CHAPTER FOUR

Demographic Features of *Alouatta pigra* Populations in Extensive and Fragmented Forests

Sarie Van Belle and Alejandro Estrada

INTRODUCTION

The black howler monkey of Mesoamerica, *Alouatta pigra*, is a primate species endemic to the area shared by Mexico, Belize, and Guatemala (Horwich and Johnson, 1986; Rylands *et al.*, chapter 2). Eighty percent of the geographic range of *A. pigra* is found in Mexico, specifically, the states of Tabasco and Chiapas, and it is the only *Alouatta* species present in the Yucatan peninsula (Smith, 1970; Horwich and Johnson, 1986; Watts and Rico-Gray, 1987; Rylands *et al.*, this volume).

Until now, information on population parameters for *A. pigra* and on its conservation status was only available from three localities in Belize. The Community Baboon Sanctuary (CBS), an area of about 4700 ha, encompasses remnants

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Sarie Van Belle • Department of Zoology, University of Wisconsin-Madison, 250 N Mills Street, Madison, WI 53706. **Alejandro Estrada** • Estación de Biología Los Tuxtlas, Instituto de Biología, Universidad Nacional Autónoma de México.

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of riparian forest along the Belize River and small rainforest fragments amidst agriculture fields and pasture lands (Horwich *et al.*, 2001a; Ostro *et al.*, 2001). Another site, Monkey River, in southern Belize, is a forest fragment, 52 ha in size (Pavelka *et al.*, 2003). The third site, Cockscomb Basin Wildlife Sanctuary, is a large reserve of 34,700 ha, but the howler population was re-introduced after *A. pigra* had gone extinct (Horwich, 1998; Ostro *et al.*, 2001). Data on *A. pigra* in undisturbed extensive forests (>5 km^2) exist only from two sites throughout its geographic distribution. For these sites, only mean troop size and population density were reported. One is the Muchukux forest in the state of Quintana Roo, Mexico (Gonzalez-Kirchner, 1998). The other is Tikal National Park in Guatemala (Coelho *et al.*, 1976; Schlichte, 1978). Basic population parameters, such as population density, population size, and age–sex composition of social groups, are poorly known for *A. pigra* existing in extensive forests. Such information is essential to understand the behavior and life history traits of this primate species (Strier, 2003a).

Throughout much of the geographic distribution of *A. pigra*, tropical rainforests have been degraded, fragmented, and converted to agriculture and pasture lands. Currently, it is estimated that only 28% tropical forest cover remains in Mexico, 59% in Belize, and 26% in Guatemala (Estrada *et al.*, chapter 1). Deforestation is continuing at a rate of −1.10% in Mexico, −2.32% in Belize, and −1.71% in Guatemala (Estrada *et al.*, chapter 1). The drastic conversion of tropical forests to anthropogenic landscapes places populations of this regionally endemic primate species at risk. *A. pigra*'s IUCN conservation status has been revised recently from "least concerned" in 2000 to "endangered" due to habitat loss and better available information (Cuarón *et al.*, 2003). However, the paucity of data on demographic parameters, ecology, and behavior of *A. pigra* in both natural protected habitats and in habitats associated with marked human disturbance makes conservation assessments of this primate species particularly difficult (Estrada and Coates-Estrada, 1988; Rylands *et al.*, 1995).

In this chapter, we present information on population density, troop size, and age–sex composition of eight populations of *A. pigra* existing in extensive forest tracks in Mexico and Guatemala. We assess the variability in these demographic parameters for populations of *A. pigra* existing in fragmented landscapes by contrasting these population characteristics for two of the populations living in extensive forest with those living in the abutting fragmented landscape. Finally, we compare literature reports of troop composition and population density of *A. pigra* populations in fragmented landscapes with the information for the eight sites of extensive forests.

METHODS

Sites and Data Collection

Between 2000 and 2003, population surveys of *A. pigra* were conducted in the eight sites located in extensive forest reserves in southern Mexico [El Tormento (ET), Calakmul (CAL), Palenque (PAL), Montes Azules along Rio Lacantun (LMA), Reforma ejido's reserve near Rio Lacantun (LRE), and Yaxchilán (YAX)] and in northern central Guatemala [Municipal Reserve Salinas Nueve Cerros, Lachuá ecoregion (LAC) and Tikal (TIK)] (see Baumgarten, 2000; Estrada *et al.*, 2002a,b,c; Barrueta, 2003; Barrueta *et al.*, 2003; Rosales Meda, 2003; Estrada *et al.*, 2004). We refer to extensive forest as forests >8.5 km^2 and protected by local governments.

Four of the sites (ET, LAC, LRE, and PAL: Figure 1) were large forest patches surrounded by anthropogenic landscapes dominated by pasture lands and agriculture fields. The other four sites were part of several larger reserves (>300 km^2) connected to each other to form the largest protected forested landmass in Mesoamerica of about 4 million hectares of tropical rainforest (Estrada *et al.*, 2004). All sites, including these sites in this large landmass, are sufficiently far apart (>100 km) to consider the primate populations as independent demographic units (Table 1).

In addition to the primate populations surveyed in extensive forest tracks, we surveyed *A. pigra* populations living in two fragmented landscapes abutting two of the extensive reserves, Palenque in Mexico, and Lachuá in Guatemala (Figure 1). Forest fragments refer to unprotected forests <4 km^2. In Palenque, we surveyed 22 forest fragments occupied by black howler monkeys. These had a mean area of 10.9 ± 9.4 ha (range 1.9–35 ha) (see Estrada *et al.*, 2002b, for details). In Lachuá, we surveyed 26 fragments in which black howler monkeys were present. The fragments had a mean area of 66 ± 109 ha (range 1.0–387 ha) (see Rosales Meda, 2003 for details).

Primate Surveys

At each site, we determined the relative location of all troops, defined as a social unit having at least one adult male and one adult female, living in the study area. This was accomplished using early morning (05:00–07:00 h) triangulation of their morning choruses and subsequent ground surveys (see Estrada *et al.*, 2004; Estrada *et al.*, chapter 19). Each troop was followed and counted repeatedly until a consensus of troop size and age and sex composition was

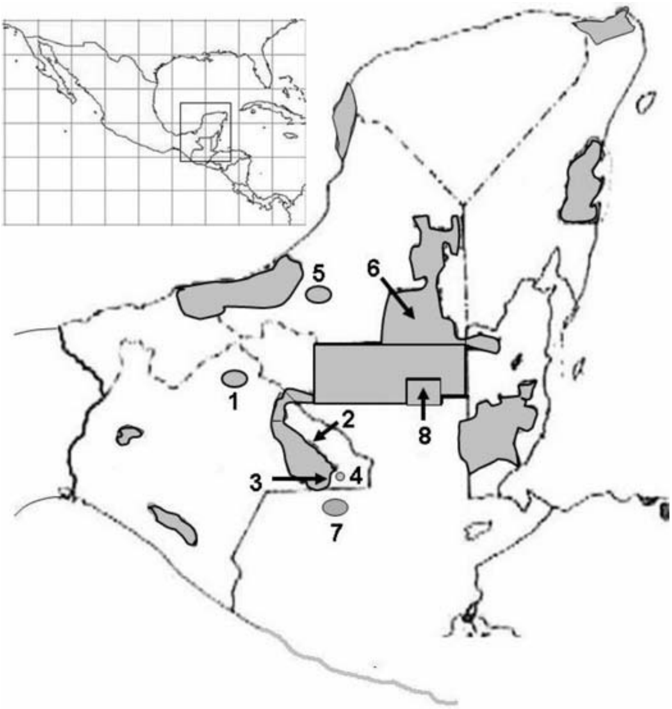

Figure 1. A map of southern Mexico, Belize, and northern Guatemala with the locations of the eight extensive forests sites studied. In Mexico: **1**: Palenque National Park; **2**: Yaxchilán National Monument; **3**: Montes Azules along Rio Lacantun; **4**: Reforma Community Reserve; **5**: El Tormento; **6**: Calakmul Biosphere Reserve; In Guatemala: 7: Municipal Reserve Salinas Nueve Cerros; **8**: Tikal National Park. The shaded areas indicate the system of national protected areas in southern Mexico, Belize, and northern Guatemala.

reached. Troops were searched for on subsequent days to confirm their composition and approximate location to reduce the probability of counting a troop more than once.

Individual howler monkeys in troops were classified as infants (clinging ventrally or dorsally to mother), juveniles (independent of mother and ¼–½ the size of adults), and adults (all large and robust individuals) (Izawa *et al.*, 1979). The sex of adults and juveniles could be reliably determined. Solitary individuals and extratroop social units encountered were noted. We cannot be certain that we encountered all solitary individuals or extratroop units since they are more silent and less conspicuous than larger and more vocal units.

Table 1. Features of study sites investigated. Study area refers to the area encompassed by our surveys at each site

Site[a]	Reserve area (ha)	Study area (ha)	Annual rainfall (mm)	Dry season	Mean ± SD temperature (°C)
Calakmul	700,000	400	820	November–April	25.0 ± 2.2
El Tormento	1400	1400	1380	December–May	24.1 ± 2.0
Lacantun-MA	300,000	836	2874	February–April	25.2 ± 1.8
Lacantun-RE	1700	450	2874	February–April	25.2 ± 1.8
Lachuá	850	850	2252	February–May	26.3 ± 0.6
Palenque	1771	600	2200	January–April	26.4 ± 2.2
Tikal	57,600	500	1762	December–April	25.0 ± 8.5
Yaxchilán	2700	100	1951	December–April	25.5 ± 2.2

[a] Calakmul: Archeological Mayan site in center of the Biosphere Reserve Calakmul; El Tormento: Forestry Reserve "El Tormento"; Lacuntun-MA: Montes Azules Biosphere Reserve by river Lacantun; Lacantun-RE: Community reserve of Reforma by river Lacantun; Lachuá: Municipal Reserve Salinas Nueve Cerros; Palenque: Palenque National Park; Tikal: Tikal National Park; Yaxchilán: Natural Monument Yaxchilán.

Data Processing and Statistics

For each site, mean troop size and mean troop composition were calculated. The mean adult sex ratios and mean number of infants per adult female and juveniles per adult female were calculated based on the ratios for each troop. The juvenile sex ratio per site was calculated from the sum of juvenile males and females encountered in all troops to avoid losing information from troops with juveniles of one sex only. Overall mean troop size, troop composition, and the above mentioned ratios were calculated from the population means for the eight extensive forest sites. We expressed population density figures (individuals/km^2, including solitary individuals and extratroop units) in terms of the area sampled. For two sites (LMA and YAX), density calculations include the area sampled from boat surveys along the rivers abutting the study area (see Estrada *et al.*, 2004, for details).

Mean troop composition and density of *A. pigra* populations were compared between extensive forests and forest fragments occurring in the two fragmented landscapes we investigated (Lachuá and Palenque) and in the fragmented landscape of the CBS, Belize, as reported by Ostro *et al.* (2001).

Comparisons among populations in extensive forests and between populations in extensive versus fragmented forests were assessed via the nonparametric Kruskal–Wallis test and Mann–Whitney *U* test. The Spearman rank

Table 2. Relative percentage of each age–sex class, including solitary individuals, within each *A. pigra* population in extensive forest (AM: adult male; AF: adult female; JM: juvenile male; JF: juvenile female; J: juvenile, sum of JF and JM; I: infant; IMM: immature, sum of J and I)

Site[a]	AM	AF	JM	JF	J	I	IMM
Calakmul	34.4	29.5	13.1	9.8	23.0	13.1	36.1
El Tormento	28.7	36.0	10.7	7.3	18.0	17.4	35.4
Lacantun-MA	36.0	40.0	4.0	8.0	12.0	12.0	24.0
Lacantun-RE	37.5	43.8	6.3	6.3	12.5	6.3	18.8
Lachuá	32.2	32.9	NA[b]	NA[b]	24.5	10.5	35.0
Palenque	33.1	27.2	11.8	14.0	24.3	14.0	38.3
Tikal	27.8	32.2	6.7	13.3	20.0	20.0	40.0
Yaxchilán	42.6	29.6	7.4	5.6	13.0	14.8	27.8
Mean	34.0	33.9	8.6	9.2	18.4	13.5	31.9
SD	4.8	5.7	3.3	3.3	5.4	4.2	7.5

[a] See Table 1 for site information.

[b] Juvenile sex not noted for Lachuá.

correlation was used to assess relations between demographic parameters and density (WinSTAT 3.0, 1994; SPSS 12.0, 2003).

RESULTS

Population surveys at these sites resulted in a total of 801 black howler monkeys encountered in the eight extensive forests studied. Of these, 769 individuals were members of 120 troops, and 32 were solitary or in extratroop social units. Thirty-four percent were adult males and 34% were adult females, 18% were juveniles, and 14% were infants (Table 2).

Troop Composition of Extensive Forest Populations

For the populations investigated, the overall mean troop size was 6.57 ± 1.20 individuals (Table 3). A troop had on average 2.07 ± 0.41 adult males, 2.26 ± 0.33 adult females, 1.28 ± 0.48 juveniles, and 0.96 ± 0.44 infants (Table 3). The overall mean adult sex ratio in a troop was 1.36 ± 0.20 females per male (Table 4). The mean juvenile sex ratio for the populations was 1.18 ± 0.58 juvenile females per juvenile male (Table 4). Troops had on average 1.10 ± 0.39 immatures per adult female or 0.65 ± 0.28 juveniles and 0.46 ± 0.16 infants per adult female (Table 4).

Troop size in the eight populations varied from 2 to 12 individuals, and the number of adult males and females in a troop both ranged from 1 to 5. Unimale

Table 3. The mean age and sex composition of troops and mean troop size of *A. pigra* populations living in extensive forests. (*N*: number of troops; *n*: individuals counted; Sol. Ind.: solitary individuals; AM: adult male; AF: adult female; J: juveniles; I: infants; IMM: immatures including infants and juveniles; bold only for clarity)

Site[a]	*N*	*n*	Sol. Ind.		AM	AF	J	I	IMM	Troop size
Calakmul	8	60	1	**Mean**	**2.50**	**2.25**	**1.75**	**1.00**	**2.75**	**7.50**
				SD	0.93	0.71	1.28	0.53	1.49	1.93
				Range	1–3	2–4	0–3	0–2	0–4	4–9
El Tormento	26	173	5	**Mean**	**1.77**	**2.46**	**1.23**	**1.19**	**2.42**	**6.65**
				SD	0.82	1.14	0.76	0.90	1.24	2.28
				Range	1–4	1–5	1–3	0–3	0–5	3–11
Lacantun-MA	13	72	3	**Mean**	**1.85**	**2.31**	**0.69**	**0.69**	**1.38**	**5.54**
				SD	0.80	0.63	0.63	0.75	0.96	1.51
				Range	1–3	1–3	0–2	0–2	0–3	3–8
Lacantun-RE	12	61	3	**Mean**	**1.75**	**2.33**	**0.67**	**0.33**	**1.00**	**5.08**
				SD	0.75	1.23	0.65	0.49	0.95	2.07
				Range	1–3	1–5	0–2	0–1	0–3	2–10
Lachuá	24	134	9	**Mean**	**1.58**	**1.92**	**1.46**	**0.63**	**2.08**	**5.58**
				SD	0.83	0.65	0.83	0.65	1.06	1.84
				Range	1–4	1–3	0–3	0–2	0–4	3–10
Palenque	19	128	8	**Mean**	**2.05**	**1.91**	**1.74**	**1.00**	**2.71**	**6.74**
				SD	0.91	1.03	1.37	0.94	1.88	2.77
				Range	1–4	1–4	0–4	0–3	0–4	2–12
Tikal	10	88	2	**Mean**	**2.30**	**2.90**	**1.80**	**1.80**	**3.60**	**8.80**
				SD	0.67	0.99	0.79	0.92	1.17	2.15
				Range	1–3	1–4	1–3	1–3	2–5	6–12
Yaxchilán	8	53	1	**Mean**	**2.75**	**2.00**	**0.88**	**1.00**	**1.88**	**6.63**
				SD	1.58	0.53	0.64	0.76	1.13	3.13
				Range	1–5	1–3	0–2	0–2	1–4	4–10
Total	120	769	32	**Mean**	**2.07**	**2.26**	**1.28**	**0.96**	**2.23**	**6.57**
				SE	0.41	0.33	0.48	0.44	0.83	1.20

[a] See Table 1 for site information.

Table 4. Mean adult sex ratio (AF/AM), mean adult female:juvenile ratio (J/AF), mean adult female:infant ratio (I/AF), and mean adult female:immature ratio (IMM/AF) of troops, percentage single male troops (% 1 AM), and density (individuals/km^2) of *A. pigra* populations living in extensive forests (bold only for clarity)

Site[a]		AF/AM	JF/FM	J/AF	I/AF	IMM/AF	% 1 AM	Density (individuals/km^2)
Calakmul	**Mean**	**1.25**	**0.75**	**0.88**	**0.50**	**1.38**	**25.0**	**15.2**
	SD	1.21		0.64	0.27	0.74		
El Tormento	**Mean**	**1.67**	**0.68**	**0.60**	**0.50**	**1.10**	**38.5**	**12.7**
	SD	1.11		0.38	0.40	0.61		
Lacantun-MA	**Mean**	**1.49**	**2.00**	**0.31**	**0.35**	**0.65**	**38.5**	**44.1**
	SD	0.80		0.30	0.31	0.51		
Lacantun-RE	**Mean**	**1.47**	**1.00**	**0.27**	**0.18**	**0.46**	**41.7**	**25.6**
	SD	0.92		0.31	0.32	0.48		
Lachuá	**Mean**	**1.40**	**NA**[b]	**0.85**	**0.35**	**1.21**	**58.3**	**15.8**
	SD	0.63		0.60	0.38	0.79		
Palenque	**Mean**	**1.14**	**1.06**	**1.07**	**0.54**	**1.61**	**31.6**	**23.0**
	SD	0.87		0.99	0.50	1.33		
Tikal	**Mean**	**1.40**	**2.00**	**0.68**	**0.71**	**1.38**	**10.0**	**17.8**
	SD	0.75		0.30	0.51	0.65		
Yaxchilán	**Mean**	**1.08**	**0.75**	**0.50**	**0.54**	**1.04**	**25.0**	**12.8**
	SD	0.94		0.38	0.42	0.70		
Total	**Mean**	**1.36**	**1.18**	**0.65**	**0.46**	**1.10**		**20.9**
	SE	0.20	0.58	0.28	0.16	0.39		

[a] See Table 1 for site information.
[b] Juvenile sex not noted for Lachuá.

Table 5. Percentage of troops ($N = 120$) according to number of adult males and females for the extensive forests

	1 AM	2 AM	3 AM	4 AM	5 AM	Total
1 AF	12.5	6.7	1.7	–	–	20.8
2 AF	15.0	15.8	13.3	2.5	1.7	48.3
3 AF	5.8	8.3	5.0	–	–	19.2
4 AF	5.0	3.3	1.7	–	–	10.0
5 AF	–	0.8	0.8	–	–	1.7
Total	38.3	35.0	22.5	2.5	1.7	

troops and troops with two adult males accounted for 38.3% and 35.0% of the troops, respectively. Forty-eight percent of the troops had two adult females (Table 5). Troops with a multimale–multifemale structure accounted for 53.3%. Among these, troops with two adult males and two adult females were the most frequent (15.8%; Table 5). The percentage of unimale troops per population ranged from 10.0% (TIK) to 58.3% (LAC) (Table 4).

Comparison of Extensive Forest Populations

Mean troop sizes were significantly different among the eight populations existing in extensive forests (KW $H_7 = 21.77$, $p = 0.003$). There were no differences in the mean number of females in a troop (KW $H_7 = 11.92$, $p = 0.104$) and in the mean adult sex ratio (KW $H_7 = 10.77$, $p = 0.149$) among these populations. The difference in mean troop size was due to differences in mean number of adult males (KW $H_7 = 14.61$, $p = 0.048$), and perhaps most importantly due to differences in the mean number of immatures among the populations (KW $H_7 = 27.60$, $p < 0.0001$). Mean infant:adult female ratios did not differ significantly among populations (KW $H_7 = 12.02$, $p = 0.100$), but mean juvenile:adult female ratios did (KW $H_7 = 18.91$, $p = 0.008$).

While troop composition differed among populations, the proportion of each age–sex class, including solitary individuals, within each population was not different from the expected mean proportions for all populations (χ^2-test, d.f. = 4, $p > 0.900$) (Table 2).

For the eight populations living in extensive forests, density ranged from 12.7 to 44.1 individuals/km^2. Across all populations, mean density was 20.9 individuals/km^2 (Table 4). Mean troop size ($r_s = -0.41$, $p = 0.320$) (Figure 2), mean number of adult males ($r_s = -0.29$, $p = 0.493$), mean number of adult females ($r_s = -0.02$, $p = 0.955$), and mean number of immatures ($r_s = -0.36$, $p = 0.385$) were not correlated with population density. The percentage of unimale troops within a population ($r_s = 0.24$, $p = 0.565$), and the

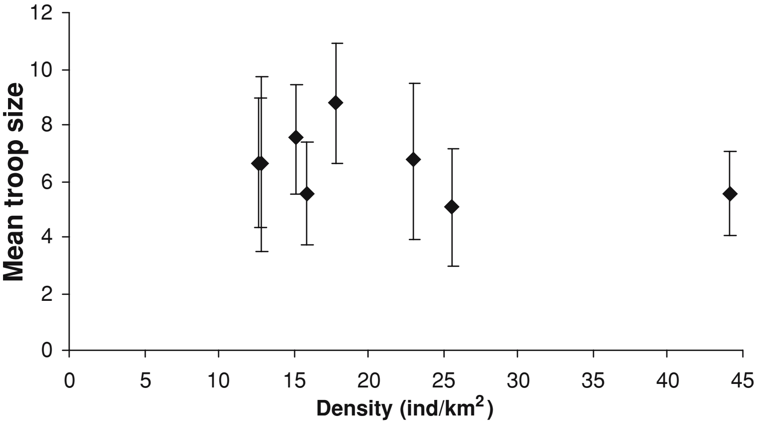

Figure 2. Relationship between mean troop size ± SD and population density for the eight populations existing in the extensive forests investigated (Spearman $r_s = -0.41$, NS).

relative age class distribution in the populations (r_s in all cases $p > 0.050$) also were not correlated with population density.

Troop Composition in Forest Fragments

Palenque, Mexico

In the 22 forest fragments occupied by black howler monkeys at Palenque, we counted a total of 115 individuals. Of these, 107 were members of 18 troops, 5 males formed 2 all male social units, and 3 males were solitary. One forest fragment harbored both a troop and an all male unit. All other fragments contained only one social unit. Troop size ranged from 2 to 15 individuals (mean = 5.94 ± 3.08 individuals, median = 5.0 individuals). A troop had on average 1.39 ± 0.50 adult males (range 1–2), 1.83 ± 0.92 adult females (range 1–4), 0.78 ± 0.81 juvenile males (range 0–3), 1.11 ± 1.08 juvenile females (range 0–4), and 0.83 ± 0.86 infants (range 0–3). Mean adult sex ratio was 1.39 ± 0.78 females per male. There were on average 1.05 ± 0.74 juveniles, 0.43 ± 0.42 infants, or 1.48 ± 0.73 immatures per adult female in a troop. Sixty-one percent of the troops had only one male. Mean ecological density was 119.2 ± 83.0 individuals/km^2, ranging between 11.3 and 315.8 individuals/km^2. While mean troop size and age–sex composition did not significantly differ between the protected forests of Palenque National Park and the fragmented landscape surrounding this reserve, mean number of adult males was significantly smaller in forest fragments than in the extensive forest ($U = 99.5$, $p = 0.018$).

Lachuá, Guatemala

The 26 forest fragments surveyed in the fragmented landscape of Lachuá yielded a total count of 225 howler monkeys, of which 223 were troop members of 43 troops and 2 were solitary males. Twenty-two fragments harbored 1 troop, and 4 fragments (50, 18, 60, and 216 ha) harbored 2, 3, 7, and 9 troops, respectively. Troop size ranged from 2 to 11 individuals (mean = 5.19 ± 1.97 individuals, median = 5.5 individuals). A troop had on average 1.63 ± 0.85 adult males (range 1–4), 1.95 ± 1.00 adult females (range 1–5), 0.30 ± 0.56 juvenile males (range 0–2), 0.51 ± 0.59 juvenile females (range 0–2), and 0.79 ± 0.94 infants (range 0–4). Mean adult sex ratio was 1.50 ± 0.99 females per male. A troop had on average 0.48 ± 0.46 juveniles, 0.41 ± 0.45 infants, or 0.89 ± 0.68 immatures per adult female. Fifty-five percent of the troops had a unimale structure. Mean ecological density was 107.18 ± 178.73 individuals/km^2, ranging between 1.0 and 700.0 individuals/km^2. There was no difference in mean troop size and age–sex composition of troops between Finca Municipal Salinas Nueve Cerros and the fragmented area abutting this reserve, except for the mean number of juveniles and mean number of juveniles per adult female, which was significantly smaller in forest fragments than in the extensive forest (J: $U = 292.5$, $p = 0.002$; J/AF: $U = 324.5$, $p = 0.010$).

Troop Composition and Population Density in Fragmented Landscapes Versus Extensive Forests

To assess the broader consistency of these patterns, we compared data available on mean population density and mean troop composition for *A. pigra* in three fragmented landscapes (CBS, LAC, and PAL) with the eight sites of extensive forest (Table 6). We found no significant difference in mean troop size ($U = 9.0$, $p = 0.540$), mean number of adult females ($U = 8.0$, $p = 0.414$), mean adult sex ratio ($U = 10.0$, $p = 0.682$), mean number of immatures ($U = 12.0$, $p = 1.000$), and mean adult female to immature ratio ($U = 12.0$, $p = 1.000$) (Figure 3). However, the mean number of adult males per troop was significantly smaller in forest fragments than in extensive forests ($U = 1.0$, $p = 0.025$) (Figure 3). Populations in forest remnants lived, on average, at ecological densities 5.4 times higher in comparison with populations in extensive forests ($U = 0.0$, $p = 0.007$).

Based on the 99 troops encountered in the fragmented landscapes of Palenque, Lachuá, and CBS (Table 7), troops with one and two males accounted for 57.6% and 34.3%, respectively. Troops with one and two females accounted for 30.3% and 46.5%, respectively. Troops with one adult male and two adult females were the most common accounting for 28.3%, while multimale–multifemale troops accounted for 31.2% (Table 7).

DISCUSSION

New survey data on population characteristics of *A. pigra* suggest considerable variability in population density and troop size. Further, data suggest important differences between populations of this howler monkey species existing in extensive and fragmented forests. In the fragmented forest, mean population

Table 6. Troop size and composition and population desnsity of *A. pigra* populations in fragmented landscapes: Belize: Community Baboon Sanctuary (CBS); Mexico: Palenque (PAL); Guatemala: Lachuá (LAC) (AM: adult male; AF: adult female; IMM: immature; bold only for clarity)

	Sites	Troops		Density (individuals/km^2)	Troop size	AM	AF	IMM	AF/AM	IMM/AF	Tot cum area (ha)	Avg frag size (ha)
CBS[a]	5	38	**Mean**	**123.2**	**5.66**	**1.40**	**2.42**	**2.21**	**1.63**	**1.08**	**171**	**42.7**
			SD	95.4	0.62	0.68	0.31	0.56	0.37	0.47		12.3
PAL	22	18	**Mean**	**119.2**	**5.90**	**1.39**	**1.83**	**2.72**	**1.39**	**1.48**	**160**	**10.9**
			SD	83.0	3.08	0.50	0.92	2.14	0.78	0.73		9.4
LAC	26	43	**Mean**	**107.2**	**5.19**	**1.63**	**1.95**	**1.60**	**1.51**	**0.98**	**1716**	**66**
			SD	178.7	1.97	0.85	1.00	1.33	1.06	0.78		109.0

[a] Ostro *et al.* (2001).

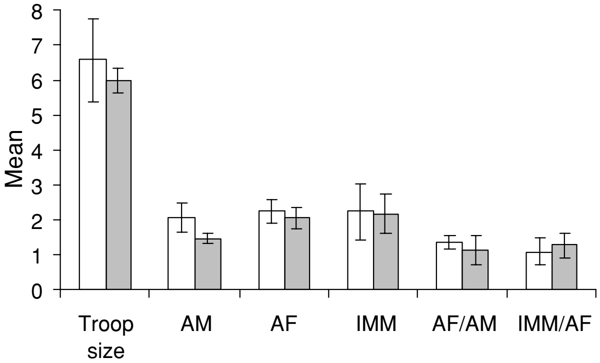

Figure 3. Comparison (Mann–Whitney *U* test) of mean troop size (± SE) and mean troop composition (± SE) between the fragmented landscapes (Community Baboon Sanctuary, Palenque, and Lachuá) (gray bars) and the eight sites of extensive forests (white bars).

Table 7. Percentage of troops ($N = 99$) according to number of adult males and females in the fragmented landscapes of Palenque, Lachuá, and Community Baboon Sanctuary

	1 AM	2 AM	3 AM	4 AM	Total
1 AF	19.2	8.1	1.0	2.0	30.3
2 AF	28.3	14.1	4.0	–	46.5
3 AF	7.1	10.1	1.0	–	18.2
4 AF	3.0	1.0	–	–	4.0
5 AF	–	1.0	–	–	1.0
Total	57.6	34.3	6.1	2.0	

density increases and mean number of adult males in troops decreases compared with the protected forests >5 km^2 in area. In the next paragraphs, we discuss some of these patterns.

Variation in Demographic Features of Populations in Extensive Forests

Black howler mean troop sizes in the extensive forests studied ranged from 5.08 to 8.80 individuals. The earlier figure of mean troop size reported for the *A. pigra* population in Tikal, Guatemala, of 6.25 individuals falls within this range (Coelho *et al.*, 1976). However, mean troop size of 3.16 individuals reported by Gonzalez-Kirchner (1998) for *A. pigra* in the Muchukux forest, Quintana Roo, Mexico, is considerably lower. In the case of Tikal, mean troop size appears to have increased, during the 30-year interval between censuses, from 6.25 individuals (Coelho *et al.*, 1976) to 8.80 individuals, associated with an increase in number of troops encountered in the study area probably in response to a population growth (Estrada *et al.*, 2004).

Until now, troop composition had only been described for troops living in fragmented forests in Belize, and troops have been depicted as predominantly monogamous (Bolin, 1981) or as larger unimale troops (Horwich *et al.*, 2001a). Data presented here suggest that most *A. pigra* troops living in extensive forests have a multimale–multifemale social structure, with two adult males and two adult females being the most common. The number of males in a troop ranged between one and five, with troops of one, two, and three adult males being the most frequent. The number of adult females in a troop, on the other hand, was less variable. Almost half of the troops encountered had two adult females, but their number also ranged between one and five. This supports the idea that in *A. pigra* female group size is limited due to either female intolerance or a limited number of female breeding opportunities in troops (Pope, 2000a,b). However, Crockett and Janson (2000) have argued that in *A. seniculus* female group size is constrained by the risk of infanticide. They suggest that troops with greater than four adult females are more attractive to extratroop males and that during male takeovers, infanticide may occur. Whether this provides an explanation of female group size in *A. pigra* remains unclear. Alternatively, Garber *et al.* (1993) have proposed that small multimale–multifemale groups, like the *A. pigra* troops in extensive forests, are likely to represent the primitive condition for platyrrhines, and that compared to Old World monkeys, in many New World monkeys female breeding opportunities within groups are more limited.

Mean troop size significantly differed among the *A. pigra* populations studied in extensive forests. This was principally due to differences in mean number of immatures, but no clear pattern in population differences in mean number of infants and juveniles could be discerned. The mean infant:adult female ratio did not significantly differ among the populations, while the mean juvenile:adult female ratio did significantly differ but this was only for the LMA and LRE populations, which had, on average, fewer juveniles per adult female in a troop compared to the other populations. Differences in mean number of immatures between populations could be attributed to differences in fertility rates, mortality rates of the young age classes, dispersal age and rate, birth seasonality (observed in *A. pigra* in CBS, Brockett *et al.*, 2000), and period of population survey (Strier, 2003a,b). Long-term monitoring of each population will be needed to assess whether populations truly differ. Notwithstanding the dissimilarities in mean troop compositions among the eight populations of extensive forest, there were no significant differences in relative number of the age–sex classes among them. Hence, our study indicates that a black howler population in extensive forests almost consistently comprises 34% adult males, 34% adult females, 18% juveniles, and 14% infants, independent of density or mean troop size.

For the extensive forest sites, *A. pigra* densities ranged from 12.7 to 44.1 individuals/km^2, and densities of 25.0 individuals/km^2 reported earlier for Tikal (Coelho *et al.*, 1976), and of 16.5 individuals/km^2 for Muchukux (Gonzalez-Kirchner, 1998) fall within this range. The lack of association between mean troop size and density implies that populations of *A. pigra* living at higher densities did not consistently have larger troops. This contrasts with data from populations of *A. caraya* in Argentina (Rumiz, 1990), of *A. palliata* in Costa Rica (Fedigan *et al.*, 1998; Fedigan and Jack, 2001), of *A. pigra* in CBS (Horwich *et al.*, 2001b), and of *A. seniculus* in Venezuela (Rudran and Fernandez-Duque, 2003), where mean troop size positively correlated to population density. These populations have been reported to have experienced significant population fluctuations, apparently caused by epidemic pathogens, such as yellow fever and botfly infestations, by food shortages, or by natural disasters such as hurricanes (Chapman and Balcomb, 1998; Rudran and Fernandez-Duque, 2003, Pavelka *et al.*, 2003; Pavelka and Chapman, this volume). It is likely that the eight populations we investigated in the extensive forests have also experienced such population fluctuations. For example, in Tikal the number of troops increased from 4 to 10, and also underwent an increase in mean troop size during the 30-year interval between the surveys by Coelho *et al.* (1976) and by Estrada *et al.* (2004).

Population growth in *A. caraya* (Rumiz, 1990), *A. palliata* (Fedigan *et al.*, 1998), *A. pigra* (Horwich *et al.*, 2001a), and *A. seniculus* (Rudran and Fernandez-Duque, 2003) has been associated with the expansion of the established troops until a maximum troop size has been reached, determined by the biotic and aboitic characteristics of the local habitat. The second stage of population increase is primarily due to formation of new and smaller troops by dispersing individuals from the established troops. When the habitat becomes saturated, recently established troops also increase their size until they reach maximum troop size (Rudran and Fernandez-Duque, 2003). It is possible that the populations of *A. pigra* investigated in extensive forests were at different growth stages, which, in combination with possible differences in maximum troop size and carrying capacity among the eight sites studied, could explain why no correlation was found between mean troop size and density. Thus, the results we described here may only indicate the extent of population fluctuations experienced by populations of *A. pigra*. Only long-term studies of *A. pigra* will offer insight into population dynamics and the processes driving these changes in troop size, composition, and density (Rudran and Fernandez-Duque, 2003; Strier, 2003a). For now, we have documented demographic baseline data on *A. pigra* populations existing in extensive forests and data on the variability of several demographic features among these populations. This information is useful in an initial assessment of how black howler populations, social groups, and individuals are influenced by habitat fragmentation.

General Fragmentation Effects

Based on a comparison between populations of extensive and adjacent fragmented forests, it appears that habitat fragmentation had certain important effects on troop composition in *A. pigra*. In Palenque, Mexico, and in Lachuá, Guatemala, mean troop sizes in fragments, although not statistically significant, were, in general, smaller than in the extensive forest. Troops living in the fragmented landscape of Palenque had, on average, fewer males than neighboring troops living in the protected forest. In Lachuá, troops living in forest fragments had, on average, half as many juveniles and juveniles per adult female as the troops dwelling in the extensive forest reserve. While the observed troop composition values in the fragmented landscapes investigated fell within the range documented for troops living in extensive tropical forests, the observed differences might be a result of demographic or environmental stochastic events, since the time of fragmentation (>30 years).

Comparing data available on mean population density and mean troop composition for *A. pigra* in three fragmented landscapes (CBS, LAC, and PAL) with data for the eight sites of extensive forest shows that the populations in forest fragments live, on average, at ecological densities 5.4 times higher in comparison with the populations in extensive forests, suggesting overcrowding (Estrada *et al.*, 2002b). However, troops in forest fragments did not differ in mean troop size and composition from those in extensive forests, except for the mean number of adult males, which was significantly smaller for populations living in forest fragments than in extensive forests. Also, unimale troops were more common (57.6%) in the fragmented landscapes than in the extensive forest reserves (38.3%). This suggests that adult males may be most sensitive to habitat saturation or isolation. For example, in a study about injuries and scars of *A. palliata mexicana* troops in forest fragments, Cristóbal-Azkarate *et al.* (2004) found that 90% of the observed injuries were facial scars on adult males. They suggested that these scars most likely result from fights during attempts of troop take-over. Injuries inflicted during these male-to-male fights can be severe and lead to the death of contestants (Crockett, 2003).

Marsh (1999) suggested that behavioral adjustment to habitat fragmentation occurs before troop composition changes in response to fragmentation. However, she found no significant difference in daily activity patterns and food diversity in the *A. pigra* troops living in different sized forest fragments in CBS, Belize. Similar results have been reported for other howler monkey species (Bicca-Marques, 2003), suggesting that *Alouatta*'s flexible diet and small home ranges make them more able to cope with habitat fragmentation than other large-bodied monkeys (Jones, 1995; Estrada *et al.*, 1999; Bicca-Marques, 2003).

Although fragmentation may have limited effects on the behavioral ecology of *A. pigra*, troops living in forest fragments are increasingly exposed to hunting and/or predation by domestic animals (e.g., alpha male was killed by a dog in CBS, Belize, Kitchen, 2004). Additionally, reduced tree species diversity may lead to nutritional stress and/or to the use of suboptimal resources. This and greater exposure to sun radiation due to continued habitat degradation may result in increased mortality (Estrada *et al.*, 1999). In Lachuá, for example, the mean number of juveniles in troops living in forest fragments was about half its counterpart for troops living in extensive forests, suggesting an important effect of fragmentation on survivorship of immatures.

Furthermore, in the fragmented landscapes dispersal opportunities may be lower. For example, most forest patches we studied harbored only one troop, and dispersal-induced-mortality is thought to increase when howlers travel in open agricultural fields and cattle pasture (e.g., *A. palliata*, Rodriguez-Toledo *et al.*, 2003). Dispersal costs may become so high that individuals may stay in their natal troop, as we suspect in the case for a troop of 15 individuals encountered in an isolated forest fragment in Palenque (Estrada *et al.*, 2002b), therefore increasing the potential of inbreeding depression.

Finally, small isolated troops are more vulnerable to typical demographic and environmental stochasticity, resulting in increased extinction probabilities for remaining isolated populations. Although observations suggest that howlers can survive in forest fragments, they may not do well in the medium and long term (Estrada *et al.*, 2002b).

While our study provides information on the variability of demographic features of the *A. pigra* populations in extensive forests, and on the influence of habitat fragmentation on these demographic features, more long-term data are needed from more *A. pigra* populations in both forest conditions to understand *A. pigra*'s population dynamics and persistence potential in habitat fragments.

SUMMARY

Until now, little information was known about demographic features of the regionally endemic black howler populations living in large tracks of tropical forests. Here, we report results from population surveys conducted in eight extensive forests sites (>8.5 km^2) in Mexico and Guatemala. We also surveyed the black howler population in the fragmented landscape bordering two of the extensive forest reserves. Based on the 120 troops encountered in the extensive forest sites, mean troop size was 6.57 (SE = 1.20) individuals (range 2–12 individuals). Troops had most commonly a multimale–multifemale social structure, with two adult males and two adult females being the most common. Population densities ranged from 12.7 to 44.1 individuals/km^2. Mean troop size and composition were not correlated to population densities. For the two fragmented landscapes bordering the extensive forests, mean densities in forest fragments were, on average, five times higher than in extensive forests. Mean troop composition was not significantly different between forest fragments and extensive forests, but data suggest a tendency of fewer males in troops living in forest fragments. Long-term monitoring in extensive forests is necessary to document variability in population dynamics and to make adequate assessments of the consequences of fragmentation on demography, behavior, and life history of *A. pigra*.

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