Demographic Changes over Thirty Years in a Red Howler Population in Venezuela

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*During a 30-year span (1969–1999) the annual growth rate of a Venezuelan red howler (*Alouatta seniculus*) population fluctuated irregularly, but its size increased, remained stable for a short while, and finally declined sharply. The increase took place in three stages, and began as an increase in the size of established groups. The next two stages of population increase were due to the formation of new groups and their subsequent increases in size. These two stages likely occurred because of habitat regeneration, which increased the areas where newly formed groups could establish home ranges. The population decline of 74% was most likely due to disease. However, new groups died out more rapidly than established groups, indicating that food shortages, especially in recently regenerated areas, may also have contributed to the population crash. The food shortages could have been caused by unpredictable periods of drought, which may explain the irregular size fluctuations of the study population. Since many howler species show irregular size fluctuations and sharp declines, their demographic features may reflect adaptations to unpredictable events like droughts and disease epidemics. On this premise we explain the preponderance of unimale groups and female-biased birth sex ratios at low densities and the dispersal of both sexes as adaptations for increasing a population rapidly after a decline. Within the population, mortality of small juvenile females was higher in multimale than in unimale groups, though medium juvenile and older immature females were better represented*

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in multimale than in unimale groups. These results may be explained in terms of group composition and the mating systems in red howlers.

INTRODUCTION

The value of conducting long-term field studies to develop a thorough understanding of primate population dynamics cannot be overemphasized. Whether the motivation is applied, as when developing Population Viability Analysis models for conservation purposes (Caughley, 1994; Cowlishaw and Dunbar, 2000; Dobson and Lyles, 1989), or theoretical, as when formulating explanations for the evolution of taxon-specific life-history traits (Charnov and Berrigan, 1993; Ross, 1991), any successful attempt to understand population dynamics will have to be based on studies spanning several generations. Only then can we expect to determine how population fluctuations affect demographic parameters. Until we know the effect of population fluctuations and understand the processes driving these changes, we will not be able to fully explain the observed species-specific life-history strategy as an adaptive response to the environment.

Given the abundant literature demonstrating that numerous taxa show regular population fluctuations (Krebs, 1996), it is surprising that this topic has not received more attention in primate investigations. This lack of attention may have been due to two reasons. One is the popular misconception that was recently refuted by Chapman and Peres (2001), that the tropics, where most primates are found, are relatively stable, especially when compared to temperate areas where population fluctuations have been investigated most extensively (Stenseth, 1999). The other is that few primate field studies have lasted long enough to cover several generations (Dobson and Lyles, 1989) or to provide the basic information needed to describe population changes in detail.

In the Neotropics, the longest nonhuman primate field studies have been conducted on howlers (*Alouatta spp.*). All 6 species of howlers have been studied for various periods of time (Kinzey, 1997) since the pioneering work of Carpenter on *Alouatta palliata* at Barro Colorado Island, Panamá (Carpenter, 1934). The mantled howler (*Alouatta palliata*) and the red howler (*A. seniculus*) have been the two most intensively studied species with some of the studies spanning a few decades (Agoramoorthy and Rudran, 1995; Clarke *et al.*, 1986, 1994; Crockett, 1996; Eisenberg, 1979; Estrada, 1982; Estrada *et al.*, 1999; Fedigan *et al.*, 1998; Fedigan and Jack, 2001; Glander, 1992; Milton, 1996; Neville, 1972; Pope, 1990, 1998, 2000; Rudran,

1979; Sekulic, 1983). Using these long-term data some authors have hypothesized that their populations may undergo fluctuations (Crockett, 1996; Crockett and Eisenberg, 1986; Milton, 1982, 1996). We contribute to an evaluation of this hypothesis by describing changes in a red howler population in Venezuela during 30 years.

Between 1969 and 1999 the study population underwent periods of expansion, stability and decline. We characterize the different stages with data on the population's size, density, rate of increase, age structure, sex ratios, and group size and composition during each stage. The study, which includes data from approximately 5 generations of howlers, allows us to address the following questions about population dynamics: Was the rate of population increase relatively stable over time? Were population parameters, e.g., group size and sex ratios, related to population density? Did sex ratios of the different age-sex classes change during the population fluctuations in a predictable manner? Is the population recovering? Are changes in population parameters related to environmental factors?

METHODS

Study Area and Population

We conducted the study at Hato Masaguaral, a cattle ranch located in Guárico State, Venezuela (8° 34' N, 67° 35' W). Hato Masaguaral's wild fauna and flora were protected from fire and deforestation by its strongly conservation-minded owner, Sr. Tomas Blohm. The ranch included two major habitat types; a continuous gallery forest along the river Guarico, and forest patches—matas—away from the river that were surrounded by seasonally inundated grasslands (Troth, 1979). Red howlers occupied both habitat types, but the census data that we present here were obtained mainly from the population inhabiting the matas. The mata population has been studied by numerous researchers: Agoramoorthy and Rudran (1992, 1995), Crockett (1984, 1985, 1996), Crockett and Pope (1993), Crockett and Rudran (1987a,b), Eisenberg (1979), Herrick *et al.* (2000), Neville (1972), Pope (1990, 1992), Rudran (1979), and Sekulic (1982, 1983).

Rainfall in the area is highly seasonal with a discrete wet and dry season from May to October and November to April, respectively (Crockett and Rudran, 1987a). The vegetation is semideciduous with many trees and shrubs losing most of their leaves by the late dry season. The elevation is about 70 m., and the monthly average temperatures varied from about 19–22°C minimum to 33–38°C maximum, with daytime temperatures being generally higher in the dry season (Troth, 1979).

Data Collection

Different investigators conducted the censuses; all were trained to classify individuals into appropriate age categories before they began collecting field data. The training helped to standardize the population structure data. Moreover, we regularly conducted ear-tagging operations involving chemical capture of red howlers period (Agoramoorthy and Rudran, 1994; Thorington *et al.*, 1979, Rudran, unpublished data), in order to facilitate unambiguous identification of individuals.

Periodic censuses of the study population began in June 1976 and continued through March 1999. In June and July 1976, and from January 1977 to October 1978, March 1979 to February 1981 and March 1985 to September 1993 we conducted population censuses more or less each month. From March 1981 to February 1985 and after September 1993 we usually conducted censuses once per year during the dry season (November–April). We located the study groups with the help of their loud calls, and if this failed, by systematically searching different parts of their home ranges. Once located, we determined group size by counting its members repeatedly until several consistent totals were obtained. Then we sexed each group member and assigned it to an age category via a classification system based on physical and behavioral characteristics of known-age individuals. We assigned individuals of both sexes to the infant category if their ages were known or estimated to be ≤10 mo. Females >10 mo are small-, medium-, and large-juveniles (SJF, MJF, LJF) or subadults (SAF) if their ages are known or estimated to be >19, 28, 37 and 46 mo, respectively. Similarly, males >10 mo are small-, medium-, large-juveniles (SJM, MJM, LJM) or subadults (SAM) if their ages are known or estimated to be <22, 34, 46 and 58 mo, respectively. Females and males whose ages are known or estimated to be >46 or 58 mo, respectively, are adults. After assigning age categories to individuals, we confirmed a group's identity via several features including their size, composition, the area where they were seen, and any members that were identifiable by natural markings or ear tags (Agoramoorthy and Rudran, 1994; Thorington *et al.*, 1979).

We also saw solitary males and females and associations of ≥2 individuals during population censuses. Whenever solitaries and associations were encountered, we recorded their locations within the study area, size, composition and individual characteristics. The individuals of an association either left the area after a while, or stayed together as a social group until they produced infants. We included the newly formed groups in subsequent population censuses, which gave rise to a gradual increase in the number of groups under investigation.

Data Analysis

Our analysis is based on published and unpublished data spanning 1969–1999. The published data are derived from Neville (1972, 1976) and Rudran (1979) and cover the period from 1969 to 1978. The unpublished data included information collected after 1978 by Rudran in 1979, 1981, 1982, 1984, 1996, 1997 and 1999 and by Rudran and colleagues: Rumiz (1985–1987), Valderrama (1988), Sestrich (1989), Agoramoorthy (1990–1992, 1994, 1995) and Kilber (1993) during other years.

During some population censuses, particularly those conducted on an annual basis, it was not possible to contact all study groups. In these cases, we assigned each missing group its average size based on counts during the previous and the following periods (mo or yr) of contact. Although we assigned sizes to missing groups we did not attempt to deduce their composition. Therefore, the groups were excluded from the analysis of population structure, for which we used only groups whose compositions were actually verified in the field.

Population size for any given year is the total number of individuals living in new and established groups during a particular month of that year. The month of choice was more or less the same during different years (between December-April) in order to standardize for within-year population size fluctuations due to demographic events. We computed population density estimates assuming that the size of the study area is 1.55 km^2 (Rudran, 1979).

We computed the annual rate of increase as the ratio of population size in two successive counts (Caughley, 1977). When two successive counts were longer or shorter than a year apart (e.g. 1976–1978), we proportionately adjusted the difference between them when calculating the annual rate of increase. We applied no adjustments for multiple comparisons since all comparisons are explicitly presented together with the raw data on which the comparisons were based.

RESULTS

Thirty-five monkeys were marked with ear-tags in 1978, and 149, 5 and 70 individuals were ear-tagged in 1981, 1985 and 1987, respectively. Between 1989–1994 an additional 75 howlers were marked with ear-tags. Ear-tags facilitated unequivocal identification of individuals and thereby improved the quality of the census data throughout the study.

Changes in Population Size, Density and Rate of Increase

During the 30-year period, the population first expanded, then remained relatively stable, and finally began a decline that continued through 1999 (Table I). Despite this general trend, the population's annual rate of increase fluctuated between one and 6% from 1970 to 1978 (Figure 1), while grew from 146 to 186 individuals, and density increased from 94 to 120 howlers/km^2. Even after this period of moderate growth, the annual rate of increase continued to fluctuate until 1989 as the population expanded and reached a maximum of 346 individuals and density of 223 howlers/km^2. In 1990 there was no increase, but during the next 3 years the population registered moderately negative rates of increase that ranged between one and 5%. This was followed by substantial reductions in size; sometimes as much as one-third of the population was lost from one year to the next beginning in 1994. By the end of March 1999 the population had been reduced to one-fourth of its maximum size and included only 90 individuals; population density was 58 howlers/km^2.

The growth of the population was at least partly due to habitat regeneration that increased the size and vegetation density of the matas within the study area. This enabled dispersing males and females to band together and to establish new groups that later grew in size as well. Both events contributed to the increase of the study population.

Changes in the Size and Number of Groups

Population growth between 1970 and 1978 resulted in part from slight increases in group size. The median size of the 13 groups observed by Neville (1972) that could unequivocally be identified by Rudran increased slightly during that period (median, range: 8, 6–12 vs. 9, 5–13, n = 13), but the difference is not statistically significant (Unpaired t-test, two tails, t = −0.282, df = 12, p = 0.783). Subsequent increases in population size were due to changes in the size and number of established groups, as well as to the addition of new groups to the study population (Table I). For instance, 59% of the population increase that occurred between 1978 and December 1981 (55 of 94 individuals) was due to the increase in median size of established groups from 8.0 (range: 4–14) to 10.5 individuals (range: 6–18, n = 22 groups, t = −4.957, df = 21, p = 0.000). Another 21% represented 20 individuals of two established groups added to the study, while the remainder belonged to 4 new groups that formed during the same period.

After the established groups reached a stable median size of 10 individuals in 1987, the population continued to expand as a result of the formation of new groups and an increase in the median size of these groups. Between

Table I. Changes in population size, population density, and size (median) and number of established and new groups

	70	72	76	77	78	79	81	84	85	86	87	88	89	90	91	92	93	94	95	96	97	99
Population size	146[a]	163[a]	182	184	186	219	280	278	294	304	322	336	346	346	328	318	314	219	212	155	117	90
Density (in d/km²)	94	105	117	119	120	141	181	179	190	196	208	217	223	223	212	205	203	141	137	100	75	58
No. groups																						
Total	19	19	21	21	22	24	28	30	33	33	34	34	36	36	36	36	33	29	29	23	18	15
Established			21	21	21	22	24	24	24	24	24	24	24	24	24	24	22	18	18	15	14	12
New					1	2	4	6	9	9	10	10	12	12	12	12	11	11	11	8	4	3
Size																						
Established			9.0	8.0	8.0	9.0	10.5	9.5	9.5	9.5	10.0	10.0	10.0	10.0	10.0	9.0	10.0	7.5	7.5	8.0	7.0	6.0
New					4	4	4.5	5.5	6.0	7.0	8.0	8.0	9.0	8.5	8.0	6.5	9.0	6.0	6.0	6.0	5.5	6.0
Min. size																						
Established			4	4	4	4	6	6	5	6	5	6	6	5	5	4	5	5	5	4	4	4
New					4	4	4	4	4	4	5	5	4	5	5	5	5	4	4	2	4	5
Max. size																						
Established			15	17	14	15	18	15	15	15	14	17	15	16	16	17	17	14	11	10	10	9
New					4	4	6	7	7	9	10	10	12	12	15	14	15	12	9	8	7	6
% groups																						
Multimale			52	43	59	54	46	40	63	64	47	41	42	49	50	55	72	32	24	38	33	7
Unimale			48	57	41	46	54	60	38	36	53	59	58	51	50	45	28	68	76	62	67	93
Mean size																						
Multimale			8.5	8.7	8.8	9.2	10.5	9.1	9.0	8.7	9.3	9.8	10.7	10.5	10.0	9.7	9.1	8.0	8.6	7.6	7.2	9.0
Unimale			9.5	5.9	7.9	9.0	9.6	9.4	6.4	7.9	8.6	9.0	8.8	8.6	8.6	8.2	8.9	6.6	6.7	6.9	6.0	5.8

Note. Values estimated from previous and/or following years are shown with one decimal.
[a] From Neville, 1976.
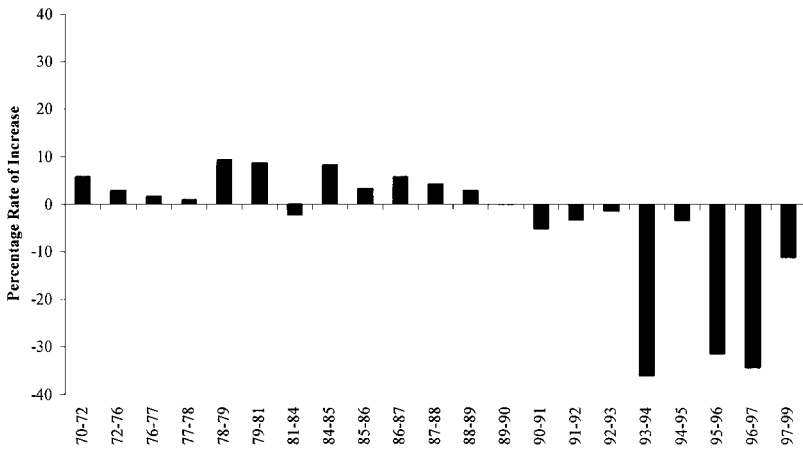
Fig. 1. Changes in Population Rate of Increase (1970–1999).

1979 and 1989 12 new groups were formed and their median size increased from 4.5 (4–6, n = 3 groups) to 9.0 (4–12, n = 12 groups).

By 1991 the population began its decline and median group sizes of new and established groups also started a decline that continued more or less through the next 8 years. Twenty-one groups disintegrated and only 15 established and new groups survived. The established groups decreased in size more slowly than new groups did (Table I), but both groups ultimately had a median size of 6 individuals per group in 1999, with established and new groups having 4–9 and 5–6 individuals, respectively. Density is a good predictor of the size of established groups ($R^2 = 0.782$, df = 18, F = 69.089, p = 0.000), as well as of new groups ($R^2 = 0.385$, df = 14, F = 8.76, p = 0.010).

Changes in Group Composition

The population consisted of unimale, and multimale groups (mean ± s.d.: 2.2 ± 0.2 adult males, range: 2–6). The sizes of both types of groups were similarly affected by changes in density, and they became larger as density increased, and smaller when density declined (Uni-male: adj $R^2 = 0.359$, F = 11.641, df = 18, p = 0.003; Multi-male: adj $R^2 = 0.521$, F = 21.628, df = 18, p = 0.000).

Multimale groups were somewhat larger than unimale groups (mean = 9.3 ± 1.0 vs 8.1 ± 1.2 individuals). Additionally, they had significantly more small- and medium- juvenile males, and more medium-juvenile, large-juvenile and subadult females than unimale groups did (Mann-Whitney tests,

Table II. Group composition of unimale and multimale groups

	Unimale	Multimale	U	z	p
Adults					
Males	1	2.2 ± 0.2	0	-5.794	**0.00**
Females	2.5 ± 0.3	2.7 ± 0.3	158.5	-1.123	0.26
Subadults					
Males	1.3 ± 0.2	1.2 ± 0.1	142	-1.647	0.10
Females	1.0 ± 0.1	1.1 ± 0.2	142.5	-1.871	**0.06**
Large juveniles					
Males	1.2 ± 0.2	1.2 ± 0.2	178.5	-0.595	0.55
Females	1.2 ± 0.5	1.2 ± 0.2	140	-1.907	**0.06**
Medium juveniles					
Males	1.2 ± 0.2	1.4 ± 0.3	113	-2.381	**0.02**
Females	1.1 ± 0.2	1.3 ± 0.4	122	-2.199	**0.03**
Small juveniles					
Males	1.2 ± 0.2	1.4 ± 0.3	87	-3.101	**0.00**
Females	1.2 ± 0.2	1.2 ± 0.2	199.5	-0.014	0.99
Infants					
Males	1.2 ± 0.2	1.3 ± 0.2	184.5	-0.429	0.67
Females	1.3 ± 0.2	1.2 ± 0.2	153	-1.28	0.20

Note. All tests are Mann–Whitney U tests for two independent samples.

two-tailed, Table II). However, there is no significant difference between the two groups in the number of adult females or the number of large juvenile and subadult males in them (Table II).

The percentage of uni- and multimale groups in the population changed over time (Table I). In 1978 there was a slight preponderance of multimale groups (Rudran, 1979). From then until 1993, the percentage of multimale groups in the population varied between 40 and 70%. When population size and density began a rapid decline in 1994, the percentage of multimale groups began to plummet and reached its lowest level of 7% by the end of the study.

All but one (11/12) of the new groups that were formed during the study had a unimale structure when first established. Unimale groups were vulnerable to male invasions, which are social changes that transformed unimale into multimale groups (Crockett, 1984; Rudran, 1979; Sekulic, 1983) and mainly affected large unimale groups. For instance, the average size of 9 unimale groups that experienced invasions between 1984 and 1985 is significantly larger than the average size of all unimale groups in the population (12.2 ± 2.6 vs 8.1 ± 1.2 individuals). Since male invasions transformed large unimale into multimale groups, only small unimale groups remained in the population between 1984 and 1985. Therefore, the average size of unimale groups was drastically reduced from 9.4 to 6.4 individuals (Table I).

Changes in Age Structure

Throughout the 30-year period, approximately half of the individuals of the study population comprised adults. (Table III). The second most numerous age-class was the juveniles, which included a third of the population, whereas the rest comprised subadults and infants. This average representation of age classes notwithstanding, the age structure during population expansion and decline were different, as indicated by the percentage of individuals in each age-sex class during both periods (Figure 2). The percentage of adult males and females is significantly lower during growth than decline as indicated by a multivariate analysis of variance using the 12 different age-classes as dependent variables (AM: $F = 3.612$, $p = 0.071$, $df = 21$; AF: $F = 8.302$, $p = 0.009$, $df = 21$). Infants of both sexes were more numerous while the population was growing than when it was declining (IM: $F = 14.208$, $df = 21$, $p = 0.001$; IF: $F = 4.043$, $df = 21$, $p = 0.057$). In the small juvenile class, males were more abundant during expansion than decline ($F = 3.603$, $p = 0.072$), whereas females showed no statistically significant change ($F = 1.422$, $p = 0.247$). Conversely, medium-sized juveniles of both sexes were more abundant during decline than during expansion (MJM: $F = 6.993$, $p = 0.016$; MJF: $F = 12.725$, $p = 0.002$). Differences between the proportions of subadults and large juveniles during growth and decline of the population a not statistically significant for either sex.

The number of adult males and females increased more or less gradually from 1970 until 1991 (Table III). Then, from 1992 to 1993 there was a 16% decline in the number of adult females that was not accompanied by a similar change in the number of adult males. The decrease did not affect all groups similarly, and was due to the loss of 24 adult females from only 14 study groups. At the same time, 17 study groups experienced no change and 5 groups actually added a total of 7 females. The decrease was partly due to the sharp decline in the number of medium juvenile females in 1990 to 8 individuals from 19 the previous year (Table III). This decline led to the low number of large juvenile females reported in 1991 and eventually in the decreased number of adult females beginning in 1993.

The number of infants has been increasing since 1994, when the population experienced its steepest decline. After producing only 3 infants in 1994, there were 7, 15, 10 and 13 infants born in 1995, 1996, 1997 and 1999, respectively.

Changes in Sex Ratios

Overall, there were more females than males in the population (Table III). In the adult class, the sex ratio was strongly biased in favor

Table III. Changes in the number of individuals in each age–sex class

	70	72	76	77	78	79	81	84	85	86	87	88	89	90	91	92	93	94	95	96	97	99
Adult																						
Males	28	30	33	30	36	37	42	42	59	61	55	55	58	59	62	57	65	26	26	29	16	16
Females	44	47	56	55	55	62	76	78	86	90	98	97	106	106	110	106	89	44	39	45	33	30
Subadults																						
Males	14	13	11	12	10	16	16	16	16	11	11	7	13	21	15	11	14	12	7	4	1	4
Females	5	6	6	4	3	6	9	8	6	4	7	6	6	10	10	8	9	1	8	2	0	2
Juveniles																						
Large males	17	8.5	13	14	14	13	10	23	8	14	8	26	28	23	13	16	18	5	17	8	9	4
Large females	15	5	4	3	6	6	9	7	10	12	9	23	18	16	8	12	8	4	7	3	2	3
Medium males		6.5	14	14	13	12	20	15	13	7	20	22	22	12	24	17	18	15	15	8	10	7
Medium females		8	7	10	9	13	12	11	16	22	18	22	19	8	17	17	30	8	7	11	7	8
Small males		8	12	9	12	7	20	18	11	22	23	20	16	27	23	17	9	8	10	9	1	1
Small females		5	9	9	12	12	26	22	10	16	19	12	11	18	18	19	15	5	8	9	1	2
Infants																						
Males	8	13	7	9	4	16	21	19	31	29	29	22	26	27	15	21	20	2	1	4	1	3
Females	15	10	9	13	12	17	19	14	28	26	25	24	23	18	13	17	19	1	0	8	7	10
Unsexed infants		3	1	2		2	0	5											6	3	2	

Note. Aug70: from Table 2 (Neville, 1976), juveniles were not distinguished by size; Jun-72: from Table 3 (Neville, 1976), Jun-76: from Tables 1 and 2 (Rudran, 1979).

Changes in Age Structure
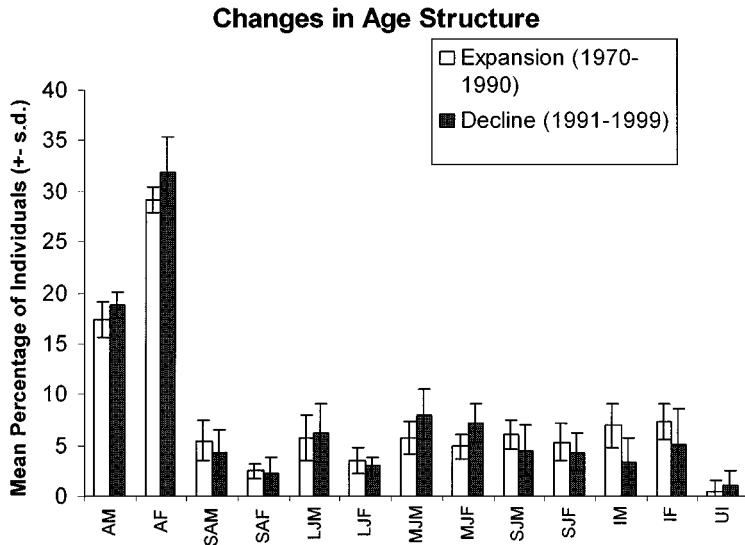
Fig. 2. Age structure of the population during growth (1970–1990) and decline (1991–1999). M: male, F: female, A: adult, SA: subadult, LJ: large juvenile, MJ: medium juvenile, SJ: small juvenile, I: infant.

of females, while among subadults and juveniles the bias was in favor of males. Sex ratios in the adult and subadult classes did not change noticeably over time and there is no apparent relationship between the proportion of males and females in the adult and subadult classes and population density (Table IV). Conversely, population density explains an important proportion of the change in the sex ratio of large and small juvenile categories. When density was low there tended to be more males than females in the large juvenile category and more females than males in the small juvenile category (Table III). In other words, population density is a good predictor of the sex ratio in the large juvenile and small juvenile categories, as indicated by linear regression analyses (Table IV).

The number of male and female infants in the population varied appreciably during different years. Relatively more females were born at the beginning and end than during the central years of the study. Changes in the ratio of male-to-female infants in the population are linearly associated with changes in density. The ratio is small, i.e. more females than males were born, when density was low, but it became large when density increased (Figure 3). Given the relatively small numbers of infants in the sample beginning in 1995 (Table III), we evaluated statistically the relationship between sex ratio and density, assigning half of all unsexed individuals to each sex. We dropped the

Table IV. Tests of linear relationships between population density and sex ratios of each age class

Ratios	R^2 adj.	Constant	Slope	F	p
AM/AF	−0.04	0.57	0.00	0.28	0.61
SAM/SAF	−0.02	4.17	0.01	0.70	0.42
LJM/LJF	0.28	4.07	0.01	8.43	**0.01**
MJM/MJF	−0.02	1.47	0.00	0.60	0.45
SJM/SJF	0.11	0.67	0.00	3.37	**0.08**
IM/IF[a]	0.77	59.24	0.00	−0.01	**0.01**
IM/IF[b]	0.86	101.36	0.00	−0.19	**0.01**
IM/IF[c]	0.52	19.55	0.00	0.21	**0.00**

[a] Unsexed infants assigned equally to both sex classes.
[b] All unsexed infants considered females.
[c] All unsexed infants considered males.

data point for 1994 from the analysis because the only 3 infants born give an extreme sex ratio (IM/IF = 2, n = 3) of doubtful biological meaning.

DISCUSSION

Our analyses confirm that the study population expanded during the 1970s and 1980s as reported elsewhere (Crockett, 1996; Crockett and Eisenberg, 1986; Pope, 1998; Rudran, 1979). After almost two decades of growth the population declined sharply in the early 1990s; and the marked increase in births during the last years could indicate that the population was beginning to recover around 1996.
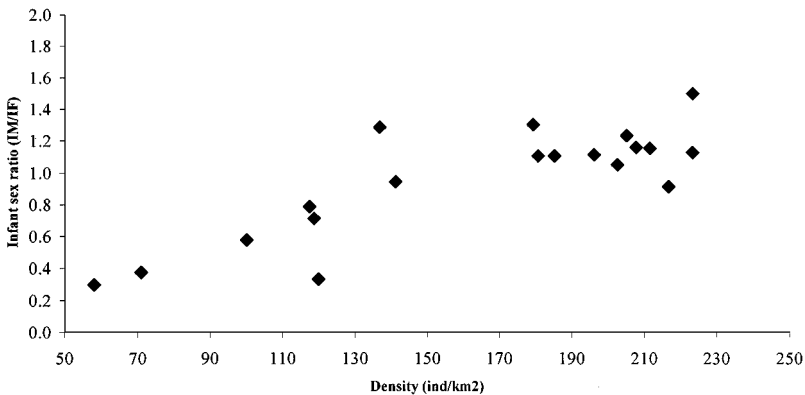
Fig. 3. Population density plotted against infant sex ratio. Unsexed infants were assigned 50–50 to each sex class.

Factors Influencing Population Growth

The population's growth was influenced by several factors, including the size and formation of social groups. Initially the population grew as a result of established groups becoming larger until they reached maximum size. The second stage of growth was primarily due to associations of dispersing males and females persisting long enough as new social groups to produce infants. The third stage of growth was mainly the result of new groups increasing in size until they reached maximum size. Group formation during periods of expansion of howler populations has also been observed in Panamá (Carpenter, 1934; Collias and Southwick, 1952), Costa Rica (Fedigan *et al.*, 1998; Fedigan and Jack, 2001) and Argentina (Rumiz, 1990).

A possible explanation for the increase in median size of established groups during the first stage of growth is that the population could have been recovering from a previous crash. Conversely, a likely explanation for the formation and expansion of new groups—the second and third stages of growth—that began in 1978 is the increase in the amount of habitat suitable for howlers within the study area. By that time, the ban on deforestation and burning had been in effect for several decades, which allowed woody plants to regenerate and increase the size of forest patches occupied by the study population. It was mainly in the recently regenerated areas and the interstices between the home ranges of established groups that new groups were able to establish themselves (Rudran, unpublished). Thus, we attribute habitat protection resulting in the gradual increase of areas suitable for red howlers to be a factor that contributed to the observed sequence of population growth. A process with similar characteristics was observed in Panamá (Collias and Southwick, 1952) and at two study sites in Costa Rica (Fedigan and Jack, 2001; Glander, 1992). We also interpret the fact that new groups were smaller than established groups to be an outcome of living in recently regenerated areas and as an indicator of the importance of habitat features, such as food availability, in regulating the size of red howler groups and populations.

Factors Influencing Population Decline

Perhaps the most convincing evidence for the cause of population decline was the discovery of 9 dead red howlers in 1996 (Rudran, unpublished). We estimate death to have occurred 3 weeks to several mo before discovery, indicating that mortality in the population was a gradual process, as would be expected from a disease epidemic or food shortage. The skeletal remains, which were almost complete, included 3 adults (one male and 2 females),

2 subadults and 4 juveniles. Six skeletans were in close proximity to one another suggesting that they belonged to a single group. The fact that all age classes experienced mortality, and that entire groups disappeared from their home ranges, suggests that disease was a factor that contributed to the decline of the study population. We could not determine the type of disease that had caused the decline.

During the period of decline, established groups decreased in size more slowly than new groups did (Table I). Furthermore, only 50% of the established groups had disintegrated by 1999, whereas 75% of the new groups had disappeared by that time. The increased susceptibility of new groups to size reduction and disintegration suggests that problems of exploiting food from recently regenerated and relatively unfamiliar areas also contributed to population decline. Dispersing female red howlers, which must have frequently obtained food from areas unfamiliar to them, ate diets that were significantly less nutritious than those of group-living females, and they also traveled farther each day, (Crockett and Pope, 1993; Pope, 1989). Similarly, new groups, which were essentially associations of dispersing individuals, may not have been sufficiently familiar with their relatively new home ranges to find adequate supplies of food, especially during periods of food shortage. Hence, they would likely have traveled farther to find food and to avoid hostile interactions with their neighbors that lived in established groups. Stress due to a poor diet, food shortage, and/or intimidation by established groups may also have increased the susceptibility of new groups to death from disease. In mantled howlers, stress due to food shortage was implicated in lowering resistance to bot-fly infestations (Otis *et al.*, 1981), which can cause mortality (Milton, 1996).

Factors Influencing Irregular Population Fluctuations

The population's growth rate fluctuated irregularly and also declined sharply at least once during 30 years. Some of the fluctuations seemed to be associated with annual rainfall, and population growth tended to slow down following a relatively dry year. For instance, the rate of increase was smaller between 1972–1978, than between 1970–1972, and was negative for the period 1981–1984, and negative again ever since 1990 (Figure 1). 1972, 1982, and 1989 were 3 of the driest years, getting 738, 998, and 966 mm of rainfall, which are significantly below the annual mean for the area (1400 mm, 1920–1997, n = 77 years, D. Thielen, pers. com.). During the 1990's, when the population's rate of increase was always negative, there were only 2 years when annual rainfall was higher than the average (1991: 1465 mm and 1996: 1507 mm).

The effects of droughts on terrestrial communities have been poorly investigated (Holmgren *et al.*, 2001), but they are gradually attracting more attention (Chapman and Peres, 2001; Leigh, 1999; Wright *et al.*, 1999). One likely effect of droughts is the reduction of red howler foods, which may have been responsible for the irregular fluctuations of the population. Food scarcity could also have led to deterioration of the general health of the individuals making them less resistant to diseases. Hence, food shortage due to droughts in combination with disease could have been the reason for the population crash in the early1990's.

If droughts and disease affected the mata population, they could also have affected the population living in the gallery forest nearby. When Neville (1972) surveyed the gallery forest population in 1970 the mean group size was 9.6. The mean group size was reduced to 4.5 by 1978 (J. Robinson pers. comm.), indicating that the gallery forest population had suffered a dramatic decline a few years earlier. In subsequent years, mean group size fluctuated between about 7.8 and 8.2 until 1987 (Crockett, 1996), and between 7.6 and 9.4 from 1988 through 1993 (X. Valderrama, K. Sestrich, and G. Agoramoorthy pers. comm., and Rudran unpublished data). There were no further surveys in the gallery forest until 1997. Because social groups were difficult to locate then, we recorded data on bouts of howling. The rates of howling declined from 423/100 hr in 1997 to 200/100 hr in 1999 and 82/100 hr in 2000. Along with the decline in howling rates, the sightings of dead howlers reported by local people during 2000 provided additional evidence that the gallery forest population had again crashed in the late 1990s.

The gallery forest population crashed some years after the mata population was affected by a similar decline. The time lag may have been due to differences in habitat features. The gallery forest is floristically richer than the mata (Troth, 1979) and offers a greater variety of foods to howlers (Crockett, 1987). Furthermore, it includes a river and a stream, which probably made the vegetation less susceptible to droughts than that of the mata. Therefore, the gallery forest population may have been able to withstand the effects of droughts and food shortages somewhat longer than the mata population could before succumbing to disease.

Several other howler populations have experienced irregular population fluctuations or crashes or both. Two other red howler populations crashed as a result of disease in Venezuela between 1992–1996 (Pope, 1998). A population of *Alouatta caraya* in northern Argentina crashed in 1982, possibly due to bot-fly infestation (Rudran, unpublished data). The population on Barro Colorado Island (BCI), Panamá, experienced a crash between 1933 and 1951; yellow fever, botfly infestation and drought are possible causes (Collias and Southwick, 1952). The population eventually recovered, but fluctuated irregularly and declined sharply at least once between 1977 and

1993 (Milton, 1996). It appeared to be regulated by unpredictable periods of food scarcity (Milton, 1982) coupled with the primary and secondary effects of bot fly parasitism (Milton, 1996). A population of *Alouatta palliata* in Santa Rosa National Park also experienced irregular fluctuations in population size, and a sharp decline during a span of 28 years (Fedigan and Jack, 2001).

Since numerous howler species experience irregular population fluctuations and periodic crashes, their demographic features may reflect adaptations or responses to cope with unpredictable events. With this premise in mind we interpret the demographic details of our study population.

Group Size and Composition

Our analysis indicated that density was a good predictor of the size of established and new groups. This result is consistent with a previous analysis based on 10 years of data from the same population (Crockett, 1996) and with information from mantled howlers (Fedigan *et al.*, 1998).

Contrary to expectations, the number of adult females in uni- and multimale groups did not differ significantly, suggesting that adult males in multimale groups may have access, on average, to fewer females than the adult male of a unimale group. Nevertheless, sexually mature males may have preferred to remain in multimale groups because they offered greater resistance to male invasions than unimale groups did (Agoramoorthy and Rudran, 1995), and thereby reduced the likelihood of infanticide, which could increase the survival of their infants. When adult males of multimale groups are related (Pope, 1990), remaining in them would also have increased the survival of their offspring, and therefore, enhance their inclusive fitness.

Because the number of adult females was similar in uni- and multimale groups, there were no differences in the number of infants produced in both types of groups (Table II). Therefore, the resistance of multimale groups to infanticide should have made their small juvenile recruitment rates higher than those of unimale groups. Despite this expectation, our results showed that multimale groups had higher rates of small juvenile recruitment only for male infants, whereas recruitment of female infants was the same as in that unimale groups. This suggests that small juvenile females were more vulnerable to death in multimale than in unimale groups. The increased vulnerability of small juvenile females in multimale groups may have been the result of aggression directed at them by unrelated adult males, as in mantled howlers (Clarke, 1982 cited in Glander, 1992). Our finding that group composition and mating systems may have been important determinants of the survival of small juvenile females helps to clarify the details of the general

impression that females of the study population experienced a high rate of mortality as juveniles (Crockett and Pope, 1993).

After the small juvenile stage, females were better represented in the older immature age classes of multimale than of unimale groups (Table II). This situation could have arisen in two different ways. One is via faster rates of dispersal of immature females from unimale than from multimale groups in order to avoid the deleterious effects of inbreeding (Packer, 1979; Pusey, 1980). This suggestion is contrary to the assumption that inbreeding avoidance is unimportant to explain female dispersal (Crockett, 1984). However, the assumption fails to consider female dispersal in the context of group composition and mating systems, which our investigations indicate may be important considerations in female dispersal. Another possible reason why there were more medium juvenile and older immature females in multimale than in unimale groups is that the presence of several adult males in multimale groups could have encouraged immature females to remain in their natal groups because of future reproductive opportunities with unrelated sexual partners. In contrast, the presence of several adult males in multimale groups may have induced subadult and large juvenile males of the groups to disperse earlier than males born in unimale groups did, thereby resulting in similar numbers of males of these age classes in both groups (Table II).

The proportion of uni- and multimale groups fluctuated throughout the study. When density was lowest towards the latter part of the study, unimale groups vastly outnumbered multimale groups (Table I). The large proportion of unimale groups at low densities, and the fact that 11 of 12 new groups were unimale when first established suggest that males prefer to monopolize a social group whenever possible. However, when density increases or a group matures, internal recruitment, male invasions, dispersal and mortality can transform unimale into multimale groups and vice versa. The transformations would depend on the peculiarities of a group's history, composition and dynamics and would therefore be hard to predict from population parameters. This may explain why the proportion of unimale and multimale groups in the population fluctuated somewhat haphazardly at medium and high densities.

Age Structure and Sex Ratios

The age structure of the population during growth and decline fitted theoretical expectations. The population included a larger proportion of infants when it was growing than when it was declining. In contrast, the population consisted of a relatively larger number of adults when it was

declining than when it was growing. At all times females outnumbered males in the adult age class, but they tended to be less numerous than males in the subadult and juvenile age classes. Sex ratios favoring females in the adult age class and males in the immature age classes, can in part, be explained by differential rates of maturation of the two sexes. However, we believe that socially mediated mortality of small juvenile females and of males at or near adulthood (Dittus, 1979, 1980) also contributed to the sex ratios and age structure of the population (Crockett and Pope, 1988; Rudran, 1979).

Between 1992–1993, there was an appreciable decline in the number of adult females without similar changes in any of the other age classes. High rates of mortality of medium juvenile females in 1990, resulting in low rates of recruitment explain only part of the decline. The rest of the decline was probably due to the death of females after reaching adulthood. A similar phenomenon occurred in another Venezuelan red howler population, Hato El Frío, where, adult female mortality was supposed to have been the result of disease (Pope, 1998).

Sex ratios varied with density, with the changes being less pronounced in the subadult or adult classes than they were among infants and juveniles. Among infants, more females than males were born at low densities, whereas the reverse was true at high densities. Since infant production is an important determinant of population increases, the proportion of adult females in a population will influence the rate of population increase. Hence, at low population densities, female biased birth sex ratios will help to enhance rates of female recruitment, which in turn will result in higher rates of population increase. Under these circumstances, adults of both sexes that produce female offspring would likely contribute disproportionately more to the gene pool and thereby increase their fitness. Furthermore, the female biased birth sex ratio would also compensate for high rates of mortality of small juvenile females that otherwise undermines their recruitment, and therefore, the rate of population increase. At high densities, when there is a full complement of breeding females in social groups, young females would find it difficult to breed in their natal groups as a result of intrasexual competition (Crockett, 1984). Moreover, seeking mates through dispersal would become difficult because saturated habitats are unlikely to provide young females with opportunities to enter established groups or to find unoccupied areas to form new groups. Conversely, breeding opportunities in saturated habitats for males would be better, because they could disperse to form male coalitions and invade other social groups or stay in their natal groups even past adulthood (Agoramoorthy and Rudran, 1993) to breed with unrelated females. Remaining in the natal group would also help to increase inclusive fitness. Under these conditions individuals that produce male offspring are likely to enhance their fitness more than those that produce female infants do. Hence

selection would be expected to favor a male biased birth sex ratio at high densities.

Skewed birth sex ratios occur in several mammals including primates (Clark, 1978; Silk, 1983), and many reasons have been suggested for the deviation from a 50/50 birth sex ratio (Clark, 1978; Clutton-Brock *et al.*, 1981; Jones, 1988; Silk, 1983; Trivers and Willard, 1973; Zschokke, 2002). In red howlers the skewed birth sex ratio appears to be a function of population density. It should be noted that the we detected influence of population density on the birth sex ratio only when data from the entire study was considered. This illustrates how information from shorter study periods could sometimes lead to erroneous interpretations of the actual situation (Crockett and Rudran, 1987b).

The ability of red howlers to adjust birth sex ratio may be an adaptation to population fluctuations experienced by the species due to periodic food shortages and disease epidemics. Recall also that survival of small juvenile females was better in uni- than in multimale groups and that unimale groups were most numerous at low densities. Therefore, when a population declines and reaches low density, adaptations such as the dispersal of both sexes, formation of unimale groups and female biased birth sex ratios would have contributed to a rapid build up of the population. It is possible that such adaptations may also be found in other howler species that experience irregular population fluctuations and that they function to build up a population rapidly after it declines.

Final Remarks

Our investigation shows that long-term studies are essential for a clear understanding of the demography of long-lived species such as red howlers. Assuming population stability based on a short- term study can lead to flawed conclusions if a population is in fact unstable or fluctuating. The duration of a study should be considered when analyzing and interpreting the results of an investigation (Chapman and Balcomb, 1998; Crockett, 1985; Fleagle *et al.*, 1999). Our long-term investigations indicate that the demographic features of our study population were influenced by social as well as environmental factors.

ACKNOWLEDGMENTS

and the Friends of the National Zoo. Rudran thanks Tomas and Cecilia Blohm for their long years of friendship and unfailing support for the red howler project that made the whole endeavor feasible. He also thanks F. Boccardo, N. A. Muckenhirn, D. S. Mack, J. G. Robinson, R. W. Thorington Jr., D. E. Wilson, C. M. Crockett, C. Saavedra, T. Pope, S. Crissey, D. Rumiz, X. Valderrama, K. Sestrich, G. Agoramoorthy and B. Kilber for various types of field assistance throughout the study. Thanks are also due to J.F. Eisenberg who helped to set up the project during its initial stages. Finally, we thank Claudia Valeggia for helping with the long and tedious process of data tabulation.

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