

POPULATION GROWTH IN THE BELIZEAN BLACK HOWLING MONKEY (*ALOUATTA PIGRA*)Robert H. Horwich¹, Robin C. Brockett^{1,2}, Roxie A. James^{1,3} and Clara B. Jones^{1,4}¹Community Conservation, Inc., RD 1, Box 96, Gays Mills, Wisconsin 54631, USA.²Zoo Atlanta, Atlanta, Georgia 30315, USA.³Kean College, Union, New Jersey 07083, USA.⁴Livingstone College, 701 W. Monroe Street, Salisbury, North Carolina 28144, USA.

Abstract

Population growth in black howling monkeys (*Alouatta pigra*) was studied in an area of 0.63 km² from 1990 to 1999 at the Community Baboon Sanctuary, Bermudian Landing, Belize, Central America. Population density increased over time, and population growth was found to be density-dependent, with a higher rate of increase between 1991-1996 than between 1997-1999. The shape of the age distribution of the population was similar across years, although the proportion of adult males in the population decreased significantly with increased population density. Changes in membership over time for 18 monkey groups suggested that population growth may also result from an increase in the number of groups and length of tenure of groups. Groups with no or only one immature (infant, juvenile, or subadult) were confined to the period of population increase. Although more male infants were estimated to have survived to the juvenile age class, the result was statistically insignificant. Interbirth intervals were within the range for other species of *Alouatta*. Our results also indicate that increased population density and consequent increases in mean group size decrease the ability of single males to monopolize female groups due, in part, to decreased opportunities for single males to found new groups. A consequence of this condition would be increased male-male competition for mates.

Key Words - *Alouatta pigra*; Belize; population growth; intrinsic rate of increase; age distribution; infant survival; male strategies.

Introduction

Alouatta pigra, the black howling monkey, has the most restricted geographical distribution of any species in the genus (Wolfheim, 1983). It is found in undisturbed and disturbed habitats of southern Mexico, northern Guatemala, and Belize (Horwich and Lyon, 1987; Wolfheim, 1983) and appears to favor riparian and seasonally flooded forests (Horwich and Johnson, 1986; Lyon and Horwich, 1996). Black howlers are classified at a low risk of extinction according to the Mace-Lande system (Rylands *et al.*, 1995), although populations may be locally endangered or extinct (Horwich *et al.*, 1993). Like all of the other species of *Alouatta* except *A. palliata* (the mantled howling monkey), *A. pigra* are generally organized into polygynous demographic subunits of one adult male and two or three adult females in addition to immatures (Crockett and Eisenberg, 1986; Wolfheim, 1983; Chapman and Balcomb, 1998; Horwich *et al.*, in press). Like other howlers, however, variation in population structure is noteworthy (Crockett and Eisenberg, 1986), ranging from single male-single female to multimale-multifemale subunits (Bolin, 1981; Horwich and Gebhard, 1983; Horwich *et al.*, in press).

As discussed by Ricklefs (1979) and Begon and Mortimer (1986), populations of organisms may be increasing in number, decreasing, or may be found at a stable equilibrium. These authors point out that population trends may be correlated with variations in food supply, climate, predators, parasites, or other factors (e.g., habitat disturbance). Changes in population numbers during a specified time period can be classified as "stabilizing" (density-dependent) or "non-stabilizing" (density-independent), and the relative role

of each in regulating population growth has been sharply debated. Density-dependent factors imply competition for limited resources such as food or space, which influences the survival and reproduction of individuals with consequent results upon the growth of populations. Predation is also generally density-dependent, varying with the density of the population, with predation pressure increasing with increases in population growth. Density-independent factors (e.g., climate) influence population growth without regard to density, and density-independent and density-dependent factors may interact. Here we report studies of population growth in the Belizean black howling monkey (*A. pigra*) and discuss the observed results in terms of current evidence for other species of the genus.

Methods

Study area, site, and animals

The study was conducted at the Community Baboon Sanctuary (CBS, 17°33'N, 88°35'W), a managed reserve of 47 km² formed in 1985 by a cooperative agreement among private landowners (Horwich, 1990). Black howlers are the only primate species found at the CBS and are not hunted there. The CBS is a mosaic of small farms, pastures, and secondary tropical moist semi-deciduous forest fragments, including riparian habitat along the Belize River (Horwich and Lyon, 1990; Lyon and Horwich, 1996). The primary study area of 0.63 km² is composed of mapped trails, including mapped and identified trees. The landscape of the CBS is continuously changing due to farming, including "milpa"

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(slash-and-burn) agricultural practices and clearing for other reasons (Lyon and Horwich, 1996). Nonetheless, large areas of the CBS are revegetating, providing habitat for the monkeys. From 1985 to 1999, home ranges have contracted, and maps demonstrate that population increase has resulted in howlers settling previously unoccupied habitat, in new units settling in areas of home range overlap between existing groups, and in the increase of home range overlap (R. Horwich, unpublished data). Consistent with these observations, our maps show that colonization is the primary outcome of bisexual dispersal (Horwich *et al.*, 2000), similar to polygynous *A. seniculus* in Venezuela (Pope, 1992) and differing from polygynandrous *A. palliata* at La Pacifica, Costa Rica, which primarily immigrate into existing groups (Glander, 1992). Howlers are generally regarded as "pioneer species" (Eisenberg, 1979).

Details of the study site can be found in Horwich and Lyon (1990) and Silver (1998; also see Silver *et al.*, 1998). In brief, forest rhythms are seasonal, with new leaf production occurring mainly during the early rainy season (late May or early June). In the Belize District of northern Belize, flower production demonstrates a large peak during the dry season (February through May), with a second, smaller peak occurring about one month after the initiation of the rainy season. Fruit is available to black howlers in every month, but availability peaks near the end of the dry season and shortly after the initiation of the rainy season. Silver (1998; also see Silver *et al.*, 1998) found that fruit accounted for about 41% of the diet of black howlers at the CBS while young leaves made up about 37% of the diet for these wholly herbivorous monkeys.

During our studies, we were able to discriminate four habitat types inhabited by black howlers: late successional, early successional, pasture, and marsh. Both late successional and early successional habitats are dominated by *Coccoloba hondurensis* ("black grape") and *Inga vera* ("bri-bri") with three other species having a relative dominance >5% (*Lonchocarpus* sp. 1, *Guazuma ulmifolia*, *Cohuna orybigna*) (Silver, 1998). The habitats were discriminated by canopy height and canopy cover. Late successional canopy height was estimated to vary from 60 to 100 feet while early successional canopy height was <50 feet. Late successional canopy cover varied from 50 to 100%, while early successional cover was less than 25%.

Data collection and analysis

A. pigra have been studied at the CBS since 1979 (Bolin, 1981), with systematic research beginning in 1983 (Horwich and Gebhard, 1983). Researchers surveyed and mapped a 4.05 km² area from 1985 to 1989, concentrating on the 0.63 km² study area from 1990-1999, the time period comprising the present report. Data for 1994 were incomplete and therefore eliminated from our analyses. In the study site, more than 1500 trees have been tagged and mapped. Marking of animals and related genetic and morphometric studies began in 1990, and an estimated 5,000 h of observation time has been devoted to the black howlers at the CBS by our research group. The surveys were initiated by R.H.H. and his field assistants, and were continued yearly until 1992 when monthly censusing and mapping of home ranges were undertaken by

R. H. H. and R. C. B. and their field assistants. *Ad libitum* behavioral observations were also made during these periods of study, concentrating especially on male takeovers, patterns of dispersal, and social behavior within groups (Brockett *et al.*, 1999; Brockett *et al.*, 2000; Horwich *et al.*, 2000). Age/sex classification followed the system of Clarke (1990) for *A. palliata*, and sub-adults were counted as juveniles. Unmarked individuals were identified by scars, broken bones, or other distinguishing features (e.g., ectoparasites), a possible source of error in the present study.

Our census protocol depended upon enlarged topographic maps (1:1,200) of the study site upon which repeated sightings of monkeys were marked daily for the duration of each study period. We defined a demographic group as any bisexual unit of two or more (reproductive) individuals on a home range. "True censuses" (Smith, 1966) were possible because we had the manpower to count every individual black howler monkey encountered in the target areas, because black howlers are relatively sedentary and faithful to their home range, because howlers are relatively easy to locate due to their vocalizations, because we assumed that mortality and recruitment were negligible during the census periods, and because we assumed that each individual of the focal population had an equal likelihood of being counted. Our maps yielded quadrats which were assigned to survey parties of 2-5 fieldworkers daily, and efforts were concentrated between 0600-1100 and 1400-1700 when black howlers are most active. Survey parties initiated their search in the study area walking at ~1,250 m/h on parallel transects through the forest ~20 m apart. One member of each search party walked ~15 m behind the other surveyors, most of whom were familiar with the habits of black howlers and were experienced field workers, local inhabitants, or students. Return walks and rotation of observers between transects on different days were conducted opportunistically, a possible source of error. When an individual or group of monkeys was sighted, observers recorded pertinent information (e.g., identity or distinguishing marks, age/sex classification, time, weather conditions, behaviors) and remained in the vicinity of the individual or group for at least 1 h. Individual and group positions were recorded on maps for later analysis and estimation of home range sizes. Surveys were rarely conducted in the rain. Because of the frequency of surveys at this site and the large number of fieldworkers involved, we believe that our data represent a confident assessment of black howler population numbers at the CBS.

Our measures of population density are "crude density" estimates (numbers/total area). Two-tailed statistical tests are used for statistical analyses, and level of significance was set at 5%.

Results

Growth rate of population

Figure 1 shows population size and population density for the nine survey years. The intrinsic rate of population increase was computed for two time periods: 1991 to 1996 and 1997 to 1999. Population increase from 1991-1996 was 0.07, from 1997-1999, 0.01. These results indicate that population growth for black howlers at the CBS is density-dependent (see Ricklefs, 1979, p.324), demonstrating an initial period of modest increase,

possibly as a result of recovery from the 1979 population crash and slowing with time. Population growth from 1990 to 1999 may partially reflect growth in howler numbers occasioned by cooperative conservation agreements with landowners at the CBS.

Age distribution of the population

Figure 1 shows the age distribution (percent of individuals in different age classes) of the black howler population at the CBS from 1990 to 1999. If the proportions of the immature age classes (infants, juveniles, and subadults) are summed, immatures represent a relatively large proportion of adults in the population for all years, suggesting that the population is neither rapidly increasing nor declining.

In an attempt to assess the stability of the population over time, a chi square test of proportions was performed for each age classification across the nine years of study. Significant differences in proportions of infants, juveniles, subadults, or adults across years would indicate that density-independent factors are in effect. Insignificant differences across years would suggest that density-dependent factors shape population architecture in important ways. No comparisons were statistically significant (Infants: $\chi^2 = 14.27$, $df = 8$; Juveniles: $\chi^2 = 8.35$, $df = 8$; Subadults: $\chi^2 = 9.8$, $df = 8$; Adults: $\chi^2 = 6.27$, $df = 8$). This pattern implies a stable age distribution and a population that is not rapidly expanding (Odum, 1971).

What is the relationship between increasing population density and age/sex class? While proportions of infants ($r = 0.36$, $df = 7$) and juveniles ($r = 0.64$, $df = 7$) are positively correlated with population density, these coefficients are not statistically significant. Proportions of subadults per year are negatively correlated with increasing population density ($r = -0.32$, $df = 7$), a statistically insignificant coefficient. Proportions of adult females are negatively correlated with increasing population density ($r = -0.34$, $df = 7$); however, this coefficient is, likewise, not statistically significant. Proportions of males in populations are negatively and significantly correlated with increasing population density ($r = -0.78$, $P < 0.02$, $df = 7$). Thus, as population density increased, the proportion of males in black howler populations at the CBS decreased from 1990 to 1999. Coefficient of determination (r^2) equals 0.61. Thus, 61% of the variance in male population numbers is attributable to population density. This relationship is complicated, however, by the observation that, as population density increases, the proportion of groups with >1 male ("multimale groups") increases ($r = 0.59$, $df = 7$, n.s.). Overall, increased population density leads to a decreased proportion of adults in the population ($r = -0.78$, $P < 0.02$, $df = 7$), primarily accounted for by decreases in the proportion of adult males.

Changes in group membership

Table 1 exhibits changes in group membership by age/sex class from 1990 to 1999. Eight (44%) groups had a relatively brief tenure on the study site (≈ 5 years) showing that extinction of groups is a relatively common occurrence during the early years of population increase. This finding suggests that population growth may also result from an increase in the number of groups and length of tenure of groups. The number of groups in the study site increased from 11 to 16 from 1990 to 1999. While

net changes in group membership across years are often positive, net changes across years are small (generally fewer than 5 individuals). The same row as well as inspection of specific groups also indicates that juveniles, subadults, and adults of both sexes emigrate from and immigrate into groups (Brockett *et al.*, 2000).

A related finding of our study demonstrates that of the 128 group counts between 1990 and 1999, 24 (19%) exhibited no or only one immature (infant, juvenile, or subadult). All of these groups were observed from 1990 to 1996 during the period when rate of increase was highest. This result may reflect the establishment of new groups during the phase of population expansion.

Related demographic events in populations

Figure 2 shows our results for mean group size per census year, mean number of males per group per census year, and mean number of adult females to mean number of adult males per

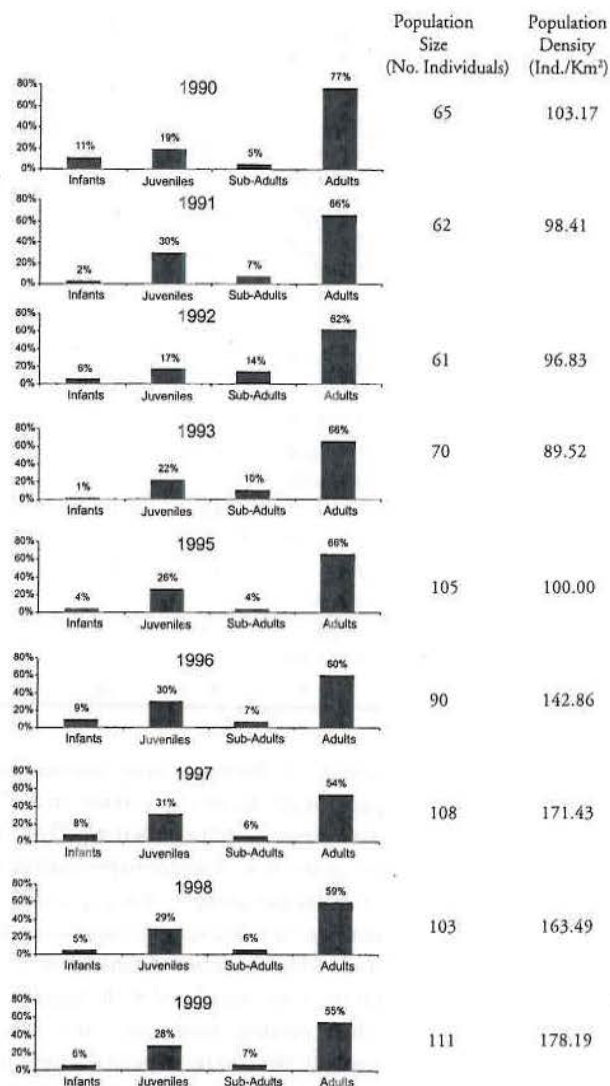


Figure 1. Age distribution per census year (1990 - 1999) for the black howling monkey (*A. pigra*) at the CBS. Population size per year (number of individuals) and population density (individuals/km²) per year displayed to right of each yearly histogram.

Table 1. Changes in group membership of black howlers at the Community Baboon Sanctuary, 1990-1999. Numbers represent net annual changes in each age/sex class for period of group tenure on study site (dates).

| GROUP | AGE/SEX CLASS | | | | | | | | TOTAL |
|-------------------|---------------|----------------|----------------|--------------|---------------|------------------|------------------|----------------|-------|
| | Adult Males | Subadult Males | Juvenile Males | Infant Males | Adult Females | Subadult Females | Juvenile Females | Infant Females | |
| School 1990-99 | 0 | 0 | 0 | 0 | 0 | +2 | -1 | 0 | +1 |
| Baizar 1991-96 | +1 | 0 | -1 | +1 | 0 | 0 | +2 | +1 | +4 |
| Fig 1990-99 | 0 | 0 | +1 | +1 | 0 | 0 | +1 | +1 | +4 |
| Joseph 1995-99 | 0 | 0 | 0 | +1 | 0 | 0 | -1 | +2 | +2 |
| Swamp 1990-99 | +1 | +2 | +1 | 0 | +2 | 0 | 0 | 0 | +6 |
| Baptist 1990-99 | -1 | +1 | +3 | +1 | 0 | 0 | +1 | +1 | +6 |
| Roxie 1995-99 | 0 | 0 | -1 | +2 | 0 | 0 | 0 | 0 | +1 |
| Vincente 1995-99 | -1 | 0 | -1 | 0 | 0 | 0 | 0 | 0 | -2 |
| River 1995 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Wade 1990-99 | +1 | +1 | +1 | +1 | -1 | 0 | +1 | +1 | +5 |
| Bamboo 1990-99 | -1 | 0 | -2 | +2 | -3 | -3 | -2 | 0 | -9 |
| Marsh 1990-95 | -1 | +1 | +1 | 0 | 0 | 0 | +1 | 0 | +2 |
| Della's 1090-99 | 0 | -2 | -3 | +4 | -1 | 0 | 0 | 0 | -2 |
| Y 1990-99 | -1 | +1 | -1 | +1 | 0 | 0 | +1 | 0 | +1 |
| Peninsula 1990-99 | -1 | +1 | +5 | +1 | -1 | 0 | -4 | +4 | +5 |
| No. A 1990-99 | +1 | 0 | +3 | +2 | -1 | 0 | -1 | 0 | +4 |
| A 1990-95 | +1 | 0 | +1 | +1 | -1 | 0 | 0 | 0 | +2 |
| Ghost 1993-99 | +1 | +1 | +1 | 0 | -1 | 0 | +2 | +1 | +5 |
| TOTAL | 0 | +6 | +8 | +18 | -7 | -1 | 0 | +11 | +35 |

census year. Mean group size per year correlates positively with population density. ($r = 0.64$, $df = 7$, n.s.). Coefficient of determination (r^2) equals 0.41. Thus, 41% of the variance in group size is attributable to population density. Mean number of males per group in the population demonstrates a weak positive correlation with population density ($r = 0.26$, $df = 7$, n.s.). Mean number of females:mean number of males per group is not correlated with population density ($r = -0.12$). These findings show that, on average, mean group size is strongly affected by population density and that, on average, numbers of males per group remain relatively stable. Adult sex ratio in the population appears to be independent of population density.

Infant survival and mortality

Based upon an analysis of individually recognized adult females, infant survival was approximated by comparing the number of infants of each sex born in each group per year against the number of juveniles counted in the subsequent year. Thus, if an infant was born in one year and the juvenile age/sex class was not increased by one in the subsequent year, the infant was presumed to have died. Forty-four (44) infants were born from 1990 to 1998. Nineteen (19) infants survived (43%), 12 (63%) of these males (binomial test= 0.0961). Thus, survival appears to affect male and female infants equally.

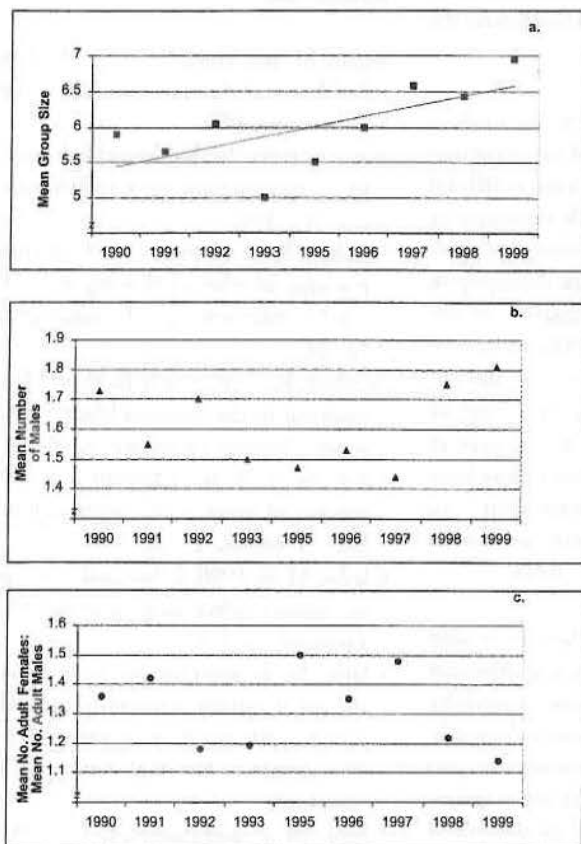


Figure 2. Changes in *A. pigra* population characteristics, 1990-1999 (a, mean group size per census year; b, mean number of males per census year; and, c, mean number of adult females: mean number of adult males per census year.)

Interbirth intervals

Mean interbirth interval (IBI) for the present study was 19.4 months ($N = 64$ IBIs for 32 individually identified females, range = 10-35 months).

Discussion

The present report demonstrates density-dependent population growth for black howlers at the CBS. Figure 1 appears to demonstrate a stable profile. It would be a mistake, however, to consider this description of the population's status as a permanent state or as a linear progression of population growth to be maintained indefinitely. Bolin's (1981) description of a low-density population decimated by a density-independent event (a cyclone) was no more a starting point than is our study the description of an end-point. As Crockett's (1996) report of population growth in the red howling monkey (*A. seniculus*) shows, historical events, both density-dependent and density-independent, affect the dynamics of populations, often in a non-linear manner. Similar conclusions can be drawn from reports for *A. caraya*, the black and gold howling monkey (Rumiz, 1990) and *A. palliata*, the mantled howling monkey (Milton, 1982; Clarke and Zucker, 1994). As a further comparison, it would be instructive to analyze age distributions of Venezuelan *A. seniculus* (Crockett, 1996) and of Costa Rican *A. palliata* (Clarke *et al.*,

1986; Clarke and Zucker, 1994), particularly since environmental perturbations that might have led to temporary or permanent changes in the age distribution are known or suspected for these populations.

Strier (2000) argues that demographic processes are complex in species exhibiting bisexual dispersal (e.g., *Alouatta*) due to the consequences within and between groups of alternative strategies for the establishment of new groups. Decisions by individuals to join existing groups or to found new breeding units may influence sex ratios of immatures and adults as well as their survivorship and fecundity. Table 1 reflects these demographic changes during the study period. Of course, changes can occur in the structure and composition of specific groups due to variations in microsite factors without leading to changes in population parameters. This condition is evident by comparing Figure 1 with Table 1. Group composition varies over time, apparently without major changes in population architecture over time. For *A. pigra* at the CBS, population expansion occurs as a result of bisexual dispersal and the founding of new groups (Horwich *et al.*, in press; Brockett *et al.*, 2000) as reflected in Table 1. These patterns are characteristic of *Alouatta* and may account for the often cited plasticity of their social organization (e.g., Crockett and Eisenberg, 1986).

The finding that increasing population density is positively correlated with increasing numbers of multimale groups has been observed in another study at the CBS (Ostro *et al.*, in press) and has important implications for an interpretation of population growth at the site. Ostro and her colleagues argue that a male's options and decisions will change with changes in population density. Our results support this interpretation and suggest that further studies on the causes and consequences of variations in the number of males in howler groups would be worthwhile (see Nunn, 1999). Overall, increased population density leads to a decreased proportion of adults, in particular, adult males, in the population. It appears, then, that population growth may decrease the ability of single males to monopolize a female group, leading to more multimale groups, possibly as a result of increased male-male competition for females as population density and, possibly, crowding increase. This condition would also result in some males being expelled from the population. Our finding that mean number of males per group in the population decreases with population density can be viewed as a consequence of increased group size with increases in population density.

As Strier (2000) notes, mechanisms of dispersal and group establishment may also have consequences for life history parameters (survival and fecundity). More than 50% of infants died in our study. Our estimates of infant survival (43%) are closer to Clarke and Glander's (1984) findings (55%) for mantled howlers in Costa Rica than Crockett and Rudran's (1987) (>80%) for Venezuelan red howlers. It is interesting to note that population density is high at both the CBS and Hacienda la Pacifica. Our data are similar to those of Crockett and Rudran (1987) with respect to survival of infants as a function of sex. For both black howlers at the CBS and red howlers, a larger proportion of male infants survive, although the results are not significant for *A. pigra*, possibly due to small sample size. Mantled howlers exhibit the opposite pattern (Clarke and Glander, 1984), a finding that

may relate to differences in social organization between black and red howlers, on the one hand and mantled howlers on the other.

Mean interbirth interval observed in the present study is comparable to those reported for other species of the genus (20-22.5 months) by Strier (2000, Table 7.3). The range in IBIs for black howlers at the CBS indicates that female reproductive physiology is highly plastic and capable of responding to variable population events such as infanticide and stochastic demographic processes such as fluctuations in population density. Crockett (1998) reports that the reproductive potential of howler monkeys is high relative to body size since reproductive parameters such as IBIs are short relative to body size. Citing the literature, she suggests that this condition may represent adaptation to "opportunistic habits", recurrent yellow fever epidemics, or relatively small brain size (to body size ratio). The greater reproductive potential of howlers may in part explain their success in disturbed conditions (Crockett, 1998).

In conclusion, population growth in the black howler monkey at the CBS is density-dependent, and population architecture as measured by the proportion of infants, juveniles, subadults, and adults in the population across years appears to be stable. Further studies are required to describe the environment's impact upon *A. pigra* at the CBS and to compare and contrast its specific features with those of its congeners. Our research also documents changes in group membership across years which impact population growth and indicates possible causes and consequences of these changes, including bisexual dispersal, increased group size, increases in the number of groups over time, and increases in the length of tenure of groups. The mechanisms of these patterns require investigation. Our studies, like those of Clarke and Glander (1984) on mantled howlers at Hacienda la Pacifica, exhibit high infant mortality. This pattern is consistent with life history tactics that favor adult over juvenile (including infant) survivorship, as reported for *A. palliata* at Hacienda la Pacifica by Jones (1997). The factors underlying these results require investigation within and between species of *Alouatta*. Finally, similar to the findings of Ostro *et al.* (in press), our findings indicate that population growth may have significant consequences for the reproductive tactics of adult males. In particular, increased population density may increase male-male competition for groups and their resident adult females, and may influence a single male's ability to monopolize female groups.

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