POPULATION STRUCTURE AND GROUP PRODUCTIVITY OF THE BELIZEAN BLACK HOWLING MONKEY (*ALOUATTA PIGRA*): IMPLICATIONS FOR FEMALE SOCIOECOLOGY. HORWICH, R.H., BROCKETT, R.C., JAMES, R.A. AND JONES, C.B.

Key words: *Alouatta pigra*, Belize, population structure, population density, group productivity, density-dependence, relative reproductive success, female sociality

Abstract

The assembly and architecture of populations are functions of decisions made by individuals for the optimization of lifetime survival and reproductive success. We analyzed the results of 12 longitudinal surveys (209 group counts) of Belizean black howling monkeys (*Alouatta pigra*) at the Community Baboon Sanctuary (CBS) in an attempt to describe population structure and group productivity over time. Similar to previous reports of black howlers at several sites, modal group size was found to be one adult male and 2 adult females. Group size ranged from 2 to 16 and maximum female group size was 4 as reported for other species of polygynous *Alouatta*. Population density ranged from 8.14-178.19 individuals per km^2, one of the highest densities ever recorded for *A. pigra*. Group size was significantly positively correlated with population density, and 52 % of the variance in group size was explained by population density. Female group size and number of immatures per group were positively correlated. An analysis of the least squares regression line for female group size and the number of immatures per group found 9 of 12 surveys experiencing density-dependent conditions. Relative reproductive success, the mean number of immatures:females per female group size, decreased with increasing female group size suggesting that females in larger groups are at a disadvantage due to decreases in survivorship and/or fecundity. Again, density-dependent conditions appeared to be operating. Our analysis of gains and losses to 19 groups from 1995-1997 suggests that the black howler population at the CBS is at equilibrium or slightly increasing, primarily as a result of recruitment of immatures (infants, juveniles, and/or subadults). If female black howlers at the CBS experience density-dependent conditions, they may undergo significant food competition contrary to predictions of the "ecological model" for folivorous primates. The different conditions predicted by the least squares regression analysis (density-dependence, density-independence, or an advantage to large groups) may define the domains of selective pressures generating variations in group size as a function of decisions made by individuals optimizing inclusive fitness. These and other findings have important implications for female social relations in *Alouatta*. At present we cannot distinguish between competition for limiting food resources and infanticide as the proximate mechanism limiting female group size in black howlers and other polygynous howlers.

Introduction

First principles of ecology indicate that the size and composition of groups change in response to temporal environmental heterogeneity and may have important consequences for the survival and fecundity of organisms (ROUGHGARDEN, 1979;

PULLIAM and CARACO, 1984). Population abundance and structure (including group size) through time is an attribute of resource predictability (ROUGHGARDEN, 1979). High resource predictability combined with high resource quality, relatively homogeneous spatial dispersion of resources, and resource tracking by the animal population is expected to favor resource defense (e.g., contest competition or territoriality) by individuals or small groups, on average, whereas low resource predictability combined with large distance or high variation in distance between patches may make resources indefensible, yielding large average group size (PULLIAM and CARACO, 1984; EMLEN and ORING, 1977; SCHOENER, 1971; ROUGHGARDEN, 1979). Since temporal unpredictability of resources may be positively correlated with spatial uncertainty ("patchiness"), foraging in groups may reduce average searching time per individual group member; thus, environmental predictability will be inversely correlated with group size (PULLIAM and CARACO, 1984; WITTENBERGER, 1980; SCHOENER, 1971). The advantages of group life (e.g., increased predator defense) should also increase directly with an increase in group size (PULLIAM and CARACO, 1984; WITTENBERGER, 1980). In the present report, we measure population structure and group productivity of black howling monkeys; however, few data are available on the dispersion and quality of their resources in time and space.

Population structure has significant consequences for genes and the individuals that carry them (HEWITT and BUTLIN, 1997). Population structure may be evident as subdivision into demographic subunits or groups which represent an evolutionary compromise among those parameters yielding optimal inclusive fitness to individuals (WILSON, 1975; WITTENBERGER, 1980; DUNBAR, 1996; PULLIAM and CARACO, 1984). As WILSON (1975) points out, the frequency distribution of group sizes will be a function of those phenomena leading individuals to join and to leave groups combined with the selection pressures on individual responses to these forces. The parameters determining modal group size, thus, are ultimately expressed as adaptations of individuals to local environments (WITTENBERGER, 1980; WILSON, 1975; DUNBAR, 1996).

In the same local conditions, males and females may adopt different adaptive tactics and strategies due to the constraints of anisogamy, differential investment in gametes between the sexes (TRIVERS, 1972). Anisogamy has consequences for group size since, all other things being equal, females are expected to adopt those behavioral programs conferring the greatest benefits from the conversion of resources, especially food, into offspring, while the distribution of males is expected to map onto the dispersion of females or their resources in order to optimize fertilization success (EMLEN and ORING, 1977; BRADBURY and VEHRENCAMP, 1977; WRANGHAM, 1980; WITTENBERGER, 1980; also see SCHOENER, 1971). While the availability of energy will ultimately limit group size for populations in density-dependent conditions (WILSON, 1975; WITTENBERGER, 1980), modal population structure and female social relations are expected to be a function of resource distribution, abundance, and quality in time and space as well as other factors (e.g., predation, male coercion, habitat saturation [STERCK et al., 1997; WRANGHAM, 1986; van SCHAIK, 1989).

Several authors have studied variability in *Alouatta* population structure (da SILVA, 1981; ESTRADA, 1982; THORINGTON, 1984; CURDTS, 1993; CLARKE

1994; CROCKETT, 1996; CHAPMAN and BALCOMB, 1998; FEDIGAN, 1998). Explanations for observed differences in population dynamics within and between howler species have been attributed most commonly to historical factors such as disease, anthropogenic effects (e.g., deforestation or hunting), or phase of population growth rather than to habitat productivity. CHAPMAN and BALCOMB (1998) conclude that longitudinal studies of the same population are required to understand the causes and consequences of primate population structure. Here we report the results of long-term surveys of black howling monkeys (*A. pigra*) at one Central American location in an attempt to assess the relationship between population structure and the sizes of demographic subunits and potential benefits and costs to individuals, particularly females, and to assess our findings in terms of female socioecology.

Methods

Study Area, Site, and Animals

A. pigra is confined to Belize, northern Guatemala, and southeastern Mexico and is 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). Black howlers have been found in polygynous (single breeding male) or polygynandrous (multimale-multifemale) groups (CROCKETT and EISENBERG, 1986; OSTRO et al., 1999), and studies of demography, ecology, genetics, social organization and behavior are in their early stages (e.g., BOLIN, 1981; HORWICH, 1983; JAMES et al., 1998; OSTRO et al., 1999; HORWICH et al., 2000).

The present study was conducted at the Community Baboon Sanctuary (CBS), Belize District, Belize, C.A. (17°33' N, 88°35' W), a managed reserve of 47 km² formed in 1985 by 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 forest fragments, including riparian habitat along the Belize River (HORWICH and LYON, 1990). The landscape of the CBS is continuously changing due to farming, including "milpa" (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 1985-1999, home ranges have contracted, and our 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).

Details of the study site can be found in HORWICH and LYON (1990) and SILVER (1998). In brief, forest rhythms are seasonal, with new leaf production occurring primarily during early rainy season (late May or early June). In the Belize District of northern Belize, flower production demonstrates a large peak during dry season (February through May), with a second, smaller peak occurring about one month after the initiation of 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) 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.

Data Collection and Analysis

A. pigra have been studied since 1979 (BOLIN, 1981) at the CBS, with systematic research beginning in 1983 by R.H.H.. Researchers surveyed and mapped a 4.05 km² area from 1985-1989 and the 0.63 km² primary study site from 1990-1999 where trails were cut and > 1500 trees were identified 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., R.C.B. and their field assistants. The 1988 census was conducted by B. Hartup (University of Wisconsin, Madison), and the 1993 census was conducted by S. Koss (Community Conservation, Inc.). Several surveys were eliminated from analysis due to incomplete data sets. Selected units and lone individuals, in particular, emigrating juveniles, were followed closely at specific times. Ad lib. behavioral observations were also made during these periods of study, concentrating, especially, on male takeovers, patterns of dispersal, and social behavior within groups (see BROCKETT et al., 1999; HORWICH et al., in press; BROCKETT et al., 2000a,b]. Age/sex classification followed the system of CLARKE (1990) for *A. palliata*, and sub-adults were counted as juveniles except for the analysis in Table 3 in which age/sex classes are treated separately. "Immatures" include infants, juveniles, and/or subadults. 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, and line-transect censuses were conducted following standard methods devised for the survey of primate populations (NATIONAL RESEARCH COUNCIL, 1981). We defined a demographic group as any bisexual unit of two or more (reproductive) individuals residing on a home range. For purposes of statistical analysis, we employed female group size (the number of females per group) after WITTENBERGER (1980) since polygamy is a direct function of female social relations, even where males herd females (e.g., *Papio hamadryas* [see WITTENBERGER, 1980, p. 199]). "True censuses" (counting all individuals in the study area) (SMITH, 1966) were possible because we had the manpower to count every individual black howler monkey encountered in the study areas, because black howlers are relatively sedentary and faithful to their home range, because black howlers are relatively easy to locate due to their sonorous 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 ≈ 1,250m/h on parallel transects through the forest ≈ 20 meters apart. One member of each search party walked ≈ 15 m behind the other surveyors, most of whom were familiar with the habits of *A. pigra* and were experienced field workers, students, or local inhabitants. Return walks and rotation of observers between transects on different days were conducted opportunistically, a possible

source of error. When an individual or group 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. Positions of individuals and groups encountered 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, it is likely that our data represent a confident assessment of population numbers at the CBS.

Our measures of population density are "crude density" estimates (numbers/total area). For comparative analysis, we considered BOLIN's (1981) census to be temporally independent of our 1995 survey; thus, certain conclusions rely upon comparisons of these two studies. Correlation and linear regression analyses treated each census as an independent event, similar to previous studies of howlers (CROCKETT, 1996; also see CHAPMAN and BALCOMB, 1998, Table IV). Significance level was set at 5 % for all tests, and all tests are two-tailed unless noted otherwise. Other details of our quantitative analyses can be found in the Results.

Results

Population Structure

Frequency distribution of group sizes. The frequency distributions of group sizes for Bolin's [1981] 1979 survey and our 1995 census are displayed in Figures 1a and 1b, respectively. A total of 55 individuals in 11 groups were counted in 1981 while 105 individuals in 19 groups were counted in 1995. In 1979, mean (±s.d.) group size was 4.23±1.59 individuals (range= 2-7); in 1995, mean (±s.d.) group size was 5.53±2.34 (range= 2-12) (t_{30}= 1.76, P<.05, one-tailed). Coefficients of dispersion (CD) were .60 and .99 in 1981 and 1995, respectively. Thus, the 1979 census exhibited a dispersion of group sizes displaying a "repulsed" distribution having more observations than expected at the center of the distribution and fewer than expected at the tails and suggesting that the standard deviation is less than expected by chance alone (SOKAL and ROHLF, 1981). The 1995 census exhibited a dispersion of group sizes displaying an essentially Poisson distribution in which the variance approximates the mean.

For all surveys, group size ranged from 2 to 16 with mean group size ranging from 4.23 to 6.94 (Table 1). Coefficients of dispersion (Table 1) are generally repulsed except in 1995, 1996, and 1997.

Population density. Population density ranged from 8.14 to 178.19 individuals per km^2 (Table 1). Population density increased from 1979 to 1999 and current densities represent the highest reported for black howlers at any site (see CROCKETT and EISENBERG, 1986; CHAPMAN and BALCOMB, 1998). The trends that we report suggest that population density at the CBS may be stabilizing since 1995 suggesting that saturation of the monkeys may have reached or is close to carrying capacity.

Similar to findings for *A. palliata* and *A. seniculus* (CROCKETT and EISENBERG, 1986; also see ZUNINO, this issue), population density across years is posi-

tively and significantly correlated with mean group size (r= .72, p<.002, df= 10). As population density increases, so does group size, on average. The coefficient of determination (r^2) equals .52. Thus, 52 % of the observed variation in group size is a function of population density.
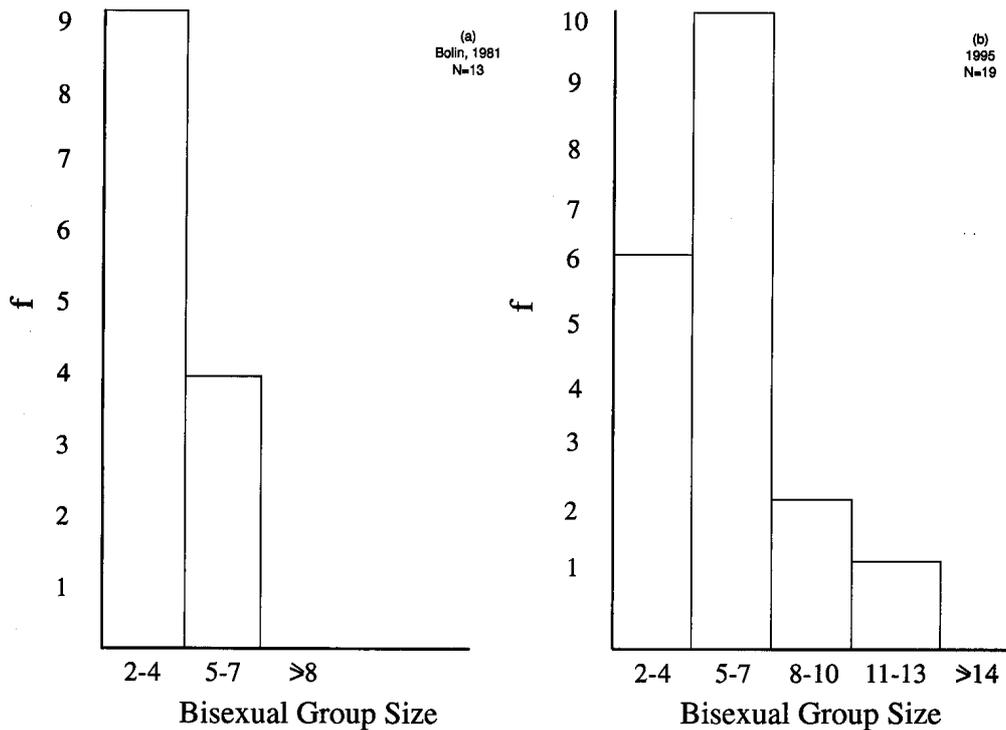

Fig. 1: Frequency distributions of group sizes for two surveys of Belizean *A. pigra* (1979 and 1995).

Intrinsic rate of increase can be compared for two time periods to assess whether population growth at the CBS is density-dependent after the method presented by RICKLEFS (1979, p. 324). Computing intrinsic rate of increase for the time period 1990-1999 during which time the size of the study site was invariant, intrinsic rate of increase for the period 1990-1996 was .05, from 1997-1999, .004. Thus, population increase at the CBS was density-dependent, with an early period of modest increase and a later period of equilibrium.

Composition of groups. Table 1 displays the adult sex ratio (mean no. males/females) for each census. The adult sex ratio ranges from 1:1.07 in 1979 to a high of 1:1.65 in 1995. Modal number of males is 1 in every census except 1990 and 1996 when modal number of males was 2, and modal number of females is 2 in every census except 1979 and 1992. In 1979 modal female group size was 1, and in 1992 female

group size demonstrated a bimodal distribution of 1 and 3. *A. pigra* at the CBS, thus, demonstrate a polygynous group structure with a modal group size of one adult male and one to three adult females, consistent with other reports of black howlers (CROCKETT and EISENBERG, 1986; WOLFHEIM, 1983; CHAPMAN and BAL-COMB, 1998). Interestingly, consistent with other reports on polygynous *Alouatta* (CROCKETT and EISENBERG, 1986; CROCKETT, 1996; CROCKETT and JAN-SON, 2000; G. ZUNINO, personal communication, 2000; C.B. JONES, unpublished data), we have never observed an adult female group size > 4. Thus, adult female group size in polygynous howling monkeys is highly conserved.

For the survey as a whole, the number of males per group ranges from 1 to 4 (Table 1). The number of males per group is not related to the number of females per group (r= .04, df= 207, n.s.). Thus, males do not appear to remain in groups or to immigrate into groups based upon the size of the female group.

Table 1: Population characteristics (1979-1999) of Belizean black howler monkeys (*Alouatta pigra*). Range in parenthesis.

	1979	1985	1988	1990	1991	1992	1993	1995	1996	1997	1998	1999
Study Area km^2	7	4.05	4.05	0.63	0.63	0.63	2.10	0.63	0.63	0.63	0.63	0.63
No. Groups	13	24	22	11	11	10	36	19	15	16	16	16
Pop. Density	8.14	31.85	33.33	103.17	98.41	96.83	89.52	166.67	142.86	171.43	163.49	178.19
Mean No. Females (range)	1.15 (1-2)	1.75 (1-3)	2.18 (1-4)	2.36 (1-4)	2.18 (1-4)	2.00 (1-3)	1.83 (1-4)	2.21 (1-4)	2.07 (1-4	2.13 (1-4)	2.13 (1-4)	2.06 (1-4)
Mean No. Males (range)	1.08 (1-2)	1.29 (1-2)	1.45 (1-4)	1.73 (1-2)	1.55 (1-3)	1.70 (1-4)	1.67 (1-4)	1.47 (1-2)	1.53 (1-2)	1.44 (1-2)	1.75 (1-3)	1.81 (1-3)
Mean No. Immatures (range)	2.00 (0-4)	2.38 (0-5)	2.50 (0-6)	1.81 (1-5)	1.91 (2-8)	2.40 (1-5)	1.72 (0-4)	1.84 (0-6)	2.40 (0-7)	3.19 (1-10)	2.56 (1-5)	3.06 (1-6)
Mean Group Size (range)	4.23 (2-7)	5.38 (2-10)	6.09 (3-11)	5.91 (4-10)	5.64 (2-8)	6.10 (3-9)	5.22 (2-9)	5.53 (2-12)	6.00 (3-13)	6.75 (4-16)	6.44 (4-11)	6.94 (4-11)
CD*	0.60	0.79	0.75	0.59	0.65	0.53	0.66	0.99	0.98	1.27	0.66	0.62
Mean No. Males/Females	1:1.07	1:1.35	1:1.50	1:1.37	1:1.41	1:1.18	1:1.11	1:1.65	1:1.35	1:1.48	1:1.21	1:1.14
r**	0.33	0.55***	0.49***	0.35	0.35	0.00	0.04	0.56***	0.46	0.81***	0.40	0.13
b_{yx}****	1.18	0.06	0.72	0.57	0.42	0.00	0.06	0.85	0.97	2.40	0.60	0.28

CD* = Coefficient of dispersion (variance/mean)
r** = Pearson Product-Moment correlation coefficient (No. adult females per group: No. immatures per group)
*** = P<.05
b_{yx}**** = Slope of the least squares regression line (No. adult females per group: No. immatures per group)

Group Productivity
Do groups with more females have more immatures? Table 1 shows that, for every year except 1992 and 1993, female group size and number of immatures is positively correlated. The positive correlation is significant for only four surveys, however (1985, 1988, 1995, and 1997, Table 1). Thus, in general, larger female group sizes are associated with more immatures per group.

An indirect test of female survivorship and/or fecundity. Increased group size may have no effect, a positive effect, or a negative effect upon female survivorship and/or fecundity (WITTENBERGER, 1980). One test of these three possible outcomes, suggesting three underlying causal mechanisms, is to employ the slope of the least squares regression line (b_{yx}, Table 1) for female group size and the number of immatures per group where a slope ≈ 1 implies density independence, a slope >1 implies that there are advantages to living in large groups, and a slope <1 implies that density-dependence may be operating (BEGON and MORTIMER, 1986; RICKLEFS, 1979; P. HERTZ, personal communication, 1986). The slope of the least squares regression line ranges from 0 in 1992 to 2.40 in 1997 exhibiting significant variability. Nine of the 12 surveys (binomial test, p= .0048) exhibit $b_{yx}<1$ suggesting that folivorous black howler females at the CBS experience density-dependence and may undergo significant competition for limiting food resources, contrary to the "ecological model" of female social relations (WRANGHAM, 1980; STERCK et al., 1997). In 1996, density-independent conditions prevailed, possibly resulting from the deforestation of an area of the study site which may have led to unstable population dynamics. Female survivorship and/or fecundity also appear to have been density-independent in 1979, a year of very low population density and, possibly, rapid rate of increase. In 1997, the only year exhibiting a slope >1, the advantage to large groups may have been a response to recovery from the clearing in 1996. This census also exhibited a clumped distribution of group sizes (Table 1) and a very high correlation between female group size and number of immatures per group which also may have resulted from individuals' decisions after habitat alteration. The clumped distribution of group sizes in 1997 suggests that the deforestation in 1996 may have led many individuals to colonize unoccupied habitat (leading to a larger number of small groups) or to join existing groups (leading to more larger groups). As pointed out above, a test of these ideas shows that recruitment of immatures primarily accounts for the differences between the years, indicating a high incidence of dispersal and a high reproductive rate.

Relative reproductive success. As displayed in Table 2, relative reproductive success (RRS) may be defined as the mean number of immatures:females per female group size JONES, 1996, p. 21). Relative reproductive success is a measure of reproductive rate and female productivity which may differ as a function of female group size. The correlation between female group size and relative reproductive success is negative (r= -.43, p<.01, df= 42) consistent with the results found by van SCHAIK (1983), ISBELL (1991) and CROCKETT and JANSON (2000). Thus, for *A. pigra* at the CBS, relative reproductive success decreases with increasing female group size, suggesting that, in general, females in larger groups are at a disadvantage, presumably because survivorship and/or fecundity decrease with increasing female group size. This conclusion is consistent with our findings reported above indicating density-dependent conditions.

Is the black howler population at the CBS increasing, decreasing, or at equilibrium? Table 3 presents all individuals gained and lost in six age/sex classes for 19 black howler groups surveyed from 1995-1997 at the CBS. Infant sex ratio is equal. The results of gains and losses to all groups reflect births, deaths, immigra-

tions, and emigrations. Gains and losses do not occur equally by age/sex class (X^2= 31.63, df= 5, p<.001). Thus, more infants are added (born) and fewer infants are lost than one would expect by chance alone. Fewer juvenile males are added and more juvenile males and females are lost than one would expect by chance alone, possibly reflecting patterns of immigration and emigration as well as mortality. Fewer adult males are added and more adult males are lost than one would expect by chance, possibly reflecting patterns of mortality, immigration, emigration, and male-male competition for group membership. The composition of adult females in groups appears to be relatively stable over time, and increases in group numbers appear to be a primary function of births. Overall, additions to groups outnumber losses, suggesting that the population of black howlers at the CBS is at equilibrium or slightly increasing, as our results for population density presented above suggest.

Table 2: Relative reproductive success (RRS) per year in Belizean black howling monkeys at the CBS.

Year	Female Group Size			
	1	**2**	**3**	**4**
1979	1.81	1.50		
1985	1.63	1.21	1.67	
1988	2.00	1.00	1.10	1.00
1990	1.00	0.75	0.89	0.50
1991	1.00	1.00	0.84	0.50
1992	2.50	1.00	0.84	
1993	1.54	1.03	0.61	0.00
1995	1.20	0.64	0.80	1.50
1996	1.75	1.50	0.67	1.75
1997	1.50	1.36	1.33	2.50
1998	1.67	1.33	0.89	1.00
1999	2.50	1.54	0.67	1.00

Table 3: Individuals added and lost for six age/sex classes in 19 black howler groups surveyed from 1995-1997 at the CBS.

	Added	**Lost**	**Total**
Adult Females	0	2	2
Adult Males	2	8	10
Juvenile Females	1	4	5
Juvenile Males	1	7	8
Infant Females	15	2	17
Infant Males	13	1	14
Total	32	24	56

Discussion

Population Structure

Belizean *A. pigra* exhibit group sizes and compositions consistent with reports from other sites (CROCKETT and EISENBERG, 1986; SILVER, 1998; OSTRO, 1998), though the present studies found population densities higher than those reported at several other sites in Central America (CHAPMAN and BALCOMB, 1998). HORWICH and LYON (1987) noted that the CBS appeared to have especially high concentrations of black howlers compared to other Central American sites. Nonetheless, densities in our study may be inflated due to the present method of calculating population density relative to the small size of our study area and because sizes of study areas are not consistent across all years.

BOLIN's (1981) report of a modal "monogamous" population structure at the CBS was interpreted by HARTUP (1989) to have resulted from "increased female mortality due to extreme environmental conditions from which the population was recovering at the time" (p. 52). Our studies support Hartup's interpretation, and we conclude that Belizean black howler population structure is comprised predominantly of polygynous subunits. We document variations in bisexual group size from 2-16 individuals which we consider to be a reflection of the potential of local conditions to support groups as well as the tendency for black howlers to utilize colonization as a mechanism of group formation after dispersal from natal or resident groups (BROCKETT et al., 2000b). This dispersal strategy has also been reported for *A. seniculus* (e.g., POPE, 1992) and for Costa Rican *A. palliata* (e.g., FEDIGAN et al., 1998). In 1997, a clumped coefficient of dispersion (Table 1), in which distributions have an excess of small and large groups, may have been the result of extensive cutting at the CBS by one landowner in 1996 significantly altering the landscape. Inspection of the data show that 28 individuals were added to groups in 1997 from 1996, 25 of these recruitment of infants and juveniles and six of these immigrating sub-adults. In addition, one new group was formed. Thus, habitat alteration may have significant consequences for the size, composition, and distribution of groups.

Our measurements of adult sex ratio also support the conclusion that Belizean black howlers are polygynous. Our studies of black howlers at the CBS suggest, however, that male turnover has increased with increasing population density and that infanticide and female dispersal may accompany changes in male tenure (BROCKETT et al., 1999; HORWICH et al., 2000; BROCKETT et al., 2000b], and the present report demonstrates that losses in adult male group membership are greater than expected while additions are less than expected by chance alone. Thus, it appears that male-male competition for group membership and consequent access to fertilizable ova are not insignificant effects, at least when population density is high. These responses require further study and may be related to the costs and benefits to females of group membership as STERCK et al.(1997) suggest.

Group Productivity

Our results indicate that females at the CBS may experience density-dependent conditions. Thus, competition for limiting resources, possibly food, may be intense for black howlers. This finding is not predicted for folivores by the ecological model and raises the possibility that female dispersal in *Alouatta* may result from avoidance of

deleterious interactions with kin. Density-dependent conditions may also depress survivorship and/or fecundity of females and may explain our finding that relative reproductive success decreases with increasing female group size.

Results of the analysis of the least squares regression line (b_{yx}, Table 1) for female group size and the number of immatures per group demonstrated a significant trend whereby 9 of 12 surveys exhibited density-dependence. The remaining groups exhibited density-independence or an advantage to large groups. These three conditions may partially explain variation in group size in black howlers and other animals since mortality of immatures and adult survivorship and fecundity may be responsive to different selective pressures over time with significant implications for life-history (STEARNS, 1992; JONES, 1997). This is a potentially important area of study since it may identify the selective regimes acting on individuals who emigrate, immigrate, colonize open habitat, and make other decisions relative to their inclusive fitness.

Relative reproductive success (RRS) ranged from 1.00 to 2.50 in the present study. In comparison, RRS for the polygynandrous *A. palliata* at two seasonal sites in Central America ranged from 0.17-1.23 (JONES, 1996). Thus, polygynous black howlers achieve a higher RRS at the low and high ends of the range of values compared with mantled howlers with a multimale-multifemale group structure. These results suggest that smaller, polygynous groups are more productive than polygynandrous groups, on average, and that reproductive success is more variable in polygynandrous groups. If female sociality is favored by small *c*(*osts*), large *b*(*enefits*), and small *N* (group size) (MAY, 1984), then, all other things being equal, higher survivorship and fecundity are expected where a (modal) polygynous population structure is found. This interpretation is supported by our findings, as discussed below.

The Evolution of Female Sociality in Alouatta

Sociality evolves under density-dependent conditions (FRANK, 1998). Population structure, including the assembly of demographic sub-units, and group productivity will be driven by female decisions regarding the optimization of inclusive fitness by the conversion of resources into offspring, and the architecture of males within and between groups will be a function of the choices that females make (see NUNN, 1999). These choices have, for most primate females, yielded patterns of association whereby the benefits of sociality usually outweigh its costs. In the primate literature, particular attention has been paid to the association between ecological factors (e.g., within- and between-group competition for resources and habitat saturation) and the nature of female relationships (e.g., the strength of bonds among females and the consequences of these for patterns of female philopatry, protection against male coercion, and defense of resources [WRANGHAM, 1980, 1986; van SCHAIK, 1989; STERCK et al., 1997]). STERCK et al. (1997) have recently tested and refined the assumptions of WRANGHAM's (1980) "ecological model". Their results have significant implications for students of *Alouatta* and other primates.

STERCK et al. (1997; see also DUNBAR, 1996) propose a model of "the dynamic relationship between group size and group growth rate in gregarious primates" (p. 295). According to this formulation, group size is an inverted-U function whereby

competition and group size increase to an equilibrium value after which selective forces counteract increasing group size towards an optimum value. Group size also has a "minimum viable" value below which groups become extinct. Productivity of the group is greatest at optimum group size. The data presented in the present report show that relative reproductive success of black howlers decreases with increasing female group size, similar to numerous other primate species (van SCHAIK, 1983; CROCKETT and JANSON, 2000). Thus, consistent with the "polygyny threshold" model (ORIANS and WILLSON, 1964], smaller female group sizes are more productive, and selective forces may have operated (e.g., increased competition for food) to limit increases in group size. An analysis of the same relationship in 11 surveys of *A. palliata* suggested that density-dependent effects were operating in 5 (binomial test, p= .1830), while the remainder exhibited either an advantage to large group size or density-independence (C.B. JONES, unpublished data). While these comparisons are indirect and tentative, they suggest that, contrary to the predictions of the ecological model, folivores may experience significant competition for food. Recent studies by KOENIG et al. (1999) on Hanuman langurs (*Presbytis entellus*) support this conclusion.

Also, contrary to the ecological model, within-group competition among folivores may favor relationships among non-kin and lead to female dispersal since mutualistic associations among relatives may increase competition for resources due to increased niche overlap (PEREZ-TOME and TORO, 1982). *Alouatta* species demonstrate female dispersal while *P. entellus* generally do not. Thus, we would predict that ecological competition is greater among howler monkeys than for Hanuman langurs. Since associations among non-kin may also favor increased reproductive rates (COLE and WIERNASZ, 1999), female dispersal by *Alouatta* females may represent an evolutionary tradeoff between the benefits of philopatry and the benefits of low relatedness.

WITTENBERGER (1980) provides theoretical models for the evolution of female sociality. The present results are consistent with two of Wittenberger's routes to female sociality. For Wittenberger's "Case 1", adult female survivorship increases as group size increases; however, reproductive rate decreases with an increase in group size, similar to our findings for the relationship between RRS and female group size. Wittenberger suggests that female survivorship may increase because of increased benefits from predator defense while reduced female reproductive rates might be a function of longer interbirth intervals, increased competition among offspring for resources, or interference behavior by other adults. The latter condition might involve infanticide by males. While our study strongly supports the conclusion that reproductive rate decreases with female group size in *A. pigra* because RRS decreases with increasing female group size, we cannot demonstrate that female survivorship increases with female group size. However, conservative female group size in polygynous howlers (≤ 4) may indicate that female survivorship is compromised when female group size is > 4, possibly creating extreme selection on a maximum female group size.

WITTENBERGER's (1980) "Case 5" predicts solitary breeding or monogamy because the costs of larger groups (e.g., increased competition for food or increased exposure to infanticide) lead to decreased female survivorship and fecundity as group size increases. BOLIN (1981) concluded that black howlers are monogamous and

16% (31/196) of the groups in our sample (1985-1999) contained just one adult male and one adult female. Further, because RRS decreases with an increase in female group size, our results suggest that reproductive rates may be highest in monogamous mating units. If this is so, why does the body of evidence suggest that black howlers at the CBS and elsewhere are polygynous? We suggest that a female group size of one may be optimal for female fecundity but that a female group size of one is unstable because of environmental heterogeneity, benefits from other sources (e.g., predator detection or access to food), pressure from female immigrants, or other factors. If Case 5 explains costs and benefits to female *A. pigra*, a maximum female group size of 4 may result from extreme selection pressure against female sociality. Our studies of grooming in black howlers at the CBS indicate that adult female social relations are relaxed or avoidant (BROCKETT et al., 2000a), consistent with this idea. At present we cannot distinguish between Case 1 and Case 5 as the most likely explanation of social relations among black howler females; however, the present analysis may apply, as well, to other polygynous howlers.

We also cannot distinguish between the alternate hypotheses that density-dependence, decreasing relative reproductive success with increasing female group size, and conservative female group size are a function of constraints imposed by limited food (van SCHAIK, 1983) or male infanticide (CROCKETT and JANSON, 2000). CROCKETT and JANSON show that for *A. seniculus*, infanticides increase with increasing female group size. Our limited data on infanticides (N= 5, observed directly or inferred) at the CBS (BROCKETT et al., 1999) demonstrate no such tendency; however, the pattern is suggestive. Three of the five infant disappearances in association with male takeovers occurred in a group containing three reproductive females. The other two infant disappearances occurred in groups containing one reproductive female each. However, in one of these cases, the resident male was usurped by two sub-adult males and in the second case, the usurping male had tried unsuccessfully to enter two other groups containing two and three reproductive females, respectively. Thus, entering groups with few reproductive females may represent an alternative male behavior when more attractive and beneficial options are unavailable or unattainable. Our findings are consistent with both hypotheses (food limitation and infanticide) and do not undermine observations suggesting that *Alouatta* females and other folivorous primates may compete for limiting food resources (JONES, 1980; FEDIGAN et al., 1998; BROCKETT et al., 2000b; KOENIG et al., 1999; van SCHAIK, 1993; ISBELL, 1991).

A problem in differentiating the two hypotheses is that they make similar predictions. However, a possible test of the ideas may result from comparing the relationship between reproductive success and female group size in two demes of the same species in the same habitat at equivalent population densities, one in which infanticide is expressed and one in which infanticide is not expressed. If CROCKETT and JANSON's (2000) ideas are operative, it would be predicted that reproductive success would not decrease with increasing female group size in the population in which infanticide is not expressed since density-dependent competition for food would not be expected to limit population growth where constraints from infanticide are relaxed. Langurs may be an appropriate taxon for these tests. Density-dependent limits on female group size in polygynous howlers may be a function of both female-female competition for limiting food resources and infanticide.

In conclusion, *Alouatta* species present a challenge to students of socioecology because of their wide geographic distribution and success in a broad range of habitats (CROCKETT and EISENBERG, 1986). The present report of *A. pigra* at the CBS demonstrates density-dependent conditions constraining population growth and group productivity. Similar to other studies of the species, black howlers at the CBS were most likely to be organized as polygynous groups consisting of a single adult male and one to four adult females plus immatures (infants, juveniles, and/or subadults). The population densities reported here are among the highest documented for the species, and group size increased with increasing population density. Females in smaller groups displayed higher relative reproductive success, possibly due to increased survivorship and/or fecundity. It is hypothesized that density-dependent conditions at the CBS favor female sociality up to a group size of, and female group size may be limited by resources and/or infanticide. Future studies of black howlers will address questions of general importance to primatology such as: What is the intensity of ecological competition within and between groups? What tactics do females employ to avoid the costs of infanticide by males? Is the rate of female dispersal altered by habitat saturation? Why do polygynandrous *A. palliata* differ in significant ways from their polygynous congeners? Future studies will also address the particular mechanisms of group establishment as well as the temporal, spatial, and nutritional characteristics of the animals' food sources in an attempt to test the hypothesis that black howler population subdivision is a function of resource tracking of predictable, relatively high-quality and homogeneously dispersed food sources. These and other questions are extensions of the topics addressed in the present report.

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