

Growth of Mantled Howler Groups in a Regenerating Costa Rican Dry Forest

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*We examined population dynamics in mantled howlers (*Alouatta palliata*) in a regenerating tropical dry forest in Santa Rosa National Park (SRNP), Costa Rica. The population has grown at a rate of about 7% per annum during the past decade. The growth in numbers from 342 in 1984 to 554 in 1992 reflects an increase in the number of groups (from 25 to 34) and a slight increase in their average size (from 13.6 to 16.3). Population density has increased from 4.9 to 7.9 individuals per km². Santa Rosa's population density and group compositions are similar to those at several other mantled howler sites, but densities of mantled howlers are much higher at two other well-studied sites: La Pacifica and Barro Colorado Island (BCI). We relate the low density of howlers at Santa Rosa to local historical and ecological factors. Howler populations at high and low densities differ in average group size and sex ratio. At high population densities, groups are larger and include more adult females. The number of male howlers per group appears to be more strictly limited and less variable than the number of females is. However, there is greater variation in male group membership at Santa Rosa than at La Pacifica or BCI, and at Santa Rosa there are more generating forests available into which males and females can disperse and form new groups. We present case studies describing two ways in which new howler groups are formed, and we suggest that, compared to females and compared to males at high density sites, males are relatively advantaged in the uncrowded habitats at Santa Rosa and other low density sites.*

KEY WORDS: howlers; demography; Costa Rica; forest regeneration; conservation.

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INTRODUCTION

At least one-third of all New World primates are threatened with extinction (Rylands, 1995), due largely to the loss and fragmentation of suitable habitat (Mittermeier and Cheney, 1987; Dobson and Lyles, 1989; Boza, 1993; Rodríguez-Luna *et al.*, 1996). Howlers (*Alouatta*) have the broadest distribution of all Neotropical monkeys and occur in a wide range of habitat types (Eisenberg, 1979; Crockett and Eisenberg, 1987; Rodríguez-Luna *et al.*, 1996; Peres, 1997). The taxonomy of *Alouatta* is still in some dispute, with subspecies being elevated to new species on an almost-yearly basis (Crockett, 1998; Rylands *et al.*, 1995). Most of the 23 taxa (in six species groups) of *Alouatta* identified by Rylands *et al.* (1995) are considered to be at relatively low risk, but some populations of *A. coibensis* and *A. fusca* are vulnerable, endangered, or critically endangered (Rylands *et al.*, 1995; Rodríguez-Luna *et al.*, 1996; Crockett, 1998). Demographic data are sparse for many populations, but those that have been relatively well studied, primarily *Alouatta palliata* and *A. seniculus*, suggest considerable variation between sites (Heltne *et al.*, 1976; Crockett and Eisenberg, 1987; Chapman and Balcomb, 1998) and fluctuations within populations over time (Collias and Southwick, 1952; Glanz, 1982; Milton, 1982; Crockett and Rudran, 1987a,b; Crockett, 1996). Researchers have related the dynamics of howler populations to epizootics, parasites, deforestation, hunting pressure, resource fluctuations, rainfall variation, and natural disasters, such as floods, hurricanes, and droughts (Smith, 1977; Milton, 1982, 1996; Crockett and Eisenberg, 1987; Clarke and Zucker, 1994; Chapman and Balcomb, 1998; Peres, 1997). Few, if any, researchers have examined changes in howler populations in relationship to land restoration and subsequent forest regeneration, like that which follows the establishment of a protected national park in former agricultural lands where forests have been partially cleared.

We summarize 10 years of demographic data (1983–1992) on a population of Central American mantled howlers (*Alouatta palliata palliata*) in a regenerating tropical dry forest in Santa Rosa National Park (SRNP), northwestern Costa Rica. We compare our findings with those from earlier population surveys of howlers in the park (Freese, 1976; Fedigan *et al.*, 1985) and with other long-term studies of mantled howlers. The best- and longest-studied populations of *Alouatta palliata* are those on Barro Colorado Island (BCI), Panama (Carpenter, 1934, 1965; Collias and Southwick, 1952; Mittermeier, 1972; Froehlich *et al.*, 1981; Milton, 1982, 1996) and at La Pacifica, Costa Rica (Heltne *et al.*, 1976; Glander, 1980, 1992; Clarke and Glander, 1984; Clarke *et al.*, 1986, 1994; Clarke and Zucker, 1994). However, some population data from other field sites in Costa Rica are

also available for comparative purposes (Lippold, 1988, 1989; Stoner, 1994; Tomblin and Cranford, 1994).

Mantled howlers are distributed from southern Mexico and southern Guatemala, south through Central America to the west coast of Colombia and Ecuador. Chapman (1987) and Larose (1996) described them as facultative folivores, and they are usually found in the middle to upper strata of relatively tall trees in primary, evergreen, or riparian forest. Although mantled howlers eat large amounts of fruit and flowers when they can, they rely on new and mature leaves for a substantial part of their diet (Chapman, 1987; Glander, 1978, 1981; Milton, 1980, 1982; Larose, 1996). Crockett (1987, 1998) concluded that *Alouatta* are best described as folivore-frugivores. Unlike the other species of *Alouatta*, *A. palliata* definitely live in multimale groups, though it is possible that one male does most of the mating (Clarke, 1982). Both sexes disperse, usually during the juvenile stage of life (Glander, 1992).

Eisenberg (1979) considered howlers to be pioneer species, with generalized adaptations to a diversity of habitats which allow them to survive under conditions of habitat degradation and to flourish under conditions of habitat regeneration. However, Dobson and Yu (1993) characterized *Alouatta* as having a high density but a restricted distribution, and there is evidence that howlers prefer evergreen or riparian forests and are found in marginal habitats only when no other area is available [*A. palliata* (Carpenter, 1934; Stoner, 1996). *A. seniculus* (Mittermeier and van Roosmalen, 1981)]. There is also considerable evidence for dietary selectivity and conservatism, usually related to avoidance of secondary plant compounds, which may restrict the ability of howlers to utilize all available habitats (Glander, 1978; Milton, 1978, 1979; Stoner, 1996; Crockett, 1998).

On first consideration, we would expect a howler population in a recently established park to be on the increase, concurrently with habitat protection and gradual regeneration of the forest. However, our study area appears to have been experiencing a continuing drying trend over the past 50 years (Fleming, 1986), and it remains to be determined whether newly regenerated forest provides sufficient food resources to attract and to sustain new or existing howler groups. By analyzing the demographic trends in howler groups in the park during a critical early stage of forest regeneration, we assessed the potential for recovery of neotropical primate populations to reclaim habitats (Chapman *et al.*, 1989; Fedigan *et al.*, 1996; Chapman and Balcomb, 1998). In addition, by presenting basic information on natality, survivorship, population growth, and group formation in Santa Rosa mantled howlers, we hope to augment our understanding of demographic processes in this species.

METHOD

Site Description

The study area is Santa Rosa National Park in Costa Rica, the site of a regenerating tropical dry forest and an experimental megapark on reclaimed ranchland (Janzen, 1986a). The original park, established in 1971, covers 108 km² of tropical dry forest in a series of stepped plateaus from the foothills of volcanic mountains down to the Pacific coastal plain. In the late 1980s, a project was begun to buy the ranchlands surrounding the park, using a debt for nature swap (Liebow, 1993; Sun, 1988; Wallace, 1992), and the result is a greatly enlarged protected area (approximately 825 km²), which is now known as Area de Conservacion Guanacaste (ACG). The core of ACG remains Santa Rosa National Park, and the original park borders form the boundaries for our annual censuses. We refer to the study area as Santa Rosa or SRNP (Fig. 1).

Originally, the Santa Rosa area was covered by a semideciduous, tropical dry forest, with patches of semievergreen oak forest (*Quercus oleoides*) on the upper plateaus (Janzen, 1982, 1983a,b, 1986a,b). Over the past 300 years, 50% of the upper plateau was cleared for cattle pasture and planted with the African grass, *Hyparrhenia rufa*, and the forests were selectively logged, primarily for mahogany (*Swietenia macrophylla*). Since the establishment of the original park in 1971, cattle and poachers have gradually been removed, fires have been increasingly controlled, and trees have begun to grow again in abandoned pastures. The current forest in SRNP is a mosaic. It can be roughly described as primarily mixed deciduous forest dominated by *Spondias mombin*, *Luehea candida*, *Guazuma ulmifolia*, *Bursera simaruba*, and *Ficus* spp. with fragments of evergreen and riparian forest dominated by *Hymenaea courbaril*, *Masticodendron capiri*, *Manilkara zapote*, *Slonea terniflora*, and *Brosimum alicastrum*, and early secondary forest, succeeding in former pastures and usually dominated by wind-dispersed species, such as *Cochlospermum vitifolium*, *Tabebuia rosea*, and *Luehea speciosa*.

There are two distinct seasons at Santa Rosa. Almost all of the annual 900–2500 mm of rain falls in the wet season, typically from mid-May to mid-December (Janzen and Hallwachs, 1995). During the dry season the majority of nonriparian trees lose their leaves and most waterholes gradually dry. There are several seasonal streams and creeks that crisscross SRNP (Fig. 1). These flow only at the height of the rainy season and gradually become arid streambeds during the dry season, but the neighboring strips of riparian forests are more likely than other forest types to retain leaves

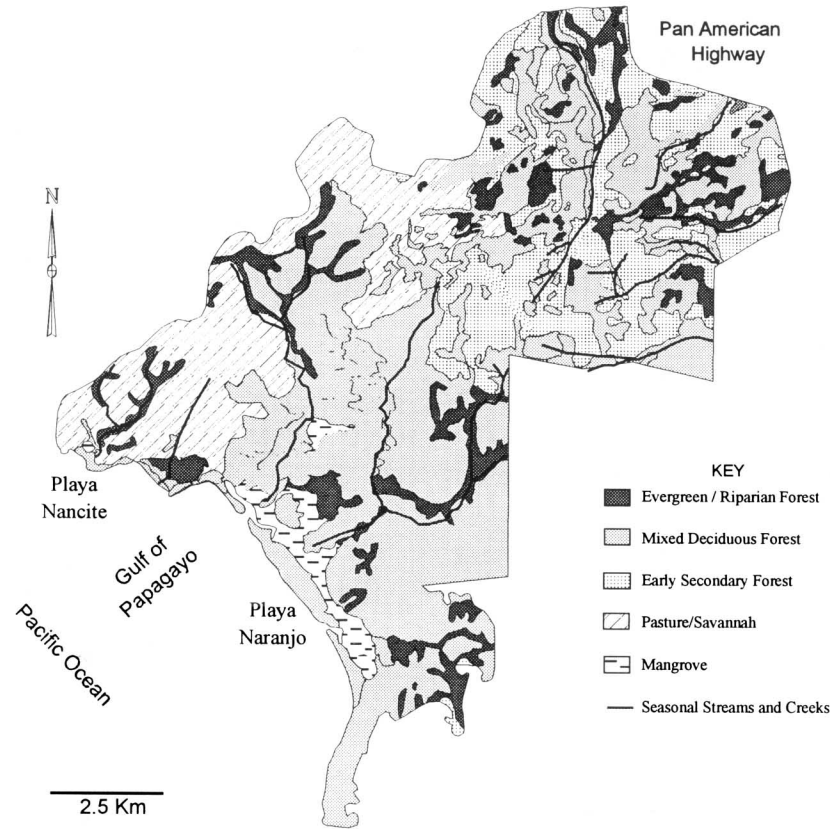


Fig. 1. Vegetation map of Santa Rosa National Park (SRNP), Costa Rica.

throughout the dry season. The riparian and evergreen forest fragments of Santa Rosa are thus important areas of food trees for howlers during the dry season. Walking along stream and creek beds is one of the best ways to locate the monkeys.

There are three primate species in SRNP: mantled howlers (*Alouatta palliata*), black-handed spider monkeys (*Ateles geoffroyi*), and white-faced capuchins (*Cebus capucinus*). Many aspects of the behavioral ecology of Santa Rosa howlers have been described (Chapman, 1987, 1988a,b; Gebo, 1992; Fedigan and Rose, 1995; Larose, 1996; Bergeson, 1996), and the long-term dynamics of the *Cebus* population at SRNP are also available (Fedigan *et al.*, 1996).

The Study Sample: Study Groups and Census Population

Our long-term study of the Santa Rosa howlers began with a brief demographic survey in 1982, followed by more complete censuses in 1983 and 1984 (Fedigan *et al.*, 1985; Fedigan, 1986; Chapman *et al.*, 1988, 1989a). In 1984, we selected three study groups for intensive behavioral and life history research, and began to habituate and to discriminate individual group members (Fedigan and Rose, 1995). In 1985, we began to record births, deaths, disappearances, and migrations, as well as details of foraging and social behavior, on a regular biweekly basis. To facilitate reliable discrimination of individuals, we captured and marked most adults within the howler study groups, and have continued to do so annually with the assistance of Glander (Glander *et al.*, 1991). The intensive biweekly data obtained from our study groups provide an accurate and detailed sample of demographic events and help us to validate the broader survey data obtained from our annual population censuses.

Between 1983 and 1992, we conducted eight annual censuses (Table I), via a modified quadrat technique that has proven useful in areas of fragmented patches of forest (National Research Council, 1981; Fedigan *et al.*, 1985; Chapman *et al.*, 1988). The censuses were almost always carried out in May and June, during which we located and counted as many of the howler groups in the park as possible. In only 2 of these years were we certain that we had searched and researched all areas of the park to the point that we could reliably call the census complete.

In the early years, we chose one area of the park at a time and either walked transects or walked all known trails and dry creek beds in the area to locate monkeys. The loud howling vocalizations of male howlers were particularly useful to locate groups, which we then counted and followed for the day. We considered any individual within 100–300 m of the group and which traveled consistently in the same direction as the group, even though in a peripheral position, to be part of the group. We used individual 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. After establishing a stable count on one group, we located its closest neighboring group and, where possible, used simultaneous contact with both groups by different observers to establish their independence. From our well-known study groups, we were able to determine average home range size (approximately 1 km²) and we used this information to estimate the ranges of the census groups.

Over time, it has become increasingly easy to relocate our census groups in successive years and to determine whether new groups have ap-

Table I. Demographic Trends in Santa Rosa Howlers from 1983 to 1992

Year	No. of monkeys counted	No. of groups counted	Average group size	Mean proportion in each age/sex class ^a						Adult M:F (sex ratio)	Infant:adult F (est. BR) ^b	Immature: adult F
				Adult male (M)	Adult female (F)	Juvenile	Infant	Adult M:F (sex ratio)	Infant:adult F (est. BR) ^b			
1983	223	19	11.7	0.19	0.52	0.13	0.16	0.39	0.35	0.65		
1984	342	25	13.6	0.22	0.44	0.20	0.14	0.52	0.33	0.83		
1985	264	16	16.5	0.22	0.37	0.25	0.16	0.63	0.43	1.18		
1986	314	20	15.7	0.20	0.41	0.21	0.18	0.51	0.46	0.98		
1987	164	15	10.9	0.22	0.39	0.20	0.19	0.58	0.51	1.11		
1988	211	12	17.6	0.21	0.43	0.18	0.18	0.50	0.46	0.88		
1990	439	28	15.7	0.24	0.41	0.19	0.16	0.60	0.42	0.94		
1992	554	34	16.3	0.24	0.41	0.16	0.19	0.66	0.47	0.90		
Mean		21	14.8	0.22	0.42	0.19	0.17	0.55	0.43	0.93		

Comparison of 1984 with 1992 (unpaired *t* test, two tailed; df = 57)

	Group size	Males	Females	Juveniles	Infants	Adult M:F	Infant: adult F	Immature: adult F
<i>T</i>	-1.079	-1.246	1.592	1.622	-2.277	-1.795	-2.148	-0.830
<i>P</i>	0.285	0.218	0.117	0.110	0.026	0.078	0.036	0.410

^aGroup sizes and proportions are means across all groups counted in each year.

^bEstimated birth rate.

peared. This method of censusing by groups does not account for single individuals that may be transferring between groups. Solitary howlers—ones >300 m from any group and traveling independently—are difficult to spot in the forests of Santa Rosa, unless they are vocalizing. As Glander (1992) noted, solitaries are often secretive and do nothing to attract attention. Because such lone individuals can range over long distances, we do not count them, as it would be possible to count solitaries twice in widely separate places on different days of the census. We estimate that we see one lone individual for each group, so the number of migrating individuals that could be found and counted in any given census is small.

For analysis, we assigned individuals to one of four age/sex classes (Clarke and Glander, 1984; Crockett and Pope, 1993; Glander, 1980): infant (<1 year), juvenile (1 to 4/5 years), adult female (>4 years), or adult male (>5 years). Although we originally divided our census data into small and large juveniles, and subadult versus fully adult individuals, most studies of mantled howlers include only one juvenile category and one adult category, so we combined small with large juveniles and subadult with fully adult individuals. Adult howlers are easily sexed, and the age classes of infants, juveniles, and adults are readily distinguished by size. The sexing of immature howlers is more difficult, and we did so only for well-known groups. Clearly, the census data are not as detailed, complete, or reliable as the daily information we collect on our study groups, but we have a reasonably accurate picture of the number of howler groups in the park, as well as their changing sizes and age/sex compositions over the study period.

Data Analysis

Although the first census took place in 1983, there were a few areas of the park that we did not search adequately until 1984, and the latter is probably more representative of the population size at the beginning of our study. Thus we compared 1984 to 1992, the most recent full census, for all analyses. Statistical analyses are based on both the numbers and the proportions in each age/sex class. However, because the number of individuals in each age/sex class are strongly influenced by overall group size, we report results based on the proportional values for group composition variables. We used *t* tests (unpaired, two-tailed) to compare group size and composition in 1984 with 1992. We used one-sample-against-the-mean tests (Sokal and Rohlf, 1981) to compare density at Santa Rosa with density at other sites. We performed a multivariate cluster analysis (SYSTAT Version 5.0, Euclidean distance, unweighted pair group linkage method) to illustrate patterns of demographic similarity between sites and a *K*-means test to con-

firm and to quantify the two major clusters. The *K*-means test identifies clusters by maximizing between-group variance relative to within-group variance across variables and performs between-cluster analysis of variance tests (ANOVAs) for each variable (SYSTAT, 1992). Alpha levels for significance are 0.05.

We calculated density estimates from a computer-generated map (CorelDraw 3.0) of Santa Rosa. The map is based on an aerial photograph and corrected by an on-the-ground survey of the forest fragments and non-forested areas in the park. We coded the map for five habitat types: evergreen/riparian forest, mixed deciduous forest, early secondary forest, pasture or savanna, and mangrove forest. We estimated available habitat for howlers (69 km²) as the proportion of the 108 km² park that is covered by evergreen/riparian (13%) and mixed deciduous forest (51%). These are the two forest types in which we commonly found howlers. They cross rapidly through early secondary forest, but forage and rest almost entirely in older growth forests.

RESULTS

Population Growth Rate

Between 1984 and 1992, the total number of howlers increased from 342 to 554, an observed rate of increase (*r*) of 0.619 over 8 years (Table I). Although we were not able to contact and to count all the groups every year, it is clear that the population grew steadily over this period, at a rate of approximately 7.7% per annum. Since 1984, the number of adult males increased by 84%, from 75 to 138, while the number of adult females increased by 51%, from 150 to 227. The density of howling monkeys in the park increased from 4.9 individuals per km² of available habitat to 7.9 individuals per km² in 1992. The number of groups increased from 25 in 1984 to 34 in 1992. Average group size increased from 13.6 to 16.3 during the same period, but the difference is not significant ($t = 1.079$, $df = -57$, $P = 0.285$).

Group Composition

Across all groups and census years, the average group size is 14.8 (range, 3–44; SD = 9.53). The average number of adult males is 3.2 (range, 1–12; SD = 2.34), and that of adult females is 6.2 (range, 1–21; SD = 3.85). The average group size and composition in each census year are in

Table I. The group composition values represent the average proportion of individuals in each age/sex class over all groups in a given year. Comparing 1992 with 1984, the average proportions of males in groups has increased slightly, while the proportions of females and immatures have decreased, but these are not significant differences. Only the proportion of infants has changed significantly, increasing from 0.14 in 1984 to 0.19 in 1992 ($t = 2.277$, $df = 57$, $P = 0.03$).

Adult sex ratios within groups ranged from 1 male to 7 females (0.14) to 4 males to 2 females (2.0). In the majority of groups, the adult sex ratio is biased toward females. The average adult sex ratio is 1 male per 1.8 females (M:F sex ratio, 0.55; Table I). The ratio of adult males to females was higher in 1992 than in 1984 (0.66 compared with 0.52), but the difference is not significant ($t = 1.795$, $df = 57$, $P = 0.078$). The ratio of immatures (infants plus juveniles) to adult females averaged 0.93 (1 immature for every 1.08 adult females), with no significant difference between 1984 and 1992 ($t = 0.830$, $df = 57$, $P = 0.410$).

Nativity and Infant Survival

We collected almost of the census data during May and June. Since howler births in Santa Rosa, howlers between January and April, May–June censuses are the optimal time to include the majority of new infants in the larger population. For each group censused, we computed a birth rate from the number of infants in the group divided by the number of adult females. The average birth rate—ratio of infants to adult females—over the years of the study is 0.43 (Table I), with a significantly higher birth rate in 1992 than in 1984 ($t = 2.148$, $df = 57$, $P = 0.036$). Our annual censuses do not discriminate individual infants or monitor their progress between years, so we were not able to calculate infant survival in the census population. However, in a sample of 54 infants born to known mothers on known dates between 1985 and 1992, infant survivorship (to age 12 months) is 70%.

There is no significant correlation between amounts of annual rainfall and births the following year in either the census population ($\rho = 0.299$) or the study groups ($\rho = 0.167$), nor are birth rates significantly correlated with the amount of early rain during May in the howler census population ($\rho = 0.359$), unlike the capuchin population (Fedigan *et al.*, 1996). In our howler study groups, for which we know most birth dates to within a few days, there were significantly more births in the dry season than in the wet season (Fig. 2; $n = 54$; two-tailed binomial test, $P = 0.0017$).

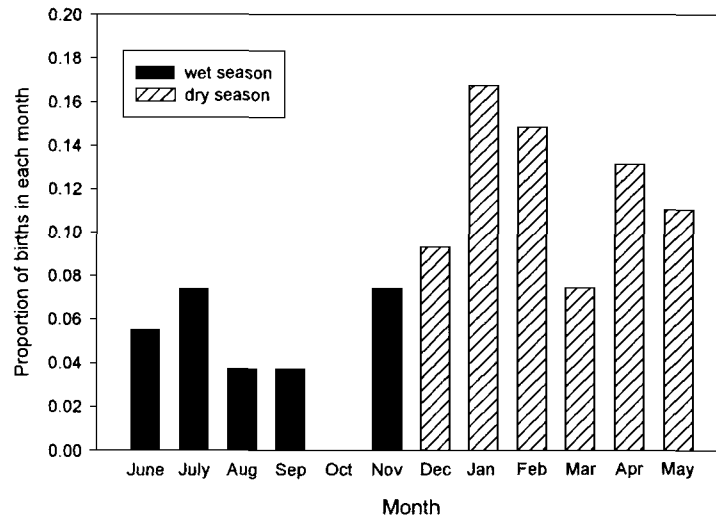


Fig. 2. The distribution of howler births in our study groups during the wet (June–November) and dry (December–May) seasons at SRNP between 1985 and 1992.

Origin and Growth of New Groups

At Santa Rosa, the origin and growth of new groups occurred via two major mechanisms: (1) fissioning of larger groups into permanent subgroups occupying adjacent ranges and (2) the dispersal of single individuals into areas of regenerating forests. In each of the latter cases, a solitary male howled over a period of weeks or months before he was joined by one or more young females. Four of the nine new groups between 1984 and 1992 formed through the fissioning of a small heterosexual subgroup from the existing group, and five new groups began with single males. Here we provide brief chronologies of two groups that we observed closely from their beginnings.

Cerco de Piedra Group (Single Male Origin)

1991: In the early dry season, a lone male appears in a patch of early secondary forest, where howlers had not been seen in the previous 20 years, and howls vigorously. A few months later he is joined by a young female. By April, the male and female are established as a resident pair and mate.

1992: The female gives birth to an infant.

- 1993: The female gives birth to a second infant.
- 1994: A second, smaller adult female joins the group, bringing it to five individuals.
- 1995: A second male appears in May and follows the group for several months. He has several prolonged howling matches with the resident male, but we observe no fighting or wounds. In July, the original female has a third infant, and the peripheral male disappears.
- 1996: In January, the second female has her first infant, bringing the group to seven individuals. Another peripheral male appears (or possibly the same male seen the previous year returned). He follows the group for several months and disappears in March. The first two offspring (now juveniles) born to the original female disappear in April. In June, a different peripheral male appears and follows the group. At this point it was comprised of five individuals (one male, two females, two infants) with one peripheral male.

Exclosure Group (Fission Origin)

- 1986: Two adult males and one adult female that were marked in the Bosque Humedo group in 1985 occupy an area of mature forest between the range of Bosque Humedo and that of a neighboring study group, Sendero. The three individuals maintain their integrity and isolation as a group for a year.
- 1987: The group is joined by another marked female from Bosque Humedo and a marked female from the Sendero group. One of the original founder males disappears. Two infants are born.
- 1988: Two marked females and one unmarked subadult male immigrate into the group. Two infants are born.
- 1992: A newly immigrant adult male defeats the remaining founder male and takes over the group.
- 1988–1996: The group maintains a size of 6–11 individuals in a small but nearly exclusive range.

Comparison of Santa Rosa and Other Mantled Howler Sites

The demographic profile of Santa Rosa howlers falls within the range of variation for mantled howler at other sites in terms of both numbers (Table II) and proportions in each age–sex class (Table III). The density of howlers at Santa Rosa is not significantly different from densities at sev-

Table II. Group Size and Numbers in Each Age/Sex Class in Mantled Howlers (*Alouatta palliata*)

Site	Year	No. of groups counted	Mean group size	Mean No.					Source
				Adult males	Adult females	Juveniles	Infants		
Santa Rosa (Costa Rica)	1972	8	8.1	1.6	3.6	2.0	0.8	Freese (1976)	
	1984	25	13.6	3.0	6.0	2.7	1.9	Fedigan (1986)	
	1992	34	16.3	3.9	6.7	2.6	3.1	This paper	
Cabo Blanco (Costa Rica)	1988	8	14.8	2.8	5.4	2.5	1.9	Lippold (1988)	
	1989	7	10.9	2.4	7.7	2.4	2.3	Lippold (1989)	
Mean			12.9	2.4	6.8	2.1	1.5		
Curu (Costa Rica)	1990	16	8.0	No data	No data	No data	No data	Tomblin & Cranford (1994)	
	1990	7	10.9	3.3	4.0	2.3	1.3	Stoner (1994)	
La Selva (Costa Rica)	1978-1981	17	9.1	3.0	4.1	1.6	1.5	Estrada (1982)	
	1972-1976	15	15.5	2.1	9.0	4.0 ^a		Clarke <i>et al.</i> (1986)	
La Pacifica (Costa Rica)	1984	16	15.7	2.6	8.3	2.2	2.2	Clarke <i>et al.</i> (1986)	
	1991 ^b	21	9.6	1.9	5.2	2.5 ^a		Clarke and Zucker (1994)	
	1991 ^a	27	12.6	2.5	6.8	3.1 ^a		Clarke and Zucker (1994)	
Mean BCI (Panama)			13.4	2.3	7.3	2.2 ^a			
	1932	23	17.3	2.8	7.4	4.0	3.1	Milton (1982)	
	1933	28	17.4	2.6	7.5	4.2	3.5	Ibid	
	1951	30	8.0	1.2	4.6	1.1	1.1	Ibid	
	1959	44	18.5	3.3	9.1	3.1	3.0	Ibid	
	1967	27	13.8	2.9	7.0	1.8	2.1	Ibid	
	1977	13	20.8	3.5	9.2	2.6	5.5	Ibid	
	1977-1993		19.4	3.1	8.5	2.5	5.2	Milton (1996)	
	Mean		16.5	2.8	7.6	2.8	3.4		
	Overall mean		13.7	2.7	6.7	2.46 ^c	2.49 ^c		
Range		8 to 20.8	1.2 to 3.9	3.6 to 9.2	1.1 to 4	0.8 to 5.5			
S.D.		4.08	0.68	1.83	0.81 ^c	1.45 ^c			

^aNumber of juveniles and infants combined and listed as "immatures."

^bLa Pacifica: 1991a, initial survey; 1991b, expanded survey.

^cExcludes combined "immature" values for La Pacifica.

Table III. Population Density and Group Composition in Mantled Howlers (*Alouatta palliata*) (for Sources See Table II)

Site	Year	Density per km ²	Group composition ^a					Adult sex ratio (M:F)	Birth rate, infants:F	Immature:F ratio ^b
			Adult male (M)	Adult female (F)	Juvenile	Infant	No data			
Santa Rosa (Costa Rica)	1972	0.9 to 1.4	0.20	0.45	0.25	0.10	0.44	0.22	0.78	
	1984	4.9	0.22	0.44	0.20	0.14	0.52	0.33	0.77	
Cabo Blanco (Costa Rica)	1992	7.9	0.24	0.41	0.16	0.19	0.66	0.47	0.84	
	1988	10.1	0.16	0.52	0.16	0.16	0.31	0.29	0.60	
	1989	6.8	0.22	0.54	0.17	0.07	0.41	0.12	0.44	
	1990	9.0	No data	No data	No data	No data	No data	No data	No data	
La Selva (Costa Rica)	1990	7 to 15	0.30	0.37	0.21	0.12	0.83	0.33	0.90	
Los Tuxtlas (Mexico)	1978-1981	23.3	0.33	0.45	0.17	0.17	0.73	0.37	0.76	
La Pacifica (Costa Rica)	1972-1976	74.3	0.14	0.58	0.26 ^c	0.14	0.24	0.29	0.48	
	1984	77.3	0.17	0.53	0.14	0.14	0.34	0.29	0.58	
	1991a ^d	63.0	0.20	0.54	0.26 ^c	0.14	0.36	0.48	0.48	
	1991b ^d	103.3	0.20	0.54	0.25 ^c	0.18	0.37	0.48	0.48	
	1992	49.0	0.16	0.43	0.23	0.18	0.36	0.42	0.96	
	1933	60.0	0.15	0.43	0.24	0.19	0.36	0.47	1.04	
BCI (Panama)	1951	16.0	0.15	0.57	0.14	0.14	0.27	0.24	0.49	
	1959	54.0	0.18	0.49	0.17	0.16	0.36	0.33	0.67	
	1967	62.0	0.21	0.51	0.13	0.15	0.41	0.30	0.56	
	1977	90.0	0.17	0.44	0.13	0.26	0.38	0.60	0.88	
	1977-1993	77.0	0.16	0.44	0.13	0.27	0.36	0.62	0.91	

^aAverage proportion in age/sex class.^bCalculated from mean values because exact numbers of immatures and females were not available from all sites.^cNumber of juveniles and infants combined and listed as "immatures."^dLa Pacifica; 1991a, initial survey; b, expanded survey.

eral other sites: Cabo Blanco, Curu, La Selva, and Los Tuxtlas (one sample against the mean test, $t = -0.583$, $df = 4$, $P = 0.591$), but is significantly less than means for La Pacifica and BCI ($t = -2.031$, $df = 9$, $P = 0.047$). Across all sites and years, group size is positively correlated with density ($r = 0.559$, $P = 0.013$), and ratio of adult males to females is negatively correlated with density ($r = -0.486$, $P = 0.041$), that is, higher-density sites have lower proportions of males in groups, whereas lower-density sites have more equal sex ratios.

We used a multivariate clustering procedure (SYSTAT 5.0) to discriminate patterns of demographic similarity and difference across sites. Because density appears to be very powerful in characterizing demographic profiles, we weighted density by a factor of 5, after standardizing values for all variables. We performed two separate analyses, with group composition indicated in terms of proportions (Fig. 3a) and numbers (Fig. 3b), respectively, in each age/sex class. In both analyses, La Pacifica and BCI fell together in a distinct cluster, while Santa Rosa and other sites formed a separate cluster. The one exception is that the BCI 1951 census [which, according to Milton (1982), reflected a small population recovering from decimation by yellow fever] fell within the Santa Rosa cluster. The two clusters (La Pc/BCI versus SR/LsTx/LaSl/Curu/CbBl) are significantly different with respect to density ($F = 104.5$, $P < 0001$), group size ($F = 11.02$, $P = 0.004$), and sex ratio ($F = 6.77$, $P = 0.019$). Groups in the Santa Rosa cluster had a significantly larger proportion of males ($F = 6.59$, $P = 0.021$), while those in the LaPc/BCI cluster had larger numbers of females ($F = 14.74$, $P = 0.001$) and infants ($F = 5.34$, $P = 0.034$).

Differences in population density may help to explain intersite differences in group composition. Howler populations and intragroup sex ratios are strongly female-biased at all sites, but there are lower proportions of adult males at the high-density sites of La Pacifica and BCI than at low-density sites such as SRNP (Table III). Groups also tend to be larger at BCI and La Pacifica (Table II). Both sex ratio and group size are correlated with density, and our cluster analysis indicates a demographic package of high density and large groups with low proportions of males relative to females.

To better understand whether lower proportions of males in high-density sites are more ascribable to variation in the number of males found in groups or variation in the numbers of females found in groups, we also examined the relative numbers of males and females in groups (Table II). Santa Rosa has one of the highest mean number of males per group, but the variation in mean numbers of males across sites is quite small, approximately one to four adult males per group. The average number of males per group in the high-density site cluster is 2.7 (range, 1.9 to 3.5; $SD =$

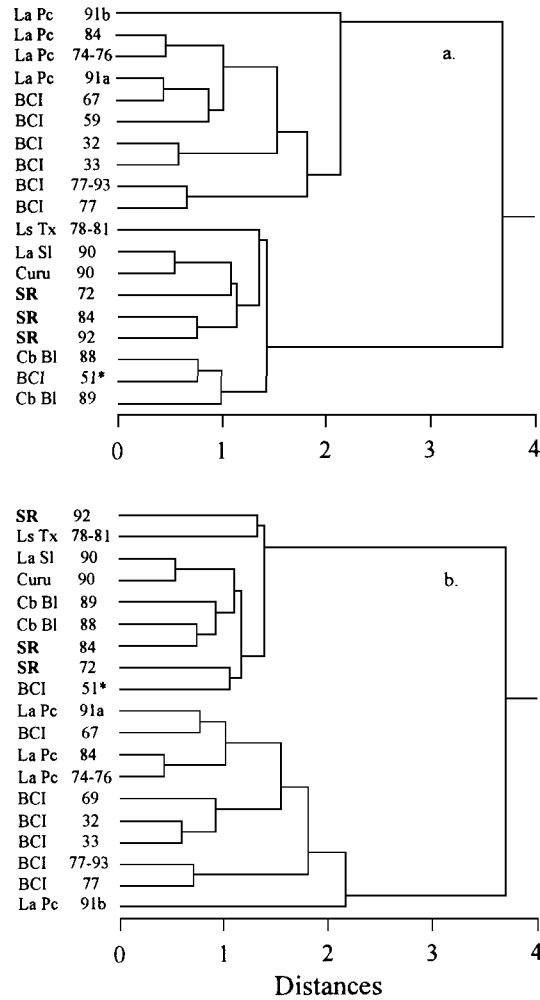


Fig. 3. Cluster analyses comparing different howler study sites based on group composition: (a) proportion of individuals; (b) number of individuals in each age/sex class. For values and site locations, see Tables II and III, respectively. *1951 was the year the howler population crashed at BCI.

0.48), while that in the low-density cluster is almost-identical, at 2.6 (range, 1.2 to 3.9; SD = 0.83). In contrast, the average number of females per groups ranges from 3.6 to 9.2, with considerable variation across sites and years. The average number of females at high-density sites is 7.8 (range, 5.2 to 9.2; SD = 1.20), compared with only 5.3 (range, 3.6 to 7.7; SD =

1.37) at low-density sites. Examination of our raw census data (at SRNP, the number of males per group ranges from 1 to 12 and the number of females ranges from 1 to 21) and that provided for several other sites (Milton, 1982; Clarke *et al.*, 1986) confirms that there is less intergroup variation in male numbers than in female numbers and that upper limits are much higher for females. Thus, the significant differences in sex ratio and proportions of males between high- and low-density sites are due to primarily larger numbers of females at La Pacifica and BCI.

DISCUSSION

Our most important finding from a conservation perspective is that the howler population within a reclaimed and regenerating habitat has increased over the past decade. The observed rate of increase of 7.7% per annum in the Santa Rosa howlers is quite high for a nonprovisioned population (Richard, 1985, pp. 244–247). However, as in the SRNP capuchin population, the number of howler males has increased more rapidly than the number of howler females, so the increase in effective population size may not be as substantial as it appears.

Population Density

It is noteworthy that the density of howlers at Santa Rosa and at four other sites is significantly lower than densities estimated for the two well-studied sites of La Pacifica and BCI. Clarke and Zucker (1994) suggested several possible reasons for the vastly different density estimates for La Pacifica and SRNP. We review them briefly and then comment on how the history of howler populations at Santa Rosa may be affecting current density estimates.

First, our density estimates of 4.9–7.9 at Santa Rosa compared to 77.3–103.3 at La Pacifica may simply reflect the range of variation within a species (Chapman and Balcomb, 1998). The inclusion of other mantled howler sites in our comparative analyses places Santa Rosa in perspective: at the low end of the density range. Second, we used an estimate of available rather than usable or total habitat, and we may be defining both our terms differently from those of researchers at La Pacifica. We defined available habitat as the proportion of the park covered by mixed deciduous and evergreen/riparian forests, the two forest types in which we commonly find howlers (Chapman and Balcomb, 1998). If we were to limit our definition of available habitat to the evergreen/riparian forest in the park, then our

density estimate would rise to 24.4 howlers per km² in 1984 and 39.9 howlers per km² in 1992. These values are still significantly below density estimates from La Pacifica. In fact, the order of difference between the two sites is such that we doubt definitions of available habitat are the source of the variation.

Another suggestion is that we failed to account for solitary individuals. While this is true, we found on average only one solitary male for each group in a census year. Even in conjunction with the more conservative definition of available habitat, this seems unlikely to be a sufficient source of the differences in density estimates.

Another point, not mentioned in Clarke and Zucker's (1994) comparison of the two sites, is that sizable populations of capuchins and spider monkeys live sympatrically with the howlers at Santa Rosa, but not at La Pacifica. Competition for food and space with other species of arboreal primates may limit the howler population at SRNP. However, there are three other species of primates living alongside the howlers at BCI, where densities estimates of *Alouatta* are almost as high as those from La Pacifica.

At both BCI and La Pacifica, there has been little or no population growth over the past 20 years (Milton, 1982, 1996; Clarke and Zucker, 1994). The howler population at BCI increased during the 1930s, was decimated by yellow fever in the late 1940s, and subsequently increased again, before stabilizing in about 1970 (Froehlich and Thorington, 1982; Glanz, 1982; Milton, 1982). Clarke and Zucker (1994) state that there is no evidence of a population increase at La Pacifica and that the larger number of groups in the second value for La Pacifica in 1991 (Table II) simply reflects a larger census over a greater area. Glander (1980, 1992) and Milton (1982) suggested that these sites are at, or close to, carrying capacity and may be saturated with howlers. La Pacifica consists of very patchy forest interspersed with agricultural fields. Some of the forest fragments are deciduous and others are riparian. BCI is made up mainly of climax evergreen or riparian vegetation or both, and even the young deciduous forest at BDI is estimated to be ≥ 100 years old (Enders, 1935; Foster and Brokaw, 1982), whereas only 13% of Santa Rosa is classified as evergreen/riparian. Eisenberg (1980) found that the mature forest at BCI supports more arboreal herbivores, including howlers, than secondary forest at Hato Masguaral, Venezuela, does. Based on a review and analysis of 80 howler populations, Chapman and Balcomb (1998) concluded that much of the variation in howler population characteristics is related to local events in the recent history of groups. They found no significant relationship between howler densities and ecological factors such as habitat productivity, seasonality, and number of sympatric species, the variables normally hypothesized to affect population densities. Perhaps the history of land and forest use

at Santa Rosa provides the best explanation of why the densities are low at this site versus La Pacifica.

The earliest estimate of the howler population at Santa Rosa is taken from surveys conducted in 1971 and 1972 (Freese, 1976). Although Freese indicates that he may not have counted all howler groups, his estimate of 70–100 howlers in 8 groups is considerably lower than 342 howlers in 25 groups that we counted a decade later. It is striking that all of Freese's groups were in the 13% of the park covered by evergreen/riparian forests, and most were on the lower plateau, toward the Pacific Ocean. In 1983, we located many groups in mixed deciduous forest in the upper plateau, closer to the Pan American Highway. It appears that something—hunting, anthropogenic fires, cattle, or greater forest destruction on the upper plateaus—had limited the howlers to low-lying, coastal-zone evergreen forest in the early years of the park and that they only later spread into mixed deciduous patches of forest and higher elevations. Even allowing for the possibility that Freese missed some groups and that we may have defined available habitat differently from him, it seems clear that the howler population expanded in size and range in the decade between 1972 and 1983. Chapman and Balcomb (1998) report on a survey of howlers in the larger Area de Conservacion Guanacaste (ACG) park, of which Santa Rosa is now one sector and concluded that the densities of howlers in different zones of the park correspond to the length of time that the zone has been protected. Santa Rosa has been protected the longest, and the howler densities in other zones are lower and more comparable to the values reported by Freese (1976).

Freese's (1976) conducted his study immediately after Santa Rosa was declared a national park in 1971, so his counts may reflect the conditions for howlers that prevailed when the area was agricultural land. At that time, the upper plateau of the park, where he found almost no howlers, was still partially cleared and planted with grasses for cattle, and the neighboring farms grew cotton crops. At least two conditions that prevailed in the Santa Rosa area in the late 1960s and early 1970s may have limited the population of howlers.

First, the mixed deciduous forests might have been young enough 25–30 years ago that there were insufficient numbers of the large trees preferred by howlers. Howlers in SRNP restrict themselves to larger trees than those used by either capuchins or spider monkeys. They do not use trees with a DBH (diameter at breast height) <20 cm, and their feeding trees have an average DBH of 63 cm (Chapman, 1988b; Larose, 1996).

Second, it is possible that there was a population crash of howlers in the area of Santa Rosa in the last 1960s, whose effects were still apparent when Freese first counted howlers in the park in 1971–1972. The evidence for this is only circumstantial, but Heltne *et al.* (1976), who conducted

howler censuses in the nearby areas of Taboga and La Pacifica from 1966 to 1971, concluded that the howlers of Guanacaste Province were a distressed and declining population—small group sizes, relatively low numbers of juveniles and infants—that were similar to the population characteristics of howlers at BCI after they were decimated by yellow fever. Heltne *et al.* (1976) checked with health authorities in Guanacaste Province, and although they found no evidence of a recent outbreak of yellow fever or other epidemics, they located a veterinarian who had been assigned to Liberia, the nearest town to Santa Rosa, 35 km away. He had received many dead howlers for autopsy in 1968–1969. Tests at the government laboratory in San Jose showed that the swollen glands of the dead monkeys were loaded with insecticides. He confirmed that 1968 and 1969 were years of heavy cotton production in the area and that large doses of insecticides were sprayed from airplanes, leading to the possibility that poisons were carried from the sprayed fields onto adjacent forested areas. Although we need better evidence than the report of one veterinarian to confirm that unusually heavy doses of sprayed insecticides might have affected the howler populations in the late 1960s, we observed in 1985 that insecticides sprayed onto cotton fields at the Santa Rosa park boundaries could drift onto the adjacent park forests where the monkeys ranged. Since that time no crop is grown in the vicinity of the park and almost all adjacent farmlands have been purchased to create the megapark: ACG.

Heltne *et al.* (1976) reported strikingly low census figures for the Taboga population in 1968 and a somewhat depressed population ($n = 50\text{--}66$) at La Pacifica in 1967–1970. Although the area covered by Heltne *et al.* (1976) is unclear, the first comprehensive counts of La Pacifica howlers in 1972–1976 indicate a much larger population of 247 individuals (Clarke *et al.*, 1986).

Whatever the causes of the low howler density found by Freese (1976) in 1972 at Santa Rosa, agricultural activity and forest destruction within the park were brought to a halt soon after its establishment. Between 1971 and 1983, when we conducted our first census, fires and poachers were brought under control and the forest was allowed to grow. Large areas of Santa Rosa are newly regenerated secondary forest, growing in abandoned pastures. One might predict that monkeys would do well in regenerating forest. Secondary forests often exhibit high plant diversity, and many colonizing species quickly produce foliage and fruit with few toxic defenses (Webb *et al.*, 1972; Hartshorn, 1978; Janzen, 1979; Fleming *et al.*, 1985). However, as Janzen (1988) and Gebhardt (1994) have documented, the new woody vegetation that grows in most regenerating pastures is made up of 90% wind-dispersed trees that do not offer fruits for vertebrates. Howlers at SRNP have a diet made up largely of fruits and flowers when

available, and they switch to mature leaves only when the other foods are not available (Larose, 1996). SRNP howlers seldom enter early secondary forest; though they will travel rapidly along a corridor of single trees to get from one forest fragment to the next. Thus, newly regenerated forests in abandoned pastures may not yet provide additional habitat for howlers. However, the mixed deciduous forests are now 26 years older than they were when the park was established, and it may be that enough of their trees have reached sufficient size for howler use. This may be why howlers are commonly found in mixed deciduous forest today, whereas they were not found in these forests when Freese (1976) conducted his survey.

Crockett (1996; Crockett and Eisenberg, 1987) described growth in a population of red howlers on ranchland at Hato Masgual, Venezuela, over a 20-year period when fires were controlled and woody vegetation was allowed to grow; conditions very similar to those at SRNP over the past 26 years. Crockett (1996) found that new groups formed from dispersing individuals rather than group fissioning; new groups are smaller than established groups; and population growth was greatest in the lower-density gallery forests where the red howlers had experienced an extreme population crash a few years before her study began.

A further factor that may have allowed howlers at SRNP to expand into regenerating forest is that the people who had ranched in the area sometimes cleared the forest differentially, allowing large fruiting trees to remain in place. As these partially cleared forests regenerate, they quickly offer habitat for monkeys—the fruiting trees are in place and as soon as trees of sufficient size for locomotion have grown, the monkeys travel into the area. One such example is the forest of Cerco de Piedra in Santa Rosa. This area was repeatedly burned and cleared before incorporation within the park and has been relatively slow to regenerate due to severe soil degradation (D. Janzen, personal communication). However, many fruiting trees, primarily figs, were left in place. This is the forest described earlier, which we had monitored for 10 years and which Freese (1976) surveyed in 1971 before the first male howler appeared and attracted a female to form a new group. There was no howler in this forest from 1971 to 1991, but we presume that Cerco de Piedra, unlike other nearby secondary forests, is now able to sustain a howler group because of the large fruiting trees scattered throughout the younger growth patch.

Group Size, Sex Ratio, and Density

Chapman and Balcomb (1998) found that across all howler species there is a relationship between group size and sex ratio such that larger groups

have proportionately fewer males. For mantled howlers at BCI, Froehlich and Thorington (1982) found that larger groups had relatively fewer males than smaller groups did, and they suggested that the number of male howlers per group is limited by social factors, such as the degree of tolerance between males (Scott *et al.*, 1978). The low variance that we found in the average number of males per group is consistent with the hypothesis that in mantled howlers, male group membership is more closely circumscribed than female membership is. If the number of male positions within groups is strictly limited, then in densely populated habitats, where there are very few opportunities to form new groups, males must either usurp or inherit existing positions within groups or fail to enter them and remain solitary, emigrate, or die. Contrariwise, females may have more options to remain in or to transfer between existing groups because groups can expand to accommodate large numbers of females. This differs from the patterns suggested for red howlers (Crockett and Pope, 1993). The number of female positions in groups is more limited in red howlers than in mantled howlers. The number of male positions in groups is also more limited in red howlers than in mantled howlers, but male red howlers have the option to transfer between groups, whereas females do not, or can do so very rarely.

Patterns of dispersal and behavioral interaction at La Pacifica and BCI confirm that there is intense competition among males for group membership (Glander, 1980, 1992; Jones, 1980, Milton, 1982, Froehlich and Thorington, 1982). Male infants at both La Pacifica and BCI appear to experience considerably higher mortality than females do (Glander, 1980; Froehlich *et al.*, 1981), and mortality at BCI peaks in young males between 5 and 7 years of age (Otis *et al.*, 1981). At La Pacifica, males disperse earlier than females do and may spend up to four times as long as solitaries (Glander, 1992). Solitary individuals are probably at increased risk of starvation or predation, and may suffer harassment by resident group members (Glander, 1992). Migration could be more costly for male howlers than for females, as males might sacrifice more reproductive opportunities. Glander (1992) suggests that females may transfer while pregnant, and males are subject to severe aggression from resident males (Jones, 1980; Glander, 1992). Transferring females are also subject to aggression but may join groups with the support of a resident male, while males typically must fight and defeat the dominant male in order to enter a group (Glander, 1980, 1992; Clarke and Glander, 1984; Clarke *et al.*, 1994). Milton (1982) reported similar patterns at BCI. Infanticide, which may be a good indicator of male reproductive competition, occurs at La Pacifica (Clarke, 1983; Clarke *et al.*, 1994).

Female howlers experience high levels of feeding competition at BCI and La Pacifica, probably as a consequence of high population density, and

associated increases in group size and restriction of home range size (Milton, 1982; Glander, 1992). Although groups in high-density sites have more infants per group simply because group size is bigger, their birth rates are not significantly greater than those of howlers at low densities, and the howler populations at BCI and La Pacifica are not growing. This indicates that an elevation in birth rate is balanced by increased mortality or emigration. At BCI, where levels of emigration are negligible, mortality clearly limits population growth, and Milton (1982) suggested that few infants survive to reproductive age. Infant survivorship at La Pacifica (Glander, 1980) is similar to the 70% found at SRNP, suggesting that death or emigration rates or both are high for older age classes. Overall, the pattern at high-density sites seems to be that males experience high levels of competition for a limited number of positions within groups, with associated high mortality or emigration or both, while females experience increased feeding competition as a result of high female recruitment and increased group size. The outcome is a strongly female-biased adult sex ratio and a relatively low intergroup mobility for males.

How does this pattern compare with that found at low-density sites such as Santa Rosa? The numbers of males in groups at SRNP are less variable than the numbers of females, and the maximum number per group (12) is much lower than the female maximum (21). However, both the upper limit and the degree of variation at SRNP exceed values at other sites (Table II). This suggests that although male group membership at SRNP is more limited than female membership, it is still less strictly limited than at BCI or La Pacifica.

At our study site, the expansion of howlers into previously unused areas and the appearance of nine new groups indicates options other than competing for positions within established groups. It appears to be primarily males that establish new groups, either by fissioning or by attracting females. Transient and secondary male dispersal also occurred in our study groups, suggesting greater male mobility at Santa Rosa than at La Pacifica, where it has not been observed (Glander, 1992). However, males at Santa Rosa also compete for breeding opportunities and for group membership. Solitary males may follow a group for several months, engaging in occasional howling matches with the dominant resident male, but without marked aggression, as described in the chronology of the Cerco de Piedra group. In other cases, severe fights occur between resident and transferring males, sometimes resulting in the takeover of an existing group by a successful challenger. This strategy may be more successful in small groups than large groups, affording good opportunities for males moving into recently colonized or marginal areas, where groups tend to be small.

Our data suggest that males are relatively advantaged in the uncrowded habitats at Santa Rosa and other low-density sites, even though all well-studied howler populations show a strongly female-biased sex ratio. Possibly the greater contribution of males to howler population growth at Santa Rosa over the span of our study relates to factors enhancing male survivorship at low densities. Whatever the reason, it appears that there are factors associated with the regenerating forests and low-density conditions at Santa Rosa that favor males, at least in the early stages of forest regeneration. Since effective population growth rates are dependent upon increases in the number of reproductive females, this has important implications in terms of primate conservation and warrants further investigation.

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REFERENCES

- Bergeson, D. J. (1996). *The Positional Behavior and Prehensile Tail Use of Aouatta palliata, Ateles geoffroyi, and Cebus capucinus*, Ph.D. dissertation, Washington University, St. Louis.

- Boza, M. O. (1993). Conservation in action: past, present, and future of the national park system of Costa Rica. *Conserv. Biol.* 7: 239-247.
- Carpenter, C. R. (1934). A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comp. Psychol. Mongr.* 10: 1-168.
- Carpenter, C. R. (1965). The howlers of Barro Colorado Island. In DeVore, I. (ed.), *Primate Behavior*, Holt, Rinehart and Winston, New York, pp. 250-291.
- Chapman, C. A. (1987). Flexibility in diets of three species of Costa Rican primates. *Folia Primatol.* 49: 90-105.
- Chapman, C. A. (1988a). Patterns of foraging and range use by three species of Neotropical primates. *Primates* 29: 177-194.
- Chapman, C. A. (1988b). Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behaviour* 105: 99-116.
- Chapman, C. A., and Balcomb, S. R. (1998). Population characteristics of howlers: Ecological conditions or group history. *Int. J. Primatol.* 19: 385-403.
- Chapman, C. A., Fedigan, L. M., and Fedigan, L. (1988). A comparison of transect methods of estimating population density of Costa Rican primates. *Brenesia* 30: 67-80.
- Chapman, C. A., Chapman, L., and Glander, K. E. (1989). Primate populations in Northwestern Costa Rica: Potential for recovery. *Primate Conserv.* 10: 37-44.
- Clarke, M. R. (1982). *Socialization, Infant Mortality, and Infant-Nonmother Interactions in Howling Monkeys (Alouatta palliata) in Costa Rica*, Ph.D. dissertation, University of California at Davis, Davis.
- Clarke, M. R. (1983). Infant-killing and infant disappearance following male takeover in a group of howling monkeys (*Alouatta palliata*) in Costa Rica. *Am. J. Primatol.* 5: 241-247.
- Clarke, M. R., and Glander, K. E. (1984). Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In Small, M. (ed.), *Female Primates: Studies by Women Primatologists*, Alan R. Liss, New York, pp. 111-126.
- Clarke, M. R., and Zucker, E. L. (1994). Survey of the howling monkey population at La Pacifica: A seven-year follow-up. *Int. J. Primatol.* 15: 61-73.
- Clarke, M. R., Zucker, E. L., and Scott, N. J., Jr. (1986). Population trends of the mantled howler groups of La Pacifica, Guanacaste, Costa Rica. *Am. J. Primatol.* 11: 79-88.
- Clarke, M. R., Zucker, E. L., and Glander, K. E. (1994). Group takeover by a natal male howling monkey (*Alouatta palliata*) and associated disappearances and injuries of immatures. *Primates* 35: 435-442.
- Collias, D. E., and Southwick, C. H. (1952). A field study of the population density and social organization of howler monkey groups. *Proc. Am. Phil. Soc.* 96: 144-156.
- Crockett, C. M. (1987). Diet, dimorphism and demography: Perspectives from howlers to hominids. In Kinzey, W. G. (ed.), *The Evolution of Human Behavior. Primate Models*, SUNY Press, New York, pp. 115-135.
- Crockett, C. M. (1996). The relation between red howler monkey (*Alouatta seniculus*) troop size and population growth in two habitats. In Norconk, M. A., Rosenberger, A. L., and Garber, P. A. (eds.), *Adaptive Radiations of Neotropical Primates*, Plenum Press, New York, pp. 489-510.
- Crockett, C. M. (1988). Conservation biology of the genus *Alouatta*. *Int. J. Primatol.* 19: 549-578.
- Crockett, C. M., and Eisenberg, J. F. (1987). Howlers: Variations in group size and demography. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 54-68.
- Crockett, C. M., and Pope, T. R. (1993). Consequences of sex differences in dispersal for juvenile red howler monkeys. In Pereira, M. E., and Fairbanks, L. A. (eds.), *Juvenile Primates. Life History, Development and Behavior*, Oxford University Press, New York, pp. 104-118.
- Crockett, C. M., and Rudran, R. (1987a). Red howler monkey birth data. I. Seasonal variation. *Am. J. Primatol.* 13: 47-368.
- Crockett, C. M., and Rudran, R. (1987b). Red howler monkey birth data. II. Interannual, habitat and sex comparisons. *Am. J. Primatol.* 13: 369-384.
- Dobson, A. P., and Lyles, A. M. (1989). The population dynamics and conservation of primate populations. *Conserv. Biol.* 3: 362-380.

- Dobson, A. P., and Yu. J. (1993). Rarity in Neotropical forest mammals revisited. *Conserv. Biol.* 7: 586-591.
- Eisenberg, J. F. (1979). Habitat, economy, and society: Some correlations and hypotheses for the neotropical primates. In Bernstein, I. S., and Smith, E. O. (eds.), *Primate Ecology and Human Origins*, Garland Press, New York, pp. 215-262.
- Eisenberg, J. F. (1980). The density and biomass of tropical mammals. In Soule, M. E., and Wilcox, B. A. (eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*, Sinauer Assoc., Sunderland, MA, pp. 35-55.
- Enders, R. K. (1935). Mammalian life histories from Barro Colorado Island, Panama. *Bull. Mus. Comp. Zool.* 78: 385-502.
- Estrada, A. (1982). Survey and census of howler monkeys (*Alouatta palliata*) in the rain forest of "Los Tuxtlas," Veracruz, Mexico. *Am. J. Primatol.* 2: 363-372.
- Fedigan, L. M. (1986). Demographic trends in the *Alouatta palliata* and *Cebus capucinus* populations of Santa Rosa National Park, Costa Rica. In Else, J. G., and Lee, P. C. (eds.), *Primate Ecology and Conservation, Vol. 2*, Cambridge University Press, Cambridge, pp. 287-293.
- Fedigan, L. M., and Rose, L. M. (1995). Interbirth intervals in three sympatric species of Neotropical monkey. *Am. J. Primatol.* 37: 9-24.
- Fedigan, L. M., Fedigan, L., and Chapman, C. A. (1985). A census of *Alouatta palliata* and *Cebus capucinus* in Santa Rosa National Park, Costa Rica. *Brenesia* 23: 309-322.
- Fedigan, L. M., Rose, L. M., and Morera Avila, R. (1996). See how they grow: Tracking capuchin monkey populations in a regenerating Costa Rican dry forest. In Norconk, M., Rosenberger, A., and Garber, P. (eds.), *Adaptive Radiations of Neotropical Primates*, Plenum, New York.
- Fleming, T. H. (1986). Secular changes in Costa Rican rainfall: correlation with elevation. *J. Trop. Ecol.* 2: 87-91.
- Fleming, T. H., Williams, C. F., Bonaccorso, F. J., and Herbst, L. H. (1985). Phenology, seed dispersal, and colonization in *Muntingia calabura*, a Neotropical pioneer tree. *Am. J. Bot.* 72: 383-391.
- Foster, R. B., and Brokaw, N. V. L. (1982). Structure and history of the vegetation of Barro Colorado Island. In Leigh, E. G., Rand, A. S., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest Seasonal Rhythms and Long-Term Changes*, Smithsonian Institution Press, Washington, DC, pp. 67-81.
- Freese, C. (1976). Censusing *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus* in the Costa Rican dry forest. In Thorington, R. W., and Heltne, P. G. (eds.), *Neotropical Primates: Field Studies and Conservation*, National Academy of Sciences, Washington, DC, pp. 4-9.
- Froehlich, J. W., and Thorington, R. W., Jr. (1982). The genetic structure and socioecology of howler monkeys (*Alouatta palliata*) on Barro Colorado Island. In Leigh, E. G., Rand, A. S., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest Seasonal Rhythms and Long-Term Changes*, Smithsonian Institution Press, Washington, DC, pp. 291-305.
- Froehlich, J. W., Thorington, R. W., Jr., and Otis, J. S. (1981). The demography of howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. *Int. J. Primatol.* 2: 207-235.
- Gebhardt, K. (1994). *Seedling Development of Four Tree Species in Secondary Tropical Forest in Guanacaste, Costa Rica*, Ph.D. thesis, Uppsala University, Uppsala.
- Gebo, D. L. (1992). Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. *Am. J. Primatol.* 26: 277-290.
- Glander, K. E. (1978). Howling monkey feeding behavior and plant secondary compounds: A study of strategies. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington, DC, pp. 561-573.
- Glander, K. E. (1980). Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.* 53: 25-36.
- Glander, K. E. (1981). Feeding patterns in mantled howling monkeys. In Kamil, A. C., and Sargent, T. D. (eds.), *Foraging Behavior: Ecological, Ethological, and Psychological Approaches*, Garland Press, New York, pp. 231-257.

- Glander, K. E. (1992). Dispersal patterns in Costa Rican mantled howling monkeys. *Int. J. Primatol.* 13: 415-436.
- Glander, K. E., Fedigan, L. M., Fedigan, L., and Chapman, C. (1991). Capture techniques for three species of monkeys in Costa Rica. *Folia Primatol.* 57: 70-82.
- Glanz, W. E. (1982). The terrestrial mammal fauna of Barro Colorado Island: Census and long-term changes. In Leigh, E. G., Rand, A. S., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest Seasonal Rhythms and Long-Term Changes*, Smithsonian Institution Press, Washington, DC, pp. 455-468.
- Hartshorn, G. S. (1978). Tree falls and tropical forest dynamics. In Tomlinson, P. B., and Zimmerman, M. H. (eds.), *Tropical Trees as Living Systems*, Academic Press, New York, pp. 617-638.
- Heltne, P. G., Turner, D. C., and Scott, N. J., Jr. (1976). Comparison of census data on *Alouatta palliata* from Costa Rica and Panama. In Thorington, R. W., Jr., and Heltne, P. G. (eds.), *Neotropical Primates: Field Studies and Conservation*, National Academy of Sciences Press, Washington, DC, pp. 10-19.
- Janzen, D. H. (1979). New horizons in the biology of plant defenses. In Rosenthal, G. A., and Janzen, D. H. (eds.), *Herbivores. Their Interactions with Secondary Plant Metabolites*, Academic Press, New York, pp. 331-350.
- Janzen, D. H. (1982). Natural history of guacimo fruits (Sterculiaceae: *Guazuma ulmifolia*) with respect to consumption by large mammals. *Am. J. Bot.* 69: 1240-1250.
- Janzen, D. H. (ed.) (1983a). *Costa Rican Natural History*, University of Chicago Press, Chicago.
- Janzen, D. H. (1983b). No part is an island: Increase in interference from outside as park size decreases. *Oikos* 41: 402-410.
- Janzen, D. H. (1986a). Guanacaste National Park: Tropical ecological and cultural restoration. Fundacion de Parques Nacionales, Editorial Universidad Estatal Distancia, San Jose, Costa Rica.
- Janzen, D. H. (1986b). The external internal threat. In Soule, M. E. (ed.), *Conservation Biology: The Science of Scarcity and Diversity*, Sinauer Associates, Sunderland, MA, pp. 286-303.
- Janzen, D. H. (1988). Management of habitat fragments in a tropical dry forest: growth. *Ann. MO. Bot. Garden* 75: 105-116.
- Janzen, D. H., and Hallwachs, W. (1995). Indicative weather data for the Santa Rosa area and Volcan Cacao, Unpublished manuscript.
- Jones, C. B. (1980). The functions of status in the mantled howler monkey, *Alouatta palliata*: Intraspecific competition for group membership in a folivorous Neotropical primate. *Primates* 21: 389-405.
- LaRose, F. (1996). *Foraging Strategies, Group Size, and Food Competition in the Mantled Howler Monkey, Alouatta palliata*, Unpublished Ph.D. dissertation, University of Alberta, Alberta.
- Liebow, E. (1993). "Debt for nature" exchanges. In Aramubulo, P., III (ed.), *Primates of the Americas: Strategies for Conservation and Sustained Use in Biomedical Research*, Battele Press, Columbus, OH, pp. 107-116.
- Lippold, L. K. (1988). A census of primates in Cabo Blanco Absolute Nature Reserve, Costa Rica. *Brenesia* 29: 101-105.
- Lippold, L. K. (1989). A wet season census of primates at Cabo Blanco Absolute Nature Reserve, Costa Rica. *Brenesia* 31: 93-97.
- Milton, K. (1978). Behavioral adaptations to leaf-eating by the mantled howler monkey (*Alouatta palliata*). In Kamil, A. C., and Sargent, T. D. (eds.), *Foraging Behavior: Ecological, Ethological, and Psychological Approaches*, Garland Press, New York, pp. 535-549.
- Milton, K. (1979). Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. *Am. Nat.* 114: 362-378.
- Milton, K. (1980). *The Foraging Strategies of Howler Monkeys: A Study in Primate Economies*, Columbia University Press, New York.
- Milton, K. (1982). Dietary quality and population regulation in a howler monkey population. In Leigh, E. G., Rand, A. S., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest*

- Seasonal Rhythms and Long-Term Changes*, Smithsonian Inst. Press, Washington, DC, pp. 273-289.
- Milton, K. (1996). Effects of bot fly (*Alouattamyia baeri*) parasitism on a free-ranging howler monkey (*Alouatta palliata*) population in Panama. *J. Zool. Lond.* 239: 39-63.
- Mittermeier, R. A. (1972). Group activity and population dynamics of the howler monkey on Barro Colorado Island. *Primates* 14: 1-19.
- Mittermeier, R. A., and Cheney, D. L. (1987). Conservation of primates and their habitats. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 477-490.
- Mittermeier, R. A., and van Roosmalen, M. G. M. (1981). Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia Primatol.* 36: 1-39.
- National Research Council, Subcommittee on Conservation of Natural Populations (1981). *Techniques for the Study of Primate Population Ecology*, National Academy Press, Washington, DC.
- Otis, J. S., Froehlich, J. W., and Thorington, R. W., Jr. (1981). Seasonal and age-related differential mortality by sex in the mantled howler monkey (*Alouatta palliata*). *Int. J. Primatol.* 2: 197-206.
- Peres, C. (1997). Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: A case study of howler monkeys (*Alouatta* spp.). *Folia Primatol.* 68: 199-222.
- Richard, A. F. (1985). *Primates in Nature*, W. H. Freeman, New York.
- Rodríguez-Luna, E., Cortés-Ortiz, L., Mittermeier, R., and Rylands, A. (eds.) (1966). *Plan de Acción para los Primates Mesoamericanos*, IUCN/SSC Specialist Primate Group, Xalapa, Veracruz, Mexico.
- Rylands, A. B., Mittermeier, R. A., and Rodríguez-Luna, E. (1995). A species list for the New World primates (Platyrrhini): Distribution by country, endemism, and conservation status according to the Mace-Land system. *Neotrop. Primates* 3 (Suppl.): 113-164.
- Scott, N. J., Jr., Malmgren, L. A., and Glander, K. E. (1978). Grouping behavior and sex ratio in mantled howling monkeys. In Chivers, D., and Herbert, J. (eds.), *Recent Advances in Primatology, Vol. 1*, Academic Press, New York, pp. 183-185.
- Smith, C. C. (1977). Feeding behavior and social organization in howling monkeys. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, Academic Press, London, pp. 97-126.
- Stoner, K. E. (1994). Population density of the mantled howler monkey (*Alouatta palliata*) at La Selva Biological Reserve, Costa Rica: A new technique to analyze census data. *Biotropica* 26: 332-340.
- Stoner, K. E. (1996). Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. *Int. J. Primatol.* 17: 1-30.
- Sokal, R. R., and Rohlf, F. J. (1981). *Biometry*, 2nd ed., W. H. Freeman, New York.
- Sun, M. (1988). Costa Rica's campaign for conservation. *Science* 23: 1366-1369.
- Systat, Inc. (1992). *Systat for Windows: Statistics, Version 5 Edition*, Systat, Inc., Evanston, IL.
- Tomblin, D. C., and Cranford, J. A. (1994). Ecological niche differences between *Alouatta palliata* and *Cebus capucinus* comparing feeding modes, branch use, and diet. *Primates* 35: 265-274.
- Wallace, D. R. (1992). *The Quetzal and the Macaw: The Story of Costa Rica's National Parks*, Sierra Club Books, San Francisco.
- Webb, L. J., Tracey, J. G., and Williams, W. T. (1972). Regeneration and pattern in the subtropical rainforest. *J. Ecol.* 60: 675-696.