Population Characteristics of Howlers: Ecological Conditions or Group History

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We examined the relative importance of ecological parameters—habitat productivity and seasonality—and group history—episodic predation, disease, and sudden habitat deterioration—to explain variation in the density and group structure of howlers (Alouatta spp.). We use data from a census of Guanacaste National Park, Costa Rica, and a literature review characterizing 80 howler populations. In Guanacaste National Park both habitat type and degree of protection affect howler density and group structure. Howlers were found at the highest density and in the largest groups in areas of semievergreen forest, which ecological sampling indicates have the most consistent level of food production. Differences in density between the sector of the park that first received protected status and more recently protected areas may be due partially to the degree of protection the areas received. We test the prediction that howler density and group structure would be influenced by habitat productivity as indexed by rainfall. Average group size and sex ratios differ among species, but female-to-immature ratios do not. Considering all censuses at one site to be independent, there are significant interspecific differences in density, with Alouatta pigra occurring at lower densities than the other species. In spite of such variability, there is no relationship between annual rainfall and howler density, and rainfall had a variable effect on group size depending on the level of independence that was considered. While such ecological comparisons are unrefined, e.g., rainfall must be used as a surrogate for habitat production, the fact that so few relationships were documented suggests that factors other than the ecological factors considered here are responsible for the observed differences in population characteristics. We suggest that much of the variability in howler population characteristics is related to events occurring in the recent

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history of the groups, such as habitat alteration, hunting, food tree crop failure, and disease.

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INTRODUCTION

In general, there is little quantitative evidence of how ecological or demographic parameters influence the structure of primate populations (Altmann and Altmann, 1979; Dittus, 1980; Glander, 1980, 1992; Milton, 1982; Crockett and Rudran, 1987a; Butynski, 1990; Isbell, 1990). However, food abundance (Dittus, 1980; Milton, 1980, 1982; Froehlich *et al.*, 1981; Crockett, 1985) and the number of competing primate species (Struhsaker, 1978; Eisenberg, 1979; Crockett, 1985) have traditionally been thought to limit primate density and thereby influence the structure of the population.

Quantification of primate communities separated either by only a few kilometers (Butynski, 1990; Chapman and Fedigan, 1990; Chapman *et al.*, 1997) or by much larger geographical distances (McKey, 1978; Oates *et al.*, 1990; Davies, 1994; Peres, 1997a,b) have typically shown large differences in the composition of the primate communities and the structure of forests, regardless of the scale of measurement. This suggests that there exists sufficient variation in forest composition to account for differences in the structures of the primate populations that inhabit them. However, researchers have increasingly become aware of the potential for a variety of other factors to influence population characteristics and social structure (Altmann and Altmann, 1979; Dunbar, 1979; Crockett, 1985, 1996; Butynski, 1990; Olupot *et al.*, 1994; Peres, 1997a,b). For example, at the onset of a long-term study of red howlers (*Alouatta seniculus*) in Venezuela, initial differences in mean troop size, adult male composition, and sex ratio existed between populations in two types of forest. An initial obvious interpretation would have been to attribute these population differences to differences in the ecological conditions of the different forests. However, continuing observations at the site revealed that the differences were at least in part due to the fact that the populations were at different phases of population growth (Crockett, 1984, 1985, 1996; Crockett and Eisenberg, 1987; Crockett and Rudran, 1987a,b).

Butynski (1990) provides a second example. He studied two populations of blue monkeys (*Cercopithecus mitis*) separated by 10 km in Kibale National Park, Uganda, and quantified the food available to each population. While there was a 10-fold difference in blue monkey densities, indices of food availability and competition suggested that food was more available

at the low-density site than the high-density site. Thus, the availability of food did not explain why blue monkey densities differed between the two sites, and Butynski attributed the low density of one subpopulation to some unknown historical event, such as a disease outbreak.

Isbell (1990) documented a sudden and short-term increase in suspected annual predation rates on vervet monkeys (*Cercopithecus aethops*) from 11 to 45%. Such episodic increases in predation as suggested by Isbell (1990) or periodic disease outbreaks as suspected by Butynski (1990) could dramatically influence group sizes and population densities.

We examined the relative importance of ecological parameters, e.g., habitat productivity, and demographic history, e.g., episodic predation, disease, or sudden habitat deterioration, in explaining variation in the density and group structure of howlers (*Alouatta* spp.). We use data from a census of Guanacaste National Park, Costa Rica, and a literature review which characterizes 80 howler populations. We censused howlers (*A. palliata*) in Guanacaste National Park between May 1987 and February 1988 and June and July 1989 (Chapman *et al.,* 1989). Largely because of the elevational change in the park–sea level to the tops of 1659-m volcanoes—a wide range of habitats is available in a small geographical area. We recorded population characteristics for neighboring howler groups in four types of habitats that are ranked by productivity and show different degrees of seasonal change.

We predicted that howler density and group structure would be influenced by the productivity of the habitat. Unfortunately, there are only limited data available on habitat productivity from different types of tropical forests (Richards, 1996). The studies that are available suggest that habitats with more rainfall have higher levels of productivity than areas with less rainfall. For example, the annual net primary productivity for dry forest averages 50–75% of that of wet forest (Hartshorn, 1983; Murphy and Lugo, 1986). Similarly, in dry forests the total plant biomass ranges between 78 and 320 tons/ha, while in wet forest, the biomass ranges between 269 and 1186 tons/ha (Murphy and Lugo, 1986). Furthermore, the total plant biomasses of desert (5.8 tons/ha) and wooded savanna habitats (30 tons/ha) are considerably less than those of forested habitats (Robin and Bazilevich, 1967). Corresponding to the increase in plant biomass associated with increased rainfall, researchers have frequently documented a positive relationship between rainfall and the diversity of the plant community. For example, Hall (1977) and Hall and Swaine (1976, 1981) documented patterns of plant diversity in Nigeria and Ghana and found that in areas where annual precipitation is ≥ 1750 mm, one can find ≤ 200 plant species in a 25×25-m plot. As areas become drier, the species richness declines, so that in areas that receive between 1500 and 1750 mm of

rain a year, there are often ≤170 species in a 25 × 25-m plot, and areas receiving between 1250 and 1500 mm of rain per year harbor between 40 and 100 plant species. Based on such studies, we index habitat productivity by annual rainfall.

It seems possible that population characteristics are determined not only by the total productivity of a habitat but also by the seasonal availability of habitat productivity. For example, considering that in dry deciduous forests, the dry season can extend for ≤6 months, during which time little if any rain falls and 60 to 75% of the trees lose their leaves (Frankie et al., 1974; Hubbell, 1979), one might expect that primate biomass would decrease with increasing seasonality.

Without long-term monitoring of a number of populations, it is difficult to evaluate the possible impact on howler populations of episodic events such as a sudden increase in predation rates, disease outbreaks, elevated hunting pressure, or rapid habitat degradation. To examine the possible importance of such factors, we review selected long-term studies on howlers and contrast populations that have been well protected for several generations within a national park to populations outside the park boundaries.

METHOD

Census

Guanacaste National Park extends from sea level to the tops of two volcanoes [1659 m (Janzen, 1986)], and the climate varies considerably depending on location in the park. In the lowlands, the dry season extends from approximately December to late May, and rainfall averages 1400 mm per year. In high-altitude volcano areas, the dry season is shorter and annual rainfall increases with altitude: at 600 m approximately 224 mm of rain fell in adjacent slopes outside of the park. Guanacaste National Park contains virtually all of the major types of dry forest habitat endemic to Central America. The most predominant forest habitat in the park is dry semideciduous forest. The majority of the trees in this type of forest drop their leaves soon after the last rains of the season and remain bare throughout much of the dry season. In several locations in the park, there are patches of nearly pristine semievergreen forest where many of the trees maintain their leaves throughout much of the dry season. The park contains several temporary and permanent rivers. These riverine areas contain strips of relatively lush vegetation and serve as important refuges for many animals throughout the dry season (Janzen, 1986). Nearly pristine forest is

found on the slopes of the volcanoes. Near the tops of the volcanoes (>1000 m) the forest is covered by cloud for most of the year, and cloud forest predominates (Janzen, 1986). Within the recently declared Guanacaste National Park is the Santa Rosa Sector, which received protected status of a national park in 1971, many years before the remainder of the part was protected. Protection of many areas started around 1986 (Janzen, 1986).

We conducted the census between May 1987 and February 1988 and in June and July 1989, for a total of 128 person-days of effort. We sampled routes of a known length throughout the park. We counted all howler groups encountered along these strips and noted the age and sex of each member. We sampled many routes several times during the study. To minimize the possibility of considering repeat counts of one group seen in different areas on different days as being separate groups, we determined whether a new sighting was within the area covered by an average group's home range. The size of an average group's home range was determined from previous work by Chapman (1989). To reduce this possibility further, we attempted to identify one or two individuals in each group, so that they could be distinguished from one another. The majority of the counts of neighboring groups are not similar, hence repeat counts were not considered to be a serious problem. However, if two neighboring groups had similar compositions, we attempted to recensus the area and to locate both groups on the same day.

It is extremely difficult to make accurate estimates of primate densities over large areas. Accordingly, the nature of this survey precludes the distinction between low densities and the absence of monkeys in an area. In addition, we visited only areas where large sections of forest were known to exist. Thus, isolated populations may be underrepresented. These sources of error contribute to inaccuracy in the absolute density estimates; however, for comparing relative densities between different areas or different forests, it should have little effect. We calculated the area covered by forest from 1:50,000 maps. Counts for the Santa Rosa Sector of the park are from Fedigan et al. (1985) and Fedigan (1987).

We noted the forest type for each group. However, many of the groups probably had home ranges that encompass several forest types. For example, groups that are found along riverine strips often make excursions into areas of dry forest. Since the proportion of each group's home range that is composed of the different forest types is unknown, we provide a description of the average density and group characteristics of groups located in the different forest types; however, we do not make statistical contrasts between forest types.

We quantified phenological patterns and seasonal changes in food abundance in three types of forest in the Santa Rosa Sector. To determine the density of trees in the different types of forest we used three 4-ha grids (10 × 10-m cell size), one in each of the different habitats. In each grid we identified all individuals of 29 potential food tree species and mapped their locations [>10-cm diameter at breast height (dbh) (Chapman and Chapman, 1990)]. The howler study group in this area spent 81% of their feeding time eating food items from these 29 tree species. To determine the phenological cycling of each species, we examined all trees once every 3 weeks during field seasons between 1984 and 1988 (36 months of observation).

To examine the possible importance of group history, we contrast populations that had been well protected for several generations within the Santa Rosa section of the park with populations outside this sector in Guanacaste National Park, which at the time of the census had just recently received protected status.

Literature Review

We reviewed published reports on population characteristics of howlers and descriptions of the ecological conditions of the areas that they inhabit. We considered the following variables: density, mean group size, sex ratio, ratio of adult females to immatures, and annual rainfall. We determined annual rainfall from either the original studies or subsequent publications by the same authors or by different authors studying in the same area.

This compilation contains several potential shortcomings typically associated with such surveys. (1) The studies are not equally divided among species: of the estimates of population characteristics, 49% are from studies of *Alouatta palliata*, 37.5% from *A. seniculus*, and only 10 and 4% from *A. pigra* and *A. caraya*, respectively. We found no estimate of population characteristics of *A. beizebul* or *A. fusca*. (2) Many of the counts are from areas that had been modified by human activities. Since human disturbances preferentially occur in certain types of habitats, it is difficult to separate differences in population characteristics occurring as a result of human interference from those occurring as a result of natural variation in environmental parameters. (3) Many of the studies provide a density estimate or data from which a density estimate could be derived but are unclear about whether the value represents ecological density (numbers/usable forest) or crude density (numbers/total area regardless whether howlers use the entire area). When it was possible to distinguish between crude and ecological density, we used only ecological density. In some

cases, authors reported crude density, though the information to calculate ecological density was available. In these cases we calculated the ecological density for the study. (4) The level at which one should consider different spatial and temporal descriptions of populations to be statistically independent is difficult to determine. For example, should descriptions of populations that are widely separated geographically, but are within the same forest, be considered independent? Similarly, at what temporal scale should multiple descriptions at the same location be considered independent? Ideally it would be desirable to have independent criteria for assessing independence; however, this will have to wait until additional studies are available.

We take two approaches. First, we consider the different researchers' criteria to be sufficient. We considered studies at what the researchers considered to be unique sites to be spatially independent. If the researcher describing the same population at different times considered the separate censuses to be sufficiently temporarily separated to make the descriptions we considered them to be independent. Second, we considered multiple descriptions at the same location made at different times not to be independent, and we averaged them to produce one value for the site.
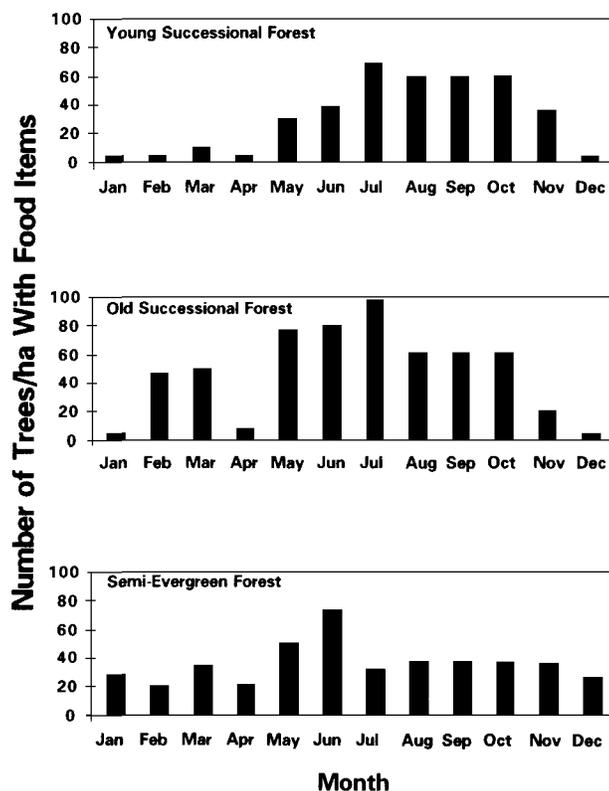
RESULTS

Census of Guanacaste National Park

Howlers live in most of the major forested areas of Guanacaste National Park. In general, all howler groups inhabited areas which contained at least some evergreen, semievergreen, or riverine forest. However, some of the areas used by howlers contained patches of semievergreen forest that are estimated to be as small as 1 ha.

Howlers are at the highest density in areas of semievergreen forest (Table I). In a 4-ha semievergreen grid in the Santa Rosa Sector, only 6 of the 29 plant species were without leaves for >1 month of the dry season. In addition, semievergreen forest had a more consistent level of food production than that of dry deciduous forest (Fig. 1). Riverine and montane forest areas had the second and third highest howler densities, respectively. Unfortunately, no quantitative data are available on the phenology of trees in these habitats. The density of howlers was lowest in areas of dry deciduous forest. Fruit production therein exhibits considerable monthly variation. Between May and November there was an abundance of fruit in dry deciduous forest, but in December, January, and April, fruit was scarce (Fig. 1). In addition, 60–75% of trees lose their leaves in the dry season (Frankie

Table I. Population Characteristics of Howler Groups Found in Different
Habitats in Guanacaste National Park, Costa Rica (Density, Individuals/km^2)

	Density	Group size	Sex ratio	Female:immature
Semievergreen	24.3	19.0	1:1.71	1:0.74
Riverine	10.1	5.4	1:1.73	1:0.69
Montane	4.0	3.5	1:1.50	1:0.50
Dry deciduous	2.7	12.1	1:2.22	1:0.88

Fig. 1. The number of trees per hectare bearing food items
available per month in dry deciduous forest and pristine
semievergreen forest in the Santa Rosa Sector of Guanacaste
National Park, Costa Rica. Two sampling areas in dry deciduous
forest are depicted: (1) young successional forest partially cleared
for fence posts 45 years ago (top) and (2) old successional forest
partially cleared 75–100 years ago (middle).

et al., 1974). This suggests that in the dry season, howlers that are limited exclusively to dry deciduous forest may experience food shortages. We recorded behavioral and demographic data on one group of howlers in the Santa Rosa sector between 1983 and 1989 (Chapman, 1988). They had access to nearly pristine semievergreen, old successional dry deciduous forest (75–100 years of regrowth), and young regenerating dry deciduous forest [40 years of regrowth following the extensive clearing of the area for fence posts (D. H. Janzen, personal communication)]. The use of semievergreen forest represented 50% of the observations for this group, while this forest type represented only 12% of the group's home range. This use of habitat differed significantly from what would be expected if the group used habitats in proportion to the area of each habitat type ($\chi^2 = 7.12$, $P < 0.05$).

The mean size of howler groups was largest in areas of semievergreen forest (Table I), reaching a maximum size of 44 individuals. Groups in dry deciduous forest were on average the second largest, followed by riverine and montane groups. There were fewer males per female in the dry deciduous forest, while the least skewed sex ratio in the groups occurred on the slopes of the volcanoes. The female-to-immature ratio did not differ considerably among habitats (Table I).

Different areas within Guanacaste National Park have experienced different degrees of human interference. The majority of the park started to receive protection around 1986; however, the Santa Rosa sector has been a national park since 1971. During much of the 25 years that Santa Rosa has been a park, efforts have been made to prevent poaching and more recently to protect the forest from fires. This protection has undoubtedly contributed to the fact that the ecological density of howlers in the Santa Rosa Sector was 7.6 times that of the remainder of Guanacaste National Park, and the crude density in the Santa Rosa sector was 15.2 times that in the rest of the park. Similarly, groups were larger in the Santa Rosa sector than in the remainder of the park (mean group size, Santa Rosa = 14.7, GNP = 4.4; $t = 4.04$, $P = 0.003$). However, neither the sex ratio ($t = 1.25$, $P = 0.22$) nor the ratio of adult females to immatures ($t = 0.27$, $P = 0.79$) differed between the Santa Rosa Sector and the rest of Guanacaste National Park (Table II).

Literature Review

Studies of howlers have been conducted from Mexico to Argentina, in habitats receiving as little as 1350 mm of rain annually to as much as 4953 mm a year (Table III). Howlers have been studied from sea level up to 2300 m and inhabit areas in which they are the only primate present, as

Table II. Population Characteristics of Howler Groups in the Santa Rosa
Sector and in the Remainder of Guanacaste National Park, Costa Rica

	Group size*	Sex ratio	Female:immature
Santa Rosa Sector	14.7	1:1.76	1:0.60
Guanacaste National Park	4.4	1:2.10	1:0.46

*$P < 0.05$.

well as areas where there are as many as 11 other primate species. Density estimates range from 0.80 to 150 individuals/km^2, with an average of 49 individuals/km^2 [in quantitative analyses, the estimate of 1050 individuals/km^2 derived from the study of Baldwin and Baldwin (1972, 1976) was omitted]. The average size of the howler groups varied between 2 and 23 members, with an average of 10.7 animals; however, groups as large as 44 individuals have been reported by Fedigan et al. (1985), and Chapman (1988, 1989). Similarly, the proportion of males to females ranges from 1:0.71 to 1:4.11 and the female-to-immature ratio varies from 1:0 to 1:1.8 (Table III).

Average group size differs among species, with Alouatta palliata having larger groups than any of the other species (Scheffe, <0.05; Table IV). Similarly, groups of Alouatta palliata have proportionately fewer males per female than either A. pigra or A. seniculus do (Table IV). However, across all species, there is a positive relationship between group size and sex ratio ($r = 0.50$, $P < 0.001$). Thus, the differences observed in sex ratio among Alouatta palliata and A. seniculus and A. pigra may be an artifact of the larger groups found in A. palliata. Among the Alouatta species there is no significant difference in female-to-immature ratios. Considering all censuses at one site to be independent, there are significant differences in the densities of the different species, with Alouatta pigra (Scheffe, <0.05) occurring at lower densities than the other species (Table IV). However, when the averages of multiple censuses are used as independent points, there is no difference in the densities of the species.

Based on the speculation that habitat productivity increases with rainfall (Murphy and Lugo, 1986), we predicted a positive relationship between annual rainfall and howler density. This prediction is not supported by the data (multiple censuses at one site considered independently, $r = -0.222$, $P = 0.175$; multiple censuses at one site averaged, $r = 0.285$, $P = 0.252$). Indeed, the direction of the relationship is opposite to that which we predicted.

One might predict that more productive habitats would support larger groups than less productive sites would. Two studies on Barro Colorado Island, Panama, and a study in Santa Rosa National Park suggest that the

Table III. Population Characteristics of Howlers (*Alouatta* spp.) Derived from a Literature Review[a]

Species	Density	Group size	Sex ratio	F:imm	Rainfall	Source and location
A. palliata	4.9	13.60	0.97	0.56	1531	Fedigan et al. (1985); Santa Rosa, Costa Rica
A. palliata	1.2	8.13	2.20	0.79	1531	Freese (1976); Santa Rosa, Costa Rica
A. palliata	89.7	13.77	2.38	0.78	1878	Rodriguez (1985); Palo Verde, Costa Rica
A. palliata	—	5.20	1.60	0.21	—	Milton and Mittermeier (1977); Coiba, Panama
A. palliata	1050.0	18.90	2.00	0.88	—	Baldwin and Baldwin (1972, 1976); Chirique, Panama
A. palliata	77.3	15.50	2.98	0.57	1450	Clarke et al. (1986); La Pacifica, Costa Rica
A. palliata	23.3	9.12	1.37	0.75	4953	Estrada (1982); Los Tuxtlas, Mexico
A. palliata	74.3	13.20	4.11	0.54	1450	Heltne et al. (1976); La Pacifica, Costa Rica
A. palliata	74.3	10.00	1.16	0.86	1450	" " "
A. palliata	74.3	12.50	3.00	0.75	1450	" " "
A. palliata	—	15.40	3.00	0.67	1450	" Toboga, Costa Rica
A. palliata	—	13.50	2.78	0.75	1450	" " "
A. palliata	—	10.00	2.92	0.76	1450	" " "
A. palliata	—	8.90	1.88	0.77	1450	" " "
A. palliata	—	13.10	2.13	0.54	1450	" " "
A. palliata	—	10.40	1.68	0.38	1450	" " "
A. palliata	—	10.80	2.89	0.31	1450	" " "
A. palliata	—	11.30	2.18	0.86	1450	" " "
A. palliata	—	9.90	1.94	0.80	1450	" " "
A. palliata	12-19	13.75	—	—	4015	Fishkind and Susman (1987), La Selva, Costa Rica
A. palliata	27.0	17.30	2.74	0.96	2730	Carpenter (1934, 1962); BCI, Panama
A. palliata	33.5	17.40	2.74	1.04	2730	" " "
A. palliata	—	18.20	2.12	1.13	2730	" " "
A. palliata	16.2	8.00	3.75	0.47	2730	Collias and Southwick (1952); BCI, Panama
A. palliata	52.5	18.50	2.76	0.65	2730	Carpenter (1934, 1962); BCI, Panama
A. palliata	62.7	14.70	1.79	0.89	2730	Chivers (1969); BCI, Panama
A. palliata	75.8	13.80	2.41	0.56	2730	Smith (1977); BCI, Panama
A. palliata	62.6	16.20	1.81	1.22	2730	Mittermeier (1973); BCI, Panama
A. palliata	91.7	20.80	2.63	0.88	2730	Milton (1982); BCI, Panama
A. palliata	—	23.00	2.34	1.16	2730	" " "
A. palliata	—	21.40	2.18	1.07	2730	" " "
A. palliata	82.2	20.20	2.55	1.16	2730	" " "
A. palliata	—	18.90	2.24	1.09	2730	" " "
A. palliata	—	18.70	2.50	1.09	2730	" " "
A. palliata	—	20.40	2.30	0.94	2730	" " "
A. palliata	—	18.90	2.55	0.98	2730	" " "
A. palliata	—	21.30	2.15	1.14	2730	" " "
A. palliata	—	16.50	2.30	0.93	2730	Bernstein (1964); BCI, Panama
A. palliata	—	9.30	1.71	0.66	2730	Altmann (1959); BCI, Panama
A. pigra	8.1	4.20	1.00	0.73	2032	Bolin (1981); Belize
A. pigra	22.0	6.22	1.27	—	2030	Horwich (1983); Belize
A. pigra	—	6.30	1.60	1.08	2032	Horwich and Johnson (1986); Belize
A. pigra	—	4.67	2.00	0.83	—	Horwich and Johnson (1986); El Jova, Mexico
A. pigra	—	5.00	2.00	1.00	1350	" Guatemala
A. pigra	5.0	6.25	1.16	1.71	1350	Coelho et al. (1976); Tikal, Guatemala
A. pigra	4.0	5.00	1.33	0.75	1350	Schlichte (1978); Tikal, Guatemala
A. pigra	13.0	5.50	2.50	0.80	—	Schlichte (1978); Coban, Guatemala
A. seniculus	23.0	5.75	1.14	1.00	2100	Defler (1981); Colombia
A. seniculus	27.0	6.80	1.15	0.75	—	Defler (1981); Colombia
A. seniculus	114.0	7.50	0.71	1.00	—	Neville (1972); Trinidad
A. seniculus	15.0	9.00	1.25	1.80	1947	Gaulin and Gaulin (1982); Colombia
A. seniculus	21.9	3.30	1.97	0.56	2705	Green (1978); Colombia
A. seniculus	20.4	3.30	—	0.00	2705	" "
A. seniculus	30.0	—	—	—	2080	Terborgh (1983); Manu, Peru
A. seniculus	15.0	5.00	—	—	3050	Neville (1976); Peru
A. seniculus	2.7	5.40	1.20	0.60	—	Izawa (1976); Upper Amazon
A. seniculus	—	5.40	1.59	0.79	—	Izawa (1976); Upper Amazon
A. seniculus	30.5	5.40	—	—	—	Freese et al. (1982); Peru/Bolivia
A. seniculus	24.0	5.40	—	—	—	" "
A. seniculus	8.0	8.00	—	—	—	" "
A. seniculus	120.0	19.00	—	—	—	" "
A. seniculus	20.3	5.00	1.43	0.80	—	Klein and Klein (1976); Colombia
A. seniculus	25.6	6.30	—	0.92	1424	Braza et al. (1981); El Frio, Venezuela

Table III. Continued

Species	Density	Group size	Sex ratio	F:imm	Rainfall	Source and location
A. seniculus	36.0	7.70	2.08	—	1693	Crockett (1984); Hato Masaguaral, Venezuela
A. seniculus	50.0	8.30	2.26	—	1693	Crockett and Eisenberg (1987); Venezuela
A. seniculus	53.0	7.80	1.93	—	1693	" "
A. seniculus	85.0	8.70	1.80	—	1693	Eisenberg (1979); Hato Masaguaral, Venezuela
A. seniculus	150.0	8.90	1.47	1.64	1693	Rudran (1979); Hato Masaguaral, Venezuela
A. seniculus	112.0	10.50	1.81	—	1693	Crockett (1984); Hato Masaguaral, Venezuela
A. seniculus	115.0	9.70	1.70	—	1693	Crockett and Eisenberg (1987); Venezuela
A. seniculus	180.0	9.10	1.83	—	1693	Crockett and Eisenberg (1987); Venezuela
A. seniculus	—	6.90	1.62	1.00	1693	Neville (1972, 1976); Hato Masaguaral, Venezuela
A. seniculus	—	8.50	1.60	1.38	1693	" " "
A. seniculus	—	8.80	1.50	1.33	1693	" " "
A. seniculus	—	7.90	1.78	1.44	1693	" " "
A. seniculus	—	9.00	1.08	1.57	1693	" " "
A. seniculus	—	9.00	2.12	1.29	1693	" " "
A. caraya	130.0	8.05	2.02	—	1400	Thorington et al. (1984); Argentina
A. caraya	—	7.90	0.88	0.69	—	Pope (1966/68); Argentina
A. caraya	0.8	2.00	—	—	—	" "

[a]Density, individuals/km^2; sex ratio, females per male, F:imm, adult female/all immatures; annual rainfall, mm.

size of groups of *Alouatta palliata* is related to food availability. Leighton and Leighton (1982) showed that the size of feeding aggregates is related to the size of the food patch and Gaulin *et al.* (1980) found a relationship between the size of howler groups and the density of food resources. Chapman (1989) predicted the size of foraging subgroups from the density and distribution of food resources. When one considers multiple censuses at a single site as independent, as the annual rainfall increased, the size of howler groups increased ($r = 0.394$, $P = 0.001$). In contrast, when one averages repeat censuses at the same site, there is no relationship between rainfall and howler group size ($r = 0.120$, $P = 0.624$).

DISCUSSION

The howlers in Guanacaste National Park were at the highest density and in the largest groups in areas of semievergreen forest, which have the most consistent level of food production. This indicates that howlers may do better in less seasonal habitats. However, comparative studies of both folivorous lemurs (Ganzhorn, 1992) and *Alouatta* (Peres, 1997b) suggest that biomass increases with increasing seasonality. This suggests that the importance of seasonality may change depending on the scale that is being considered, and possibly the mechanisms behind the patterns may also change. On a continental or intercontinental scale, Ganzhorn (1992) proposed that clouds reduce irradiance and thus the rate of photosynthesis. Accordingly, he suggests that leaf quality might be negatively correlated

Table IV. Population Characteristics of Four Species of *Alouatta*[a]

Species	Density		Group size		Sex ratio		Female:immature	
	MC	MCA	MC	MCA	MC	MCA	MC	MCA
A. caraya	65.4	65.4	6.0	6.0	1.45	1.45	0.69	0.69
A. palliata	52.2	48.5	14.5	12.2	2.34	2.18	0.80	0.66
A. pigra	10.4	10.9	5.4	5.3	1.61	1.81	0.99	1.1
A. seniculus	55.6	34.0	7.6	7.1	1.59	1.36	1.05	0.93
F	3.93	0.96	27.2	6.37	10.5	3.82	2.52	1.98
P	0.02	0.43	<0.01	0.002	<0.01	0.03	0.07	0.15

[a]Density, individuals/km^2; sex ratio, males per female. MC, multiple censuses at one site conducted in different years are considered independently; MCA, multiple censuses at one site conducted in different years are averaged.

with annual cloud cover and possibly as a correlate, also rainfall. Alternatively, tree communities in less seasonal habitats could have a lower proportion of deciduous species. Deciduous trees may protect their leaves with toxins less than evergreen species do (Janzen, 1975; Davies, 1994), and they are often preferred food items of folivores, e.g., *Colobus guereza* (Oates, 1977). Thus, more seasonal environments may have food resources that are less protected and are of higher quality than those of more evergreen habitats. At a local scale, groups that have a mix of semievergreen and dry deciduous habitats may do best. The dry deciduous habitat may provide foods of generally higher quality (Janzen, 1975; Davies, 1994), while the semievergreen habitats may provide critical food resources during brief periods when food is scarce in the dry deciduous forest.

In general, we found few relationships between the environmental and the demographic parameters that we considered. Average group size and sex ratio differ among species, but the female-to-immature ratios does not. Considering all censuses at one site to be independent, there are significant differences in the densities of the different species, with *A. pigra* occurring at lower densities than those of the other species. In spite of such variability, there is no relationship between annual rainfall and howler density, and rainfall has a variable effect on group size depending on what level of independence is considered. While such ecological comparisons are unrefined, e.g., rainfall must be used as a surrogate for habitat productivity, the fact that so few relationships are documented suggests that factors other than the ecological factors considered here are responsible for differences in population characteristics.

We suggest that much of the variability in howler population characteristics is related to events occurring in the recent history of the groups, such as habitat alteration, hunting, food tree crop failure, or disease. The census of Guanacaste National Park demonstrates the importance of considering the history of the region in which a howler population is found. The differences in ecological and crude density estimates between the Santa Rosa sector and the rest of the park may be at least partially attributed to the increased protection that the Santa Rosa sector received. Much of the variability in population characteristics of howlers in different areas may be the result of events occurring in the recent history of the group. Similarly, researchers who have considered the conservation status of howlers have highlighted the importance of human interference, particularly hunting, in determining howler densities (Peres, 1997b; Crockett, 1998). Peres (1997b) documents that hunting has a profound impact on the abundance of all large-bodied neotropical primates and describes the decline in howler density which corresponds with an increase in hunting pressure.

Events such as failure of fruit crops (Foster, 1982; Milton, 1982), disease (Collias and Southwick, 1952), hunting (Peres, 1997b), and habitat alteration may largely determine many population characteristics for a considerable time following the event. Descriptions of the dynamic history of the howler population on Barro Colorado Island, Panama, clearly illustrate the degree to which a single population can vary in size. Long-term monitoring of the population since 1977 has shown fluctuations in the estimated population size for the island from 1500 animals to <900 individuals (Milton, 1996). Before these long-term data, a population crash was inferred to have occurred in 1951 as a result of a yellow fever epidemic (Collias and Southwick, 1962). In 1970 and 1971 a fruit crop failure on the island probably caused howlers to die in unusually high numbers. Foster (1982) attributed this fruit crop failure to an unusual seasonal weather pattern involving a short and wet dry season. Foster (1982) described similar wet dry seasons followed by fruit failures and signs of famine in the howler community in 1931 and 1958.

The documented dynamic nature of the howler population on Barro Colorado Island and the inferred dynamic nature suggested elsewhere caution against making generalizations about a population based on a single census. If a single census is the only data available, it would be valuable to present any additional information, such as evidence of hunting, descriptions of habitat alterations, fruit crop failures, and evidence of disease. It seems probable, however, that the only way to begin to understand the interaction among ecology, demographic history, and primate population structure is through long-term studies that record responses to such events.

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