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RESEARCH ARTICLES

Population of the Black Howler Monkey (*Alouatta pigra*) in a Fragmented Landscape in Palenque, Chiapas, Mexico

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Little is known about the population characteristics of *Alouatta pigra* under conditions of forest fragmentation–information that is important to understanding its tolerance to habitat loss. In this work we present data on forest loss and on troop size, age, and sex composition for a population of black howler monkeys existing in the fragmented landscape surrounding the Mayan site of Palenque, Chiapas, Mexico. Two aerial photos (1:70,000) of the study area (261 km^2) taken in 1984 and 2001 were examined to assess forest loss. Between June and December 2001 and January and March 2002 we surveyed 44 forest fragments for the presence of howler monkeys. Examination of aerial photos showed that 33% of the forest present in 1984 had disappeared by 2001, and detected an increment in the number of forest fragments present in the landscape. We discovered a total of 115 howler monkeys living in 22 of the 44 forest fragments studied, of which 107 were members of 18 troops. The rest were solitary males or small groups of males living in isolated forest fragments. Troop size ranged from two to 15 individuals (mean 5.9+3.0 ind). 31% and 15% of individuals in the troops were juveniles and infants, respectively, suggesting continued reproductive activity. Howler monkey troops in the forest fragments were on average smaller (5.9 ± 3.0 ind) than troops in the nearby protected forest of the Mayan site (7.0 ± 2.8 ind). The mean density of howlers in the forest fragments was 119 ± 82.9 ind/km^2. The establishment of corridors is suggested as a possible conservation scenario for the fragmented howler population investigated, and as a conservation measure to connect this population with the howler population found in the protected forest of the Mayan site. Am. J. Primatol. 58:45–55, 2002.

Key words: howler monkeys; *Alouatta pigra*; population density; primate conservation; sex ratios; forest fragmentation

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INTRODUCTION

The impact of habitat fragmentation on individual species and communities is a major focus of ecological and conservation research in tropical organisms, including primate populations [Lovejoy et al., 1984; Offerman et al., 1995; Rylands et al., 1995; Laurance & Bierregaard, 1997; Schelhas & Greenberg, 1996; Harrison & Bruna, 1999; Clarke et al., 2002; Laurance et al., 2002]. Habitat fragmentation results in the decline of primate populations and the fragmentation and isolation of remnant populations, which, coupled with continued habitat deterioration, hunting, and continued human encroachment, puts these populations at risk [Rylands et al., 1995; Estrada & Coates-Estrada, 1996; Crockett, 1998; Estrada et al., 1999].

The rain forests of southern Mexico harbor the northernmost geographic distribution of wild primates in the Neotropics. Three species of primates are present in these habitats: *Alouatta palliata*, *A. pigra*, and *Ateles geoffroyi*. The first and the third have a broad geographic distribution in southern Mexico and Central America, but the distribution of *A. pigra* is restricted to a small area of Mesoamerica encompassed by Mexico, Belize, and Guatemala [Smith, 1970; Coelho et al., 1976]. Mexico harbors about 80% of the geographic distribution of *A. pigra*; the species is found in parts of the state of Tabasco and in northern Chiapas, and it is the only *Alouatta* species found in the Yucatán peninsula [Horwich & Johnson, 1986; Watts & Rico-Gray, 1987].

The restricted geographic distribution of *A. pigra* in Mesoamerica, and the rapid fragmentation and conversion of its natural habitat to pasture lands and agricultural fields places populations of this regionally endemic primate species at risk [Horwich & Johnson, 1986; Rylands et al., 1995]. To diagnose the current conservation status of populations of *A. pigra* in particular localities within its distributional range, we require information on troop size and density, and the age and sex composition of populations. These facts are not well known for *A. pigra* [Horwich & Johnson, 1986; Gonzales-Kirchener, 1998; Silver et al., 1998; Ostro et al., 1999, 2000; Estrada et al., 2002]. Information on forest fragmentation and rates of forest loss, coupled with the above demographic information for populations of *A. pigra*, may be essential to understand the tolerance of this primate species to habitat fragmentation [Estrada & Coates-Estrada, 1996; Cuarón, 2000].

With the aim of contributing to the above information for *A. pigra*, in this work we report data on forest loss, troop size, population density, and demographic structure for a population of *A. pigra* living in unprotected forest fragments surrounding the protected forest of the Mayan site of Palenque in Chiapas, Mexico. The results of the survey are compared to population data reported earlier for a population of *A. pigra* existing in the protected forest of the archeological site [Estrada et al., 2002].

METHODS

Study Area

The study area comprised 261 km^2, in which is located Palenque National Park (PNP), in northeastern Chiapas (17° 27′51″, 17° 30′05″ N; 99° 01′30″, 92° 04′42″ W; elevation in the study area ranges from 50 to 500 m above sea level) (Fig. 1). The protected land of PNP encompasses 17.7 km^2, of which about 6.0 km^2 consists of primary rain forest vegetation, another 4.0 km^2 consists of second-growth vegetation of different ages surrounding the primary forest, and the rest

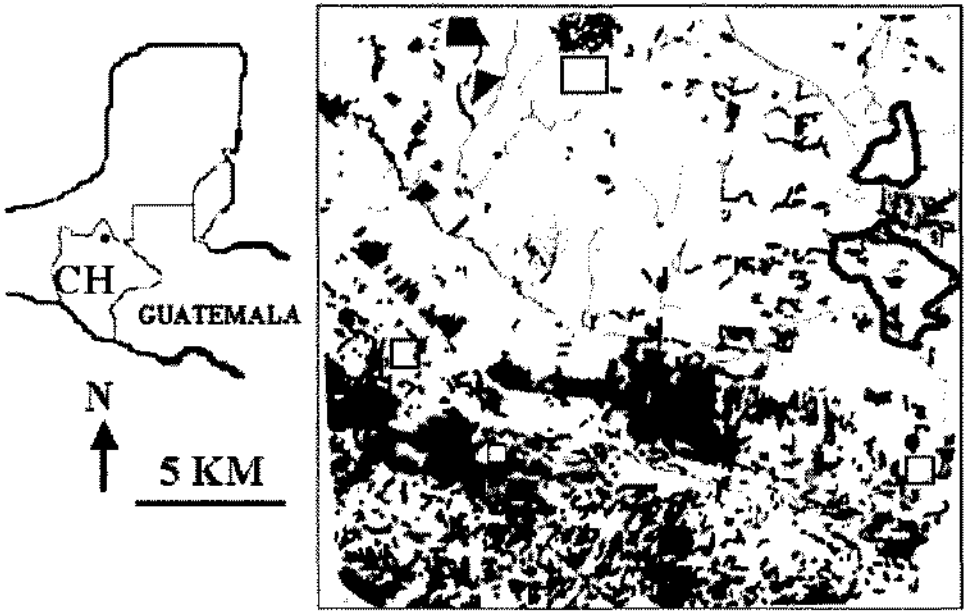

Fig. 1. Study area in Palenque (black dot in the map of southern Mexico), Chiapas (CH), Mexico (drawn from an aerial photo 1:70,000). The landscape shown encompasses 261 km^2. Remaining forests shown in black. The large forest fragment below the center of the figure is the protected forest (ca 1,000 ha) of PNP. Study sites comprised 44 forest fragments distributed in a 10-km perimeter around the PNP forest. The large area with a thick perimeter line to the right is the town of Palenque and a smaller human settlement to the north. Empty squares are small Mayan villages. Altitudinal range from north to south is 50–500 m above sea level. Thin lines are strips of residual forest vegetation along the sides of streams and rivers.

consists of introduced pasturelands [Diaz-Gallegos, 1996]. Earlier surveys by our research team in the 6-km^2 forested area of PNP discovered about 200 howler monkeys forming part of 20 troops [Estrada et al., 2002].

The land surrounding PNP is dominated by pasturelands, but clusters of forest fragments remain dispersed in the area amid pasture lands, along the sides of streams and rivers, and on the slopes of nearby mountains (Fig. 1). The climate is hot and humid, and average annual precipitation is 2,200 mm, with a drier season between January and April (average monthly rainfall = 62 ± 18 mm) and a wetter period between May and December (average monthly rainfall = 240 ± 106 mm). The mean annual temperature is 26°C (range 22–29°C).

Forest Loss

To assess rates of forest loss, we examined two black and white aerial photographs (1:70,000) of the study area (261 km^2), one taken in March of 1984 and the other in January 2001. All forest remnants present in each photograph were digitized and measured (minimum mapping unit 20×20 m) to estimate their area in hectares. For each period we counted all forest fragments present in the photographs and calculated the total area of forest vegetation they represented. We subtracted the total forest area in 2001 from the total forest

area in 1984 to determine the total area of forest vegetation lost in the 17-year interval between photographs. The isolating distance of the forest fragments investigated was measured on the aerial photos as the straight line distance to the edge of the nearest forest fragment or corridor of vegetation.

Primate Surveys

We conducted surveys of *A. pigra* in June–December 2001 and January–March 2002, in 44 forest fragments located in the study area. The forest fragments were selected randomly after dividing the study area into four quadrants following the cardinal points. The average area of these sites was 10.8 ± 14.9 ha (range 1–86 ha), and their cumulative area was 477 ha.

Surveys of howler monkeys in each forest fragment were conducted by triangulation of dawn and dusk choruses, and by walking existing trails or through the forest to reach the troop(s) detected by auditory means. Dawn and dusk choruses were monitored at each site at 0500–0700 hr and 1800–1900 hr. The direction in which howling was heard was determined with the use of a compass, taking note of orientation degrees.

The resulting information was placed on a detailed map of each site. Once triangulation was completed in the morning, we thoroughly searched the site for the troops we heard. Contacted troops were followed for 4–6 hr and repeatedly counted to confirm identification and age and sex composition. Individuals were classified as adults, juveniles, or infants (clinging to their mother). Surveys at each site lasted 3–4 days and sites were visited twice in 2001 and twice in 2002, allowing for confirmation of identity and location of troops. Population density was expressed as ind/ha or ind/km^2.

RESULTS

Forest Loss

Examination of aerial photos showed that there were 10,573 ha of rain forest vegetation in the area in 1984. In 2001, 7,121 ha remained, indicating a 33% (3,451 ha) loss of forest vegetation in the 17-year period. Most of this loss was due to conversion of the land to open fields by human activity. Data also showed the existence of 200 and 337 forest fragments in 1984 and 2001, respectively, indicating that the decrease in forest cover between these years was paralleled by an increase in forest fragments (Fig. 2). This examination also showed that all fragments >500 in size present in 1984 had disappeared, and that fragments <4.0 ha in size had increased in number in the 2001 landscape (Fig. 2).

Primate Surveys

Howler monkeys were discovered in 22 of the forest fragments investigated ($n = 44$). The mean area of these forest fragments was 10.9+9.4 (range 1.9–35 ha), and the cumulative area of these sites was 232 ha. The mean area of forest fragments without howler monkeys was 11.5 ± 19.0 ha (range 2–86 ha; cumulative area 245 ha). Forest fragments with and without howler monkeys did not differ in area ($t_{44} = 0.31$, $P < .05$). The isolating distance of forest fragments where howlers were detected ranged from 0.03 to 0.95 km (mean 0.33 ± 0.27 km). The isolation distance of forest fragments with no howler monkeys ranged from 0.61 to 2.6 km (mean 1.6 ± 0.7 km), and in 77% of the sites the isolating distance was >1.0 km.

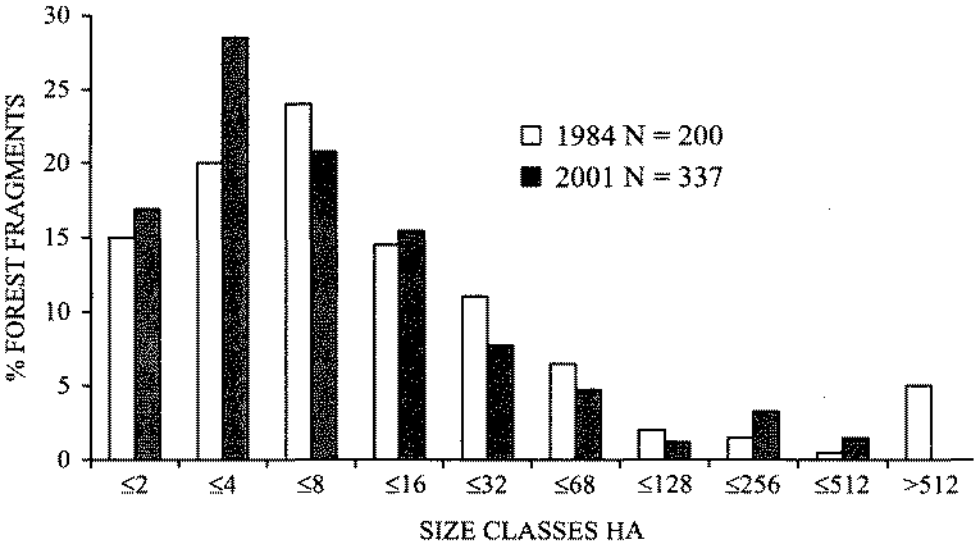

Fig. 2. Distribution of forest fragments by size classes in the landscape investigated. Note the increment in number of fragments from 1984 to 2001, the loss of fragments >500 ha in 2001, and the increase in fragments <4.0 ha in size from 1984 to 2001.

The two sets of sites differed significantly in isolating distances ($t_{44} = 7.95$, $P < .001$).

In the forest fragments with *A. pigra*, we counted 115 individuals, of which 107 were members of 18 troops. Seventeen of the forest fragments with howlers had only one troop. One forest fragment (9.5 ha) harbored one troop and a group of three males forming a separate social unit. Three solitary males (a juvenile and two adults) were discovered in three additional forest fragments 17, 19, and 22 ha in size, and in another forest fragment (4.0 ha) we found two males forming a social unit (Table I).

Troop size ranged from two to 15 individuals, and the average troop size was 5.9 ± 3.0 individuals. Sixty-one percent of the troops had one adult male only, and the rest had two adult males. Adult individuals in the troops accounted for 54% of the counts, juveniles for 31%, and infants for 15%. Twenty-three percent of the individuals were adult males, 30% were adult females, 13% were juvenile males, 19% were juvenile females, and 15% were infants (Table I).

The average age and sex composition of these troops was 1.39+0.50 adult males (range 1–2), 1.83 ± 0.92 adult females (range 1–4), 1.27 ± 0.65 juvenile males (range 1–3), 1.67 ± 0.89 juvenile females (range 1–4), and 1.36 ± 0.67 infants (range 1–3) (Table I). Seven of the troops had more than one adult female, seven troops had no juvenile males, six troops had no juvenile females, and seven troops had no infants. The overall adult male to adult female ratio was 1:1.32, and in juveniles the male to female ratio was 1:1.46 (Table I). Five troops had a 1:1 adult female to immature ratio, 11 troops had ratios >1:1, one troop had a ratio of 1:0.50, and another had a ratio of 1:0.0 (Table I).

The area of forest fragments with heterosexual troops ranged from 1.9 to 35.0 ha (mean 8.6 ± 9.3 ha). The area of forest fragments in which only solitary males and males in groups of two and three individuals were found ranged from 4–22 ha

TABLE I. Troops of *Alouatta pigra* Detected in Forest Fragments in the Landscape Surrounding the Mayan Site of Palenque, Chiapas, Mexico.

			Adult		Juvenile			
	Site area (ha)	Troop	Males	Females	Males	Females	Infants	Total
	10.7	1	1	1			1	3
	9.4	2	2	2	1		2	7
	4.8	3	2	1		1	1	5
	17.0	4	1	4	3	4	3	15
	4.0	5	1	1	1			3
	3.6	6	2	2	1	1	2	8
	3.0	7	1	1	1	2		5
	3.0	8	1	2	1			4
	7.3	9	1	1	1	1		4
	6.0	10	2	3	1	1	1	8
	35.0	11	1	1		2		4
	5.0	12	2	3	1	2	1	9
	5.0	13	1	2		1	1	5
	2.3	14	1	1				2
	3.5	15	2	3	2	1	1	9
	5.9	16	1	2		2	1	6
	33.0	17	1	1	1		1	4
	1.9	18	2	2		2		6
Total			25	33	14	20	15	107
Mean	8.9		1.39	1.83	1.27	1.67	1.36	5.94
SD	9.8		0.50	0.92	0.65	0.89	0.67	3.08
Median	5.0		1.00	2.00	1.00	2.00	1.00	5.00
Solitary males								
	17		1					1
	22				1			1
	19		1					1
Males in pairs or more individuals								
	9.4		1		2			3
	4.0		1		1			2
Total number of howlers								115

(mean 14.2 ± 7.5 ha). No relationship existed between troop size and area of the forest fragment ($r_s = 0.02$, $P = 0.45$, $n = 18$). Estimated howler densities in the forest fragments ranged from 0.11 ind/ha to 3.16 ind/ha (mean 1.1 ± 0.82 ind/ha; $n = 18$).

In comparison to the howler population in the protected forest of PNP, howler monkey troops in the forest fragments tended to be, on average, smaller than the troops in PNP. While howler troops in forest fragments had a lower number of adult males than troops at PNP (Mann-Whitney test, $P = 0.03$), forest fragments and PNP did not differ significantly in average number of adult females, juveniles, or infants per troop (Mann-Whitney test, $P > 0.05$ in all cases) (Table II).

TABLE 2. Comparison of Population Parameters for the *A. pigra* Troops Existing in the Protected Forest of Palenque National Park (PNP) and in Forest Fragements in the Surrounding Landscape

	Forest fragments	PNP
Number of sites	22	1
Cum area of sites [ha]	232	600
Number of howlers	115	136
Number of troops	18	20
Mean troop size	5.9±3.0	7.0±2.8
Troop size range	2–15	2–12
Density ind/ha	1.10±0.82	0.24
Biomass kg/ha	26.2±12.0	1.29
Mean number of		
Adult males	1.39±0.50	2.00±0.90
Adult female	1.83±0.92	1.90±1.00
Juvenile males	1.27±0.65	1.50±0.70
Juvenile females	1.67±0.89	1.50±0.50
Infants	1.36±0.67	1.60±0.70

DISCUSSION

Data from the aerial photographs showed that between 1984 and 2001 there was a continuing conversion of forest to pasture, and further fragmentation of remnant forest, with the result that the majority of the current forest fragments are less than 8.0 ha in size. Aerial photos of the study area prior to 1984 are not available, and government maps before that year do not accurately depict the areas of vegetation, which makes it difficult to assess the extent of tropical rain forest in the study area prior to 1984. However, interviews with some of the oldest members of the local Mayan villages near PNP indicated that in the past most of the area included in the aerial photo was covered with rain forest. The indigenous people also indicated that howler monkeys were common in the forested land that it is now cleared.

The mean troop size reported here for the fragmented population of *A. pigra* was smaller than that for the population inhabiting the protected forest of PNP. Smaller troop size might be an adaptation of howlers for existence in small habitat-islands [Ostro et al., 1999]. However, in continuous forests such as Muchukux, Quintana Roo, Mexico [Gonzales-Kirchener, 1998], and Tikal, Guatemala [Coelho et al., 1976], the mean troop size was 3.16 and 6.3 individuals, respectively. In fragmented riverine vegetation in Belize, troop size ranged from three to nine individuals [Silver et al., 1998]. These contrasts suggest that there is much variability in this parameter for *A. pigra*, and that it is difficult to generalize.

The presence of infants in 61% of the troops in the forest fragments suggests continued reproductive activity, and the ≥1:1 adult female to immature ratio in 16 troops suggest that most troops have an adequate reproductive potential [Clarke et al., 2002]. However, while the *A. pigra* population present in the forest fragments we surveyed seems to be surviving and reproducing, they exist in small, isolated habitat-islands. These habitats are subjected to edge effects [Murcia, 1995], such as high tree mortality [Lovejoy et al., 1984; Laurance et al.,

2002], which may result in diminishing resources (food and physical substratum) for howlers [Estrada et al., 1999]. The small size of the fragments suggests that the troops may be unable to expand their ranges to meet resource demands [Bicca-Marques & Calegaro-Marques, 1994a; Galetti et al., 1994; Crockett, 1998; Estrada et al., 1999]. In contrast, the howler population in the protected forest of PNP exists in a large forest remnant (1,000 ha, consisting of 600 ha of primary forest and 400 ha of second-growth vegetation) that allow as well for connectivity among troops through dispersal of individuals of both sexes.

Lack of connectivity among the forest fragments inhabited by the howler troops in the study area may mean less opportunities for dispersal by individuals of both sexes, with important consequences for reproductive potential and an increase in inbreeding [Beier & Noss, 1988; Lindemayer & Nix, 1993; Crockett, 1998; Estrada & Coates-Estrada, 1996; Clarke et al., 2002]. Even though howlers are known to cross open spaces to reach other forests [Crockett, 1998], in densely populated areas such as Palenque there is a high risk of predation by dogs and humans. In our work at the site since 2000 we have failed to witness any instances of howlers moving across open spaces.

To what extent the forest fragments with no howlers constitute suitable habitats for howlers is presently unknown. However, our surveys indicated that there were no major differences in the physiognomy of the vegetation between these forest fragments and those occupied by howlers. In fact, many Lauraceae, Moraceae, Sapotaceae, and Fabaceae tree species present in the forest of PNP, and known to be important in the diet of *A. pigra* [Silver et al., 1998], were found in both sets of forest fragments.

It is possible that the absence of howlers in half of the forest fragments explored may be the result of hunting, as indicated to us by interviews with local ranchers and farmers. Declines in size and number of remaining troops in forest fragments resulting from hunting have been noted for *A. pigra* populations in the Yucatan paninsula [Watts & Rico-Gray, 1987].

In PNP the *A. pigra* population occurs at densities of 23 ind/km^2, whereas at the sites investigated the estimated average density was 119 ± 82.9 ind/km^2 (range 11–316 ind/km^2). In Belize, exceptionally high densities for *A. pigra*, ranging from 47–124 ind/km^2, were detected in strips of fragmented riparian vegetation and in small forest patches [Silver et al., 1998, Ostro et al., 1999]. While this may suggest tolerance by *A. pigra* to habitat reduction and fragmentation, it also suggests a high animal load on the resources present in each forest fragment. For example, at PNP the biomass of *A. pigra* was estimated at 1.57 kg/ha [Estrada et al., 2002], while in the forest fragments studied it was 26.2 ± 12.4 kg/ha (range 7.5–54 kg/ha).

The high densities of *A. pigra* in the fragmented landscape investigated contrast with data for the same species studied in large tracts of forest such as Tikal, Guatemala, where densities for *A. pigra* were 5–9 ind/km^2 [Coelho et al., 1976], and Muchukuxt in Quintana Roo, Mexico, where densities of 16.5 ind/km^2 were reported [Gonzales-Kirchener, 1998]. It is possible that variation in this population characteristic may be related to recent group-history events (e.g., food crop failure, disease, history of habitat alteration, and hunting pressure), as has been noted for other howler species [Chapman & Balcomb, 1998].

The dietary flexibility (being as frugivorous as possible and as folivorous as necessary) [Milton, 1980; Silver et al., 1998] of *A. pigra* probably explains its ability to subsist in a variety of habitats [Horwich & Johnson, 1986; Crockett, 1998; Ostro et al., 1999, 2000], and it may explain its high tolerance to habitat fragmentation, as has been reported for other *Alouatta* species [Bicca-Marques &

Calegaro-Marques, 1994b; Galetti et al., 1994; Estrada & Coates-Estrada, 1996; Crockett, 1998; Estrada et al., 1999]. However, continued habitat loss, fragmentation, and isolation, as well as human encroachment, may put the remnant populations of *A. pigra* around PNP at risk.

Howlers existing in small forest fragments may be under dietary stress [Neves & Rylands, 1991] and may have greater parasitic infestation [Gilbert, 1994; Crockett, 1998], which may result in high mortality of young and adult individuals [Estrada et al., 1999]. This suggests that although they can survive in such habitat-islands, they may not be doing well in the long term. Our study showed that forest destruction and fragmentation still continues in the area, with important loss of forest cover and an increment in the number of very small remnants. Such fragmentation further isolates the howler troops that exist in the fragmented landscape, and increases the isolation of the protected forest of PNP.

Conservation of the howler population still living in the forest fragments investigated is important to increase the effective size of the population being preserved in PNP. The existence in the past of larger and more contiguous areas of rain forest suggests that it is very likely that the howler population at PNP and that detected in the surrounding fragments were part of a single population. This population became fragmented and isolated as the forest was converted to pasture lands by human activity.

Clearly, conservation of the *A. pigra* population around PNP requires a landscape perspective. In this scenario, we cannot ignore the conservation value of even small forest fragments [Turner & Corlett, 1996]. However, conservation planning of isolated forest fragments is incomplete, and consideration must be given to creating and sustaining connectivity [Lindemeyer & Nix, 1993; Neiman et al., 1993; Offerman et al., 1995; Harrison & Bruna, 1999; Laurance et al., 2002]. The establishment or improvement of vegetation corridors (riparian strips, windbreaks, and live fences) between isolated forest fragments in the study area may alleviate some of the pressures derived from loss of area, such as diminished suitable habitat and food resources. Importantly, it may add connectivity among isolated howler monkey troops, and among these and the *A. pigra* population preserved in the PNP forest [Beier & Noss, 1988; Saunders & De Rebeira, 1991; Estrada & Coates-Estrada, 1996; Estrada et al., 1994, 2002].

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