference and different forest types. We discuss the effects of historical interference on the primates, evaluate their potential for recovery, and provide baseline data for future studies. We show how demographic parameters vary among the primate groups in different areas and consider the degree to which habitat alterations and conspecific densities may account for the differences.

Study Sites

Lomas Barbudal National Park is 2,500 ha of largely intact tropical deciduous forest containing a number of distinct forest types including a section of riverine forest, lush areas surrounding springs, dry deciduous forest, savanna, and mesic forest (see Frankie *et al.*, 1988, for a complete listing and description of the habitat types). In 1986, the area received protected status as a national park. Prior to this date, the area was influenced by limited livestock grazing and logging (Frankie, pers. comm.). The major source of habitat disturbance has been the repeated burning of sections of the park. Many fires that are started outside of the park by ranchers as a traditional practice to maintain fields, enter the park. Other fires are deliberately started by hunters to flush animals at night. The climate of the region is highly seasonal, and from mid-December until May little if any rain falls. Rainfall ranges from 1,000-2,200 mm annually (Frankie *et al.*, 1988).

Presently, GNP is approximately 825 km² and extends from sea level to the tops of three volcanoes (1,916 m). The area represents a wide variety of habitats which have been protected for various periods of time, though the majority of the land has only recently been acquired and protected. The core of GNP, however, is Santa Rosa National Park, which has been protected since 1966. GNP contains all of the major dry forest habitats found in Central America. The predominant forest habitat in the park is dry successional deciduous forest, which represents between 20 and 400 years of regeneration (Janzen, 1986). Here the majority of the trees drop their leaves soon after the last rains of the year and remain bare throughout much of the dry season. In other areas of the park, there are patches of semi-evergreen forest which represent either very old regrowth or nearly original forest. The trees in the semi-evergreen forest typically retain their leaves throughout the dry season. In addition, the park contains a number of both temporary and permanent rivers which support relatively lush vegetation throughout the dry season. The slopes of the volcanoes are dominated by nearly undisturbed evergreen forest. The tops of the volcanoes ($>$ 1,000 m) are covered by clouds for much of the year, and cloud forest predominates. For a more detailed description of GNP, see Janzen (1986). As in Lomas Barbudal, in the drier parts of the park fire has played a significant role in determining forest structure.

The climate varies depending on the location within the park, but all regions are characterized by distinct dry and wet seasons. In the lowlands, the dry season extends from approximately December to late May. On average, 98% of the rain falls from May to November (1980-1987, range 96.7-99.2%). The rainfall has averaged 1,527 mm over the last eight years (range 914-2,340 mm; measured at Santa Rosa, Instituto Meteorológico Nacional). Near the volcanoes, the dry season is shorter and annual rainfall increases with altitude (approximately 2,838 mm, Cerro el Hacha Station, 1988).

Census Methodology

The census was conducted between May 1987 and February 1988 and in June and July 1989 for a total of 128 person-days of effort. It is extremely difficult to provide density estimates of primate populations over large areas (Chapman *et al.*, 1989; Defler and Pintor, 1985), but such estimates are required for the formulation of effective conservation plans. The size of the area to be censused and the need to sample as broad a range of habitats as possible precluded the use of repeat transect methodologies or the mapping of group home ranges. As a compromise, routes of known distances were travelled and all primate groups along these strips were counted. In GNP, an extensive network of trails and dirt roads, established when the land was used for ranching, as well as dry riverbeds, were used for the census. Lomas Barbudal has few trails, but since it is a strip of forest (approx. 10 km x 2 km), we systematically censused the area by walking across the park every 500 m and surveying all existing trails. When a primate group was encountered, the following data were recorded: the number of animals in the group, the age and sex of each member, location, habitat type, and, when possible, the group's activity prior to its seeing the observer, the distance between the observer and the animals when they were first seen, and the animals' reaction to being observed (National Research Council, 1981).

Many of the routes were sampled a number of times during the study. For *Alouatta* and *Cebus,* we attempted to minimize the error associated with duplicate counts by identifying individual animals whenever possible so that they could be recognized as belonging to a specific group, and by determining if each new sighting was within the area encompassed by the average home range size (Chapman, 1988). The counts of neighboring groups were rarely similar, and we believe that repeat counts were not a serious problem. However, if two neighboring groups were similar in composition, an attempt was made to recensus the area and locate both groups on the same day.

Spider monkeys have a social organization which is characterized by a flexible pattern of association in which subgroup size and composition are extremely dynamic (Chapman, in press; Klein and Klein, 1977). As a result, the problem of repeat counts of the same individuals could not be dealt with in the same fashion as for the other two species. Thus, when repeat visits were made along the same route, the sizes of the *Ateles* subgroups were averaged. The counts for *Alouatta* and *Cebus* for the Santa Rosa Sector were obtained from Fedigan *et al.* (1985), in which methods very similar to those described here were used.

One of the major objectives of this study was to provide baseline data for comparison with subsequent censuses in order to evaluate the appropriateness of the parks for re-establishing primate populations. We realize that the calculation of actual density estimates by different researchers at different times is difficult. However, to facilitate such a comparison we present the routes used in the census in Figures 1-4.

In addition, we present demographic characteristics of the population which can be reliably compared between researchers even if the entire census is not redone.

Density Estimates

We visited all major forested areas of Lomas Barbudal and GNP with the exception of three areas in GNP: the backside of the volcanoes, Sector Horizonte, and Rincon de la Vieja, the latter two being areas that were incorporated into the park after the majority of the study had been completed. Each of these areas is reported to have populations of all three primate species. The census involved sampling approximately 470 km of trails and transects (excluding repeat visits to areas).

Primate densities were very site-dependent, apparently influenced by both the type of habitat and the history of the area. Within GNP, *Cebus* occurred at the highest density, 5.3 ind/km². The densities of *Alouatta* and *Ateles* were slightly lower, 4.6 ind/km² and 4.5 ind/km², respectively. Figures 1-3 depict the locations of all groups encountered in the areas surveyed in GNP.

The Santa Rosa Sector has been a park since 1971, and efforts have been made to protect the area from poaching and, more recently, from fires. The density of the three species of monkeys was higher in the Santa Rosa Sector than in the rest of GNP (ratio of the density of primates in Santa Rosa to that in the remainder of GNP: *Alouatta* 7.6:1, *Cebus* 5.6:1, *Ateles* 8.1:1). The high densities found in Santa Rosa may be attributed at least in part to the increased level of protection that the area has received over the last 17 years.

Within GNP, but excluding the Santa Rosa Sector, all three primates were most common in the semi-evergreen forest island of Cerro el Hacha. This area is a 2,500 ha series of hills on the northern boundary of the park, part of which has not been cut for lumber or ranch land and consists of relatively pristine islands of forest (Janzen, 1986).

In Lomas Barbudal, the estimated density of *Alouatta* was 8.5 ind/km², the density of *Cebus* was 3.7 ind/km², and *Ateles* were absent from the park. As in Santa Rosa, the high density of howlers may be a reflection of the protection the forest has received. However, the riparian forests and the lush forest surrounding the numerous springs may also contribute to the high numbers. Such areas with year-round access to water and the associated evergreen forest may be important to the primates, particularly in the dry season. The census was conducted during the start of the rainy season, but we still commonly encountered primates in the forests bordering the springs.

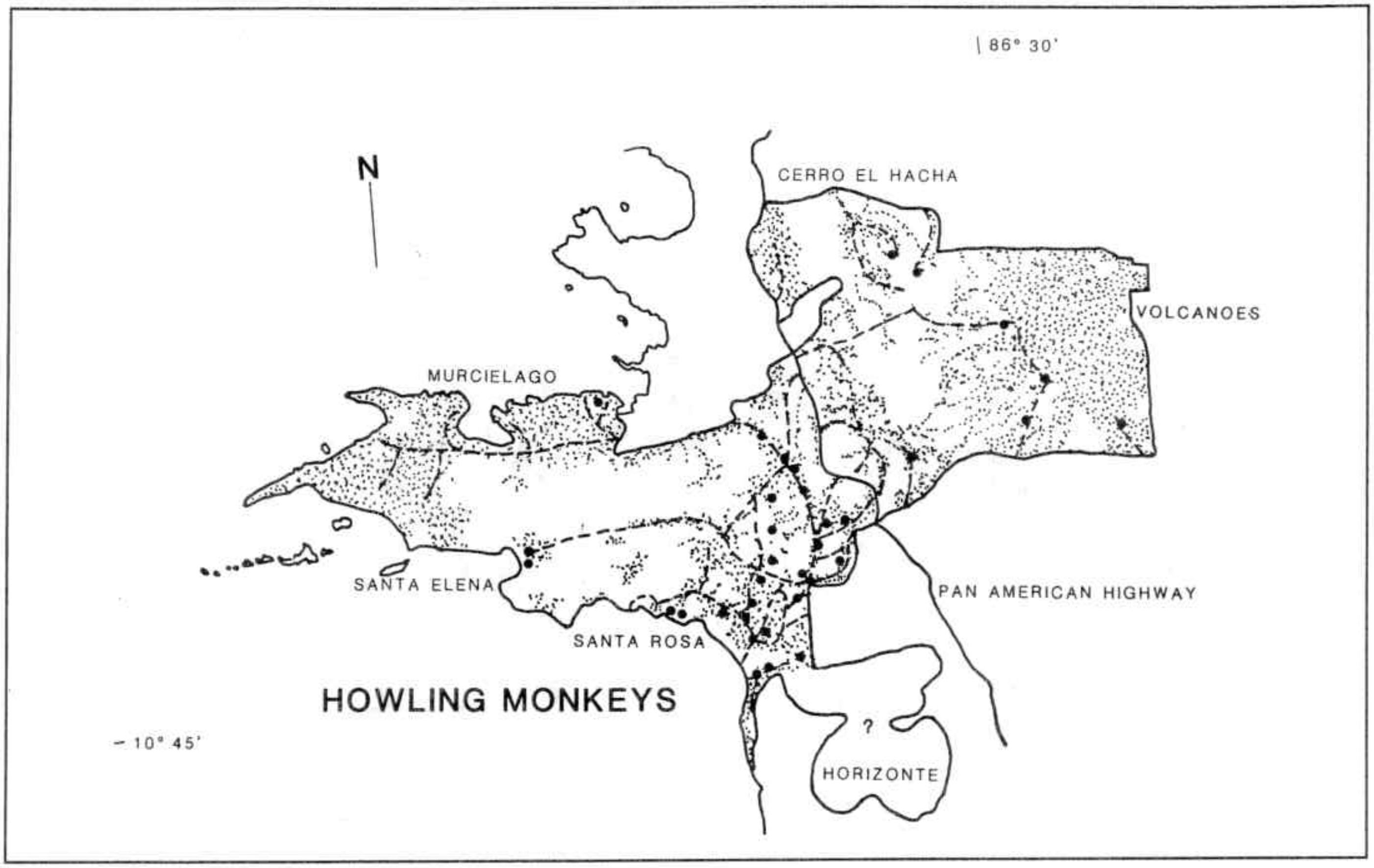

Fig. 1. A map of Guanacaste National Park, Costa Rica depicting routes censused (dashed lines), the location of forest (stippling; adapted from Janzen, 1986) and the location of *Alouatta palliata* groups (map provided by authors).

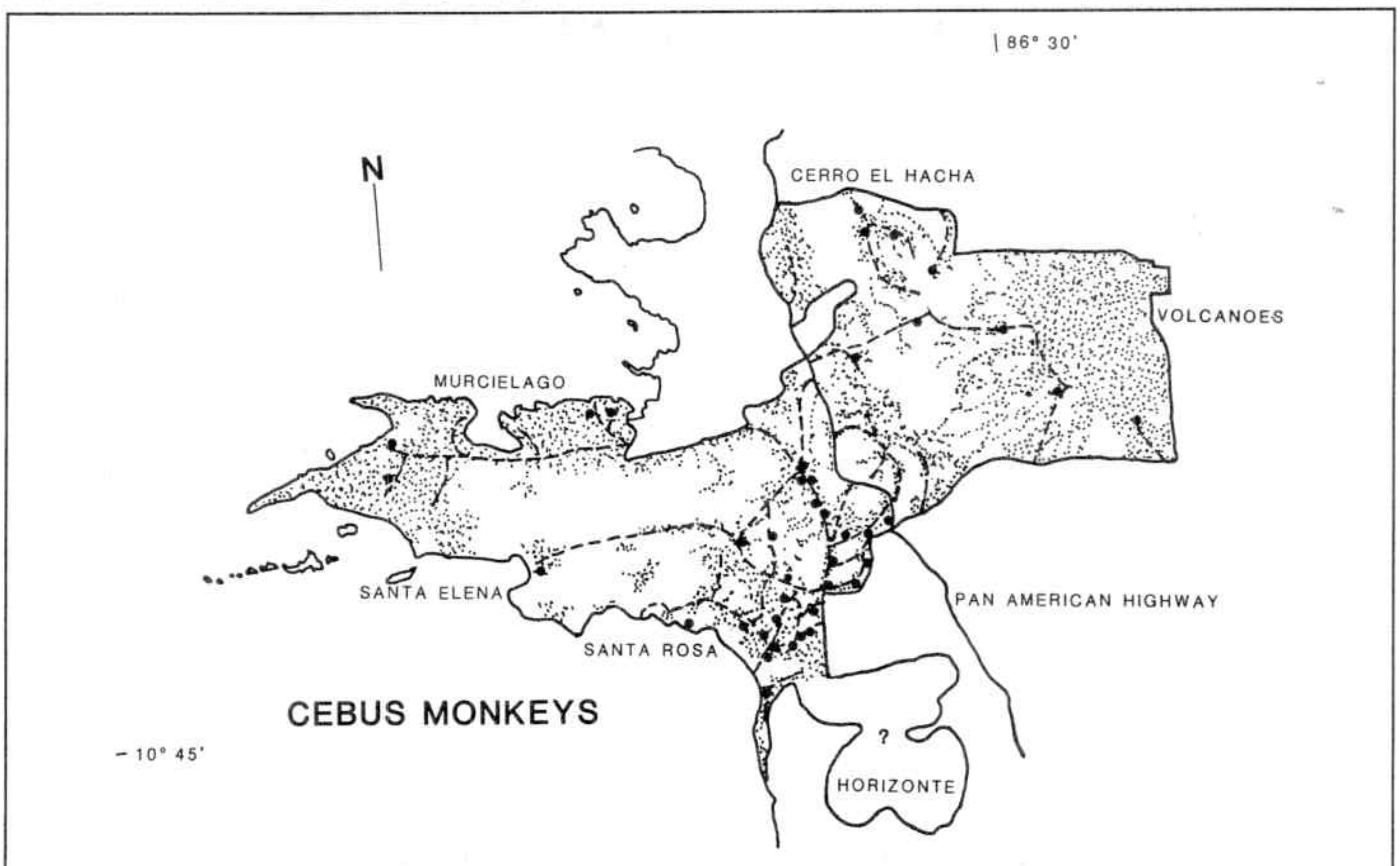

Fig. 2. A map of Guanacaste National Park, Costa Rica depicting routes censused (dashed lines), the location of forest (stippling; adapted from Janzen, 1986) and the location of *Cebus capucinus* groups (map provided by authors).

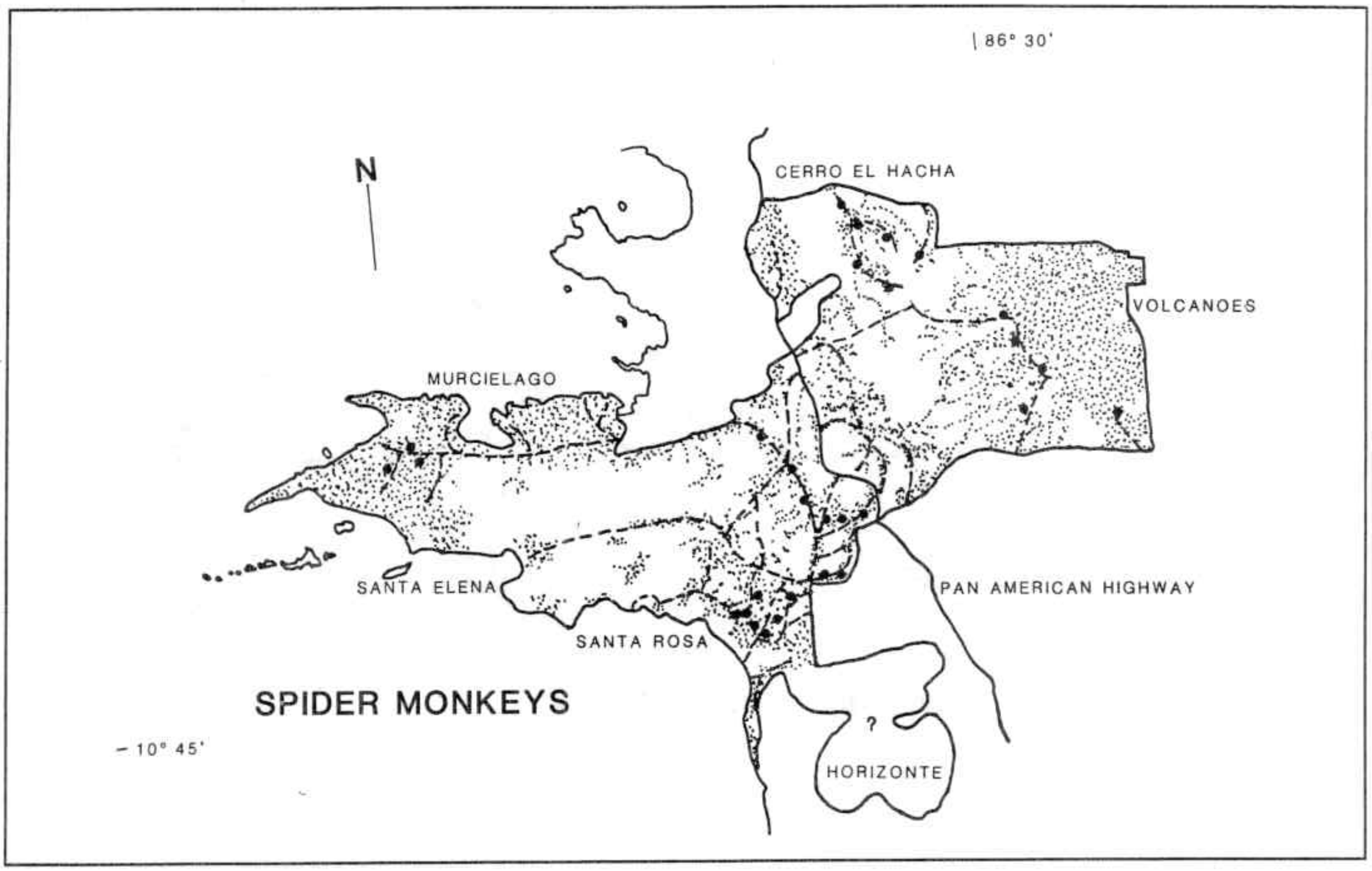

Fig. 3. A map of Guanacaste National Park, Costa Rica depicting routes censused (dashed lines), the location of forest (stippling; adapted from Janzen, 1986) and the location of *Ateles geoffroyi* sightings (map provided by authors).

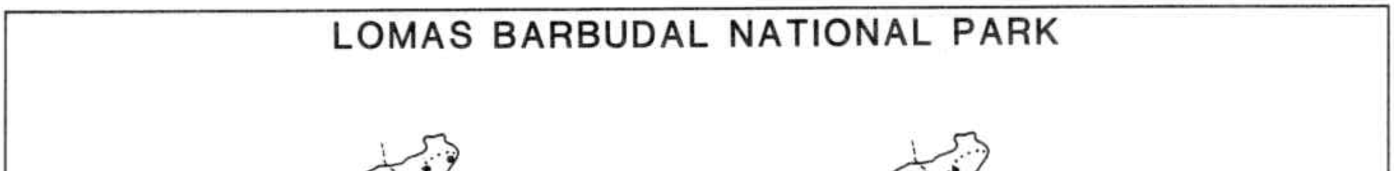

Fig. 4. A map of Lomas Barbudal National Park, portraying the routes travelled (dashed lines representing roads and dotted lines representing transects through the forest) and the location of *Cebus capucinus* groups and *Alouatta palliata* groups (map provided by authors).

There was no apparent ecological reason for the absence of spider monkeys from Lomas Barbudal. The area contains many of the fruiting tree species used by spider monkeys elsewhere. People living near the park stated that spider monkeys were found in the area as recently as 20 years ago. Today *Ateles* are present just south of Lomas Barbudal in Palo Verde National Park. Based on these observations, we suggest that spider monkeys are absent because of historical hunting practices. Hunters consider *Ateles* preferred monkey meat. This preference coupled with their slow reproductive rate and late age at maturity (Chapman and Chapman, in press) makes *Ateles* highly vulnerable to hunting pressure.

Habitat Preferences

Within GNP, spider monkeys were found in all the major forest areas of the park, with the exception of some riverine strips. Riverine areas generally contain relatively high densities of potential spider monkey food trees. Thus, there was no apparent ecological reason to explain why spider monkeys were absent from some riverine strips and not others. As with Lomas Barbudal, we suggest that they have been hunted out and, as of yet, have not re-established viable populations. Surprisingly, in the Murcielago Sector, spider monkeys were found in young (apparently 20 yr old), regenerating dry deciduous forest not more than 4 m tall. In the Santa Rosa Sector, spider monkeys are commonly found in sections of forest that are thought to represent approximately 75-100 years of regrowth.

Howlers were found throughout Lomas Barbudal and in all major forested areas of GNP with the exception of the west end of the Murcielago Sector. Howler groups tend to be found in areas that contain at least some semi-evergreen or riparian/spring forest, sometimes as little as one hectare in size.

Capuchin monkeys were found in all forested areas surveyed regardless of forest type. They ranged more widely into young successional forest than the other two monkey species and are known to routinely cross open grasslands. During the height of the dry season, capuchin monkeys typically visit areas with standing water almost daily. It seems probable that the areas used by the capuchin monkeys must contain at least some standing water during the dry season and that this requirement may limit the areas in which they occur.

Group Composition

For a comparison of group composition, we chose to include three areas which have been thoroughly described and which each have different histories of protection: Santa Rosa, protected for 17 years (Janzen, 1986), Lomas Barbudal, relatively undisturbed with the exception of fires and poaching (Frankie *et al.*, 1988); and GNP (excluding Santa Rosa) which is just now receiving protection (Janzen, 1986).

The size of spider monkey subgroups has been shown to change in relation to the availability of food resources (Chapman, in press). Since different areas were censused at different times of the year and the availability of fruit changes between seasons, a comparison of subgroup size between habitats is not valid using the available data. However, neither the sex ratio ($t=0.973$, $p=0.342$), nor the ratio of adult females to infants ($t=0.843$, $p=0.404$) differed between Santa Rosa and the remainder of GNP.

The size of howler groups was larger in Santa Rosa than in either Lomas Barbudal or in the remainder of GNP (Table 1, Scheffe $p<0.05$). In Lomas Barbudal and GNP, many of the groups encountered were composed of a male/female pair and their offspring (26% and 33%, respectively). In contrast, Fedigan *et al.* (1985) did not observe such pairs in Santa Rosa and further work in the area has revealed very few male/female pairs. There were no differences between the three areas in the sex ratios of howler groups. However, differences were found between areas in the proportion of the adult females which had clinging infants or closely associated small immatures (Table 1). A low ratio of immatures to adults has been suggested to indicate stressed populations (Estrada, 1982; Heltne *et al.*, 1976; see Clarke *et al.*, 1986 for a critique of such indices). The large proportion of females with small infants at Lomas Barbudal suggests that the population is in a phase with a high potential for growth. In contrast, the low proportion of females with young in GNP suggests that these populations may be more stressed.

As with howlers, the size of the capuchin monkey groups was larger in Santa Rosa than in either Lomas Barbudal or GNP (Table 1, Scheffe $p<0.05$). There was no difference between the three areas in the proportion of females with young. However, the sex ratio observed in Santa Rosa differed from that in the remainder of GNP (Table 1, Scheffe $p<0.05$).

Table 1. Demographic Characteristics of *Alouatta palliata* and *Cebus capucinus* in Three Areas in Northwestern Costa Rica

	Santa Rosa	GNP	Lomas Barbudal	F value
Alouatta palliata				
Group Size	14.7	4.4	7.5	11.16**
Male:Female	1:1.97	1:1.76	1:1.67	1.77
Female:Immature	1:0.60	1:0.46	1:0.80	3.23*
Cebus capucinus				
Group Size	14.1	8.8	8.1	8.70**
Male:Female	1:2.30	1:1.65	1:2.03	5.16*
Female:Immature	1:0.78	1:0.91	1:0.64	1.31

Key
*$p<0.05$
**$p<0.001$

Discussion

Census data can often be used to identify factors which may determine the abundance of species. The identification of such factors is clearly essential for the formulation of an effective conservation plan. Contrasting the observed populations, we suggest that the abundance of the three primate species is influenced by both habitat type and the history of human interference.

To place our findings in a broader perspective we collected published density estimates for each primate genus represented, *i.e. Alouatta, Ateles*, and *Cebus* (Table 2). Based on this review it is evident that the density estimates we obtained were in general lower than those obtained from other areas. The low density in northwestern Costa Rica may be due, at least in part, to the very dry and seasonal nature of the environment. If this were the only factor distinguishing northwestern Costa Rica from other less seasonal habitats, one might expect densities within certain lush microhabitats to approach the densities observed in similar habitats in other geographical areas. In a number of instances, we did find relatively high densities in lush microhabitats, but not of the magnitude necessary to account for the discrepancy in densities between the areas we surveyed and published accounts. For example, Clarke *et al.* (1986) reported that the density of howlers censused in an area that contained a large strip of riverine forest and sections of dry deciduous forest (77.3 ind/km^2) was much higher than the density of howlers in Santa Rosa National Park as calculated by Fedigan *et al.* (1985; 4.9 ind/km^2). Our survey of the riverine forest in GNP provides an estimate of 10.1 howlers/km^2, which is higher than the estimates for the overall density of howlers in Santa Rosa, but clearly far lower than the estimate provided by Clarke *et al.* (1986).

We suggest that much of the remaining difference is related to the history of human interference that the different areas and primate populations have received. The overall density of primates was higher in areas that have received protection (Santa Rosa and Lomas Barbudal) than in surrounding unprotected areas. In some protected areas, spider monkeys were seen using regenerating dry deciduous forest that was less than 4 m tall. Park guards stated that it was only recently that spider monkeys were seen in such areas. These observations are particularly encouraging to conservation efforts concerning spider monkeys. It has been suggested that this species is rarely seen in altered habitats (Wolfheim, 1983). However, our observations of spider monkeys in such young regenerating forest suggest that these monkeys have the ability to quickly recolonize altered habitats once the area receives protection.

Our results also illustrate interesting differences in the composition of groups among sites. For instance, in some areas, howlers frequently had groups containing only 1 male and female (26% Lomas Barbudal, 33% GNP excluding Santa Rosa), while in Santa Rosa this type of group structure was very rare. Although Lomas Barbudal has higher densities of howlers than Santa Rosa, the population may be well below its maximum sustainable level. The male/female pairs observed in Lomas Barbudal may be taking advantage of many openings in the habitat to establish new groups. It is common for solitary *Alouatta* males to enter an unoccupied area, call to attract a female, and thus form a new group. The large number of pairs in Lomas Barbudal may therefore represent the formation of new groups and the potential for population growth in the region.

Table 2. Population Characteristics of *Alouatta, Ateles* and *Cebus* Derived from a Literature Review

(Citations for these studies can be obtained directly from the authors, density=ind/km², sex ratio=females per male, Imm/F=immatures per female, rainfall=mm.)

Species	Density	Group Size	Sex Ratio	Imm/F	Rainfall	Source and Location
Alouatta						
A. palliata	4.9	13.60	1.97	0.56	1531	Fedigan *et al.*, 1985; Santa Rosa, Costa Rica
	1.2	8.13	2.20	0.79	1531	Freese, 1976; Santa Rosa, Costa Rica
	89.7	13.77	2.38	0.78	1878	Rodriguez, 1985; Palo Verde, Costa Rica
	—	5.20	1.60	0.21	—	Milton & Mittermeier, 1977; Coiba, Panama
	1050.0	18.90	2.00	0.88	—	Baldwin & Baldwin, 1972/76; Chirique, Panama
	77.3	15.50	2.98	0.57	1450	Clarke *et al.*, 1986; La Pacifica, Costa Rica
	23.3	9.12	1.37	0.75	4953	Estrada, 1982; Los Tuxtlas, Mexico
	74.3	13.20	4.11	0.54	1450	Heltne *et al.*, 1976; La Pacifica, Costa Rica
	74.3	10.00	1.16	0.86	1450	Heltne *et al.*, 1976; La Pacifica, Costa Rica
	74.3	12.50	3.00	0.75	1450	Heltne *et al.*, 1976; La Pacifica, Costa Rica
	—	15.40	3.00	0.67	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	—	13.50	2.78	0.75	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	—	10.00	2.92	0.76	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	—	08.90	1.88	0.77	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	—	13.10	2.13	0.54	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	—	10.40	1.68	0.38	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	—	10.80	2.89	0.31	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	—	11.30	2.18	0.86	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	—	9.90	1.94	0.80	1450	Heltne *et al.*, 1976; Toboga, Costa Rica
	12-19	13.75	—	—	4015	Fishkind & Sussman, 1987; La Selva, Costa Rica
	27.0	17.30	2.74	0.96	2730	Carpenter, 1934, 1965; BCI, Panama
	33.5	17.40	2.74	1.04	2730	Carpenter, 1934, 1965; BCI, Panama
	—	18.20	2.12	1.13	2730	Carpenter, 1934, 1965; BCI, Panama
	16.2	8.00	3.75	0.47	2730	Collias and Southwick, 1952; BCI, Panama
	52.5	18.50	2.76	0.65	2730	Carpenter, 1934, 1965; BCI, Panama
	62.7	14.70	1.79	0.89	2730	Chivers, 1969; BCI, Panama
	75.8	13.80	2.41	0.56	2730	Smith, 1977; BCI, Panama
	62.6	16.20	1.81	1.22	2730	Mittermeier, 1973; BCI, Panama
	91.7	20.80	2.63	0.88	2730	Milton, 1982; BCI, Panama
	—	23.00	2.34	1.16	2730	Milton, 1982; BCI, Panama
	—	21.40	2.18	1.07	2730	Milton, 1982; BCI, Panama
	82.2	20.20	2.55	1.16	2730	Milton, 1982; BCI, Panama
	—	18.90	2.24	1.09	2730	Milton, 1982; BCI, Panama
	—	18.70	2.50	1.09	2730	Milton, 1982; BCI, Panama
	—	20.40	2.30	0.94	2730	Milton, 1982; BCI, Panama
	—	18.90	2.55	0.98	2730	Milton, 1982; BCI, Panama
	—	21.30	2.15	1.14	2730	Milton, 1982; BCI, Panama
	—	16.50	2.30	0.93	2730	Bernstein, 1964; BCI, Panama
	—	9.30	1.71	0.66	2730	Altman, 1959; BCI, Panama
A. pigra	8.1	4.20	1.00	0.73	2032	Bolin, 1981; Belize
	22.0	6.22	1.27	—	2030	Horwich, 1983; Belize
	—	6.33	1.60	1.08	2032	Horwich & Johnson, 1986; Belize
	—	4.67	2.00	0.83	—	Horwich & Johnson, 1986; El Joval, Mexico
	—	5.00	2.00	1.00	1350	Horwich & Johnson, 1986; Guatemala
	5.0	6.25	1.16	1.71	1350	Coelho *et al.*, 1976; Tikal, Guatemala
	4.0	5.00	1.33	0.75	1350	Schliche, 1978; Tikal, Guatemala
	13.0	5.50	2.50	0.80	—	Schliche, 1978; Coban, Guatemala

Table 2. Population Characteristics of *Alouatta, Ateles* and *Cebus* Derived from a Literature Review (Continued)
(Citations for these studies can be obtained directly from the authors, density=ind/km², sex ratio=females per male, Imm/F=immatures per female, rainfall=mm.)

Species	Density	Group Size	Sex Ratio	Imm/F	Rainfall	Source and Location
A. seniculus	23.0	5.75	1.14	1.00	2100	Defler, 1981; Colombia
	27.0	6.80	1.15	0.75	—	Defler, 1981; Colombia
	114.0	7.50	0.71	1.00	—	Neville, 1972; Trinidad
	15.0	9.00	1.25	1.80	1947	Gaulin & Gaulin, 1982; Colombia
	21.9	3.30	1.97	0.56	2705	Green, 1978; Colombia
	20.4	3.30	—	0.00	2705	Green, 1978; Colombia
	30.0	—	—	—	2080	Terborgh, 1983; Manu, Peru
	15.0	5.00	—	—	3050	Neville, 1976; Peru
	2.7	5.40	1.20	0.60	—	Izawa, 1976; Upper Amazon
	—	5.40	1.59	0.79	—	Izawa, 1976; Upper Amazon
	30.5	5.40	—	—	—	Freese *et al.*, 1982; Peru/Bolivia
	24.0	5.40	—	—	—	Freese *et al.*, 1982; Peru/Bolivia
	8.0	8.00	—	—	—	Freese *et al.*, 1982; Peru/Bolivia
	120.0	19.00	—	—	—	Freese *et al.*, 1982; Peru/Bolivia
	20.3	5.00	1.43	0.80	—	Klein & Klein, 1977; 1976 Colombia
	25.6	6.30	—	0.92	1424	Breza *et al.*, 1981; El Frio, Venezuela
	36.0	7.70	2.08	—	1693	Crockett, 1984; Hato Masaguaral, Venezuela
	50.0	8.30	2.26	—	1693	Crockett & Eisenberg, 1987; Venezuela
	53.0	7.80	1.93	—	1693	Crockett & Eisenberg, 1987; Venezuela
	85.0	8.70	1.80	—	1693	Eisenberg, 1979; Hato Masaguaral, Venezuela
	150.0	8.90	1.47	1.64	1693	Rudran, 1979; Hato Masaguaral, Venezuela
	112.0	10.50	1.81	—	1693	Crockett, 1984; Hato Masaguaral, Venezuela
	115.0	9.70	1.70	—	1693	Crockett & Eisenberg, 1987; Venezuela
	180.0	9.10	1.83	—	1693	Crockett & Eisenberg, 1987; Venezuela
	—	6.90	1.62	1.00	1693	Neville, 1972, 1976; Hato Masaguaral, Venezuela
	—	8.50	1.60	1.38	1693	Neville, 1972, 1976; Hato Masaguaral, Venezuela
	—	8.80	1.50	1.33	1693	Neville, 1972, 1976; Hato Masaguaral, Venezuela
	—	7.90	1.78	1.44	1693	Neville, 1972, 1976; Hato Masaguaral, Venezuela
	—	9.00	1.08	1.57	1693	Neville, 1972, 1976; Hato Masaguaral, Venezuela
	—	9.00	2.12	1.29	1693	Neville, 1972, 1976; Hato Masaguaral, Venezuela
A. caraya	130.0	8.05	2.02	—	1400	Thorington *et al.*, 1984; Argentina
	—	7.90	0.88	0.69	—	Pope, 1966/68; Argentina
	0.8	2.00	—	—	—	Pope, 1966/68; Argentina
Ateles						
A. geoffroyi	1.5-2.2	3.80	—	—	1531	Freese, 1976; Santa Rosa, Costa Rica
	0.7	4.70	0.50	0.50	1878	Rodriguez, 1985; Santa Rosa, Costa Rica
	6-11	—	—	—	4015	Fishkind & Sussman, 1987; La Selva, Costa Rica
	45.0	—	2.23	—	1350	Coelho *et al.*, 1976; Tikal, Guatemala
	27.8	4.30	1.31	0.77	1350	Cant, 1978; Tikal Guatemala
A. belzebuth	12-15	3.50	3.00	—	—	Klein & Klein, 1976; Colombia
	14.0	—	—	—	—	Bernstein *et al.*, 1976; Colombia
	20-33	8.40	—	—	—	Izawa, 1976; Colombia
	20-33	3.34	—	—	2705	Green, 1978; Colombia
A. paniscus	6-24	—	—	—	—	Durham, 1971,72,75; Peru
	14-35	3.80	—	—	—	Janson and Terborgh; Manu, Peru
	31.0	3.20	2.53	0.57	2080	White, 1986; Manu, Peru
	8.0	—	—	—	2200	Van Roosmalen, 1980; Suriname
	—	—	2.82	1.16	2080	Symington, 1987; Manu, Peru
Cebus						
C. capucinus	5.6	14.0	2.30	1.16	1430	Fedigan *et al.*, 1985; Santa Rosa, Costa Rica
	3.5-5.0	15-20	—	—	1430	Freese, 1976; Santa Rosa, Costa Rica
	5.0-6.0	11.0	—	—	1878	Rodriguez, 1985; Palo Verde, Costa Rica
	79.2	27-30	—	—	—	Baldwin & Baldwin, 1972, 1976; Panama
	4-6	15.0	—	—	—	Fishkind & Sussman, 1987; La Selva, Costa Rica
	—	5-20	—	—	—	Milton & Mittermeier, 1977; Coiba, Panama
C. albifrons	3.8-15.3	5.3	—	—	2705	Green, 1978; Colombia
	0.2-24	2.4	—	—	—	Freese *et al.*, 1982; Peru/Bolivia
	10-34	7.5	—	—	—	Janson and Terborgh; Manu, Peru
	—	19.0	—	—	—	Izawa, 1976; Peru
C. apella	6-10	—	—	—	—	Klein & Klein, 1975; Colombia
	0.2-36	7.5	—	—	—	Freese *et al.*, 1982; Peru/Bolivia
	20-35	5.6	—	—	—	Janson and Terborgh; Manu, Peru

Conclusions

(1) A census of primate populations in protected areas in northwestern Costa Rica suggests that both the history of the region and the type of habitat play important roles in determining primate densities.

(2) Spider monkeys are the most endangered primate in northwestern Costa Rica. They were previously thought to be unable to survive in areas that had been altered by human activities. We found spider monkeys in protected young regenerating forest, suggesting that as long as they are protected from hunting and provided access to large areas of forest, or potentially connected forest patches, they can flourish in altered habitats.

(3) The observation of a large number of male/female pairs in Lomas Barbudal is consistent with the idea that the density of an animal relative to an area's productivity can alter a group's size, composition, and, potentially, its social structure.

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A General Introduction to Primate Conservation in Colombia

by Claudia L. Alderman

Bridging North and South America, Colombia contains a rich array of flora and fauna. This diversity includes an estimated 50,000 species of higher plants and over 2,800 species of terrestrial vertebrates. Similarly, more than a third of all Neotropical primate species have been found within Colombia's territory (Mittermeier, 1987). Estimates of the number of species found in the country range between 27 and 29. This discrepancy

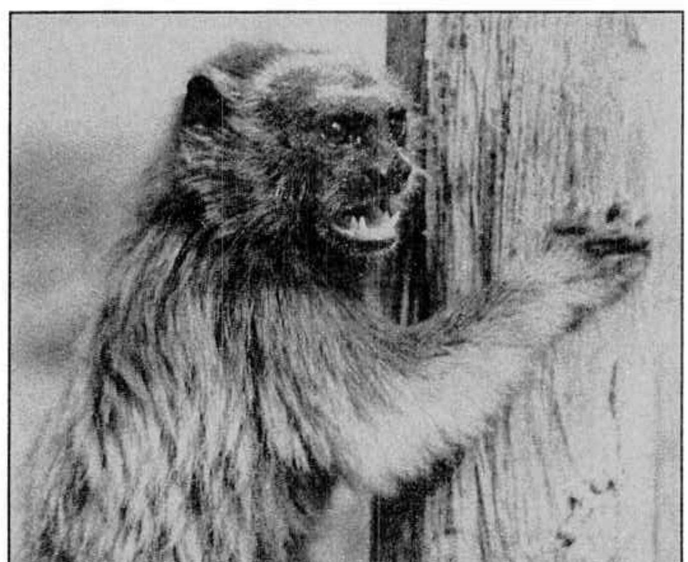

Fig. 1. The white-footed tamarin, *Saguinus leucopus*, is a callitrichid endemic to Colombia (photo by F. Medem)