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## THE BLACK HOWLER MONKEY (*ALOUATTA PIGRA*) AND SPIDER MONKEY (*ATELES GEOFFROYI*) IN THE MAYAN SITE OF YAXCHILÁN, CHIAPAS, MEXICO: A PRELIMINARY SURVEY

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### Introduction

The black howler monkey of Mesoamerica, *Alouatta pigra*, has a restricted geographic distribution in Belize, Guatemala and Mexico. The majority of its range (c. 80%) is in Mexico in parts of the states of Tabasco and Chiapas, and it is the only *Alouatta* species present in the Yucatán peninsula (Smith, 1970; Horwich and Johnson, 1986; Watts and Rico-Gray, 1987). Spider monkeys (*Ateles geoffroyi*) coexist with *A. pigra* in many areas, but because of hunting for food and to obtain pet infants, and the destruction and fragmentation of their forests, they are among the most endangered primates in Mesoamerica (Kinzey, 1998).

Information on population parameters and conservation status for *A. pigra* are available from only a few localities, namely, two sites in Belize in the Bermuda Landing and Cockscomb Wildlife Reserve (Horwich, 1998; Silver *et al.*, 1998; Ostro *et al.*, 1999, 2000), in Tikal, Guatemala (Coelho *et al.*, 1976), in the Muchukux forest in Quintana Roo, Mexico (González-Kirchner, 1998) and in Palenque, Chiapas, Mexico (Estrada *et al.*, 2002). A similar situation prevails in the case of *A. geoffroyi*, with information available only from few localities in Mexico, namely Los Tuxtlas, Veracruz (Estrada and Coates-Estrada, 1996; Silva-López and Jiménez-Huerta, 2000) and the Muchukux and Naji Tucha forests in Quintana Roo, Mexico (González-Kirchner, 1999). Some information is available on populations of *A. geoffroyi* from Tikal, Guatemala (Coelho *et al.*, 1976).

Such paucity of information and the rapid fragmentation and conversion of the natural habitat of *A. pigra* and *A. geoffroyi* to pasture lands and agricultural fields in northern Mesoamerica, coupled with intensive hunting pressure and trafficking of infants as pets, makes the task of protecting these primate species particularly difficult (Estrada and Coates-Estrada, 1988; Rylands *et al.*, 1995). Data on group size, density, and age and sex composition for populations of *A. pigra* and *A. geoffroyi* in large forest tracts and in landscapes modified by man may provide information on the variability of population parameters, and may also improve our understanding of their tolerance of habitat loss and fragmentation (Estrada and Coates-Estrada, 1996; Estrada *et al.*, 1994; Crockett, 1998; Cuarón, 2000).

In this paper we provide preliminary data on group size, population density and demographic structure for populations of *A. pigra* and *A. geoffroyi* in the protected forest surrounding the ruins of the Mayan site of Yaxchilán, Chiapas, Mexico. The data we present are part of a series of surveys of primate populations inhabiting the protected forests surrounding major Mayan archeological sites in southern Mexico (Estrada *et al.*, 2002; in prep.).

### Methods

#### Study area and sites

The study was carried out at the Mayan site of Yaxchilán, Chiapas, Mexico (16°53'N, 90°57'W, 250 m above sea level), near the Río Usumacinta, that marks the international boundary between Mexico and Guatemala (Fig. 1). There is a protected forest of about 2700 ha surrounding the Mayan site, of which 1100 ha are contained within an omega-shaped area by the river, while the rest extends inland (Fig. 1). This forest is connected to 35,000 ha of protected rain forest in the Community Reserve "La Cojolita". The climate is hot and humid, and average annual precipitation is 1951 mm, with a dry season from December to April (average monthly rainfall = 42.4 ± 12.7) and a wetter period from May to November (average monthly rainfall = 256.0 ± 100.1 mm). Mean annual temperature is 25.5 ± 2.2°C (range 21–28°C).

Tall evergreen rain forest (tree heights between 15–45 m) is the dominant vegetation at the study site (<www.conabio.gob.mx>). Abundant trees in this forest are *Brosimum alicastrum*, *B. costaricanum*, *Poulsenia armata*, *Ficus glabrata* (Moraceae), *Manilkara zapota*, *Pouteria sapota* (Sapotaceae), *Bursera simaruba* (Burseraceae), *Lonchocarpus* sp. (Fabaceae), and *Spondias* spp. (Anacardiaceae) (Meave, 1990).

The Mayan site dates back to about 500 AD (Coe, 1998). Only about 5% of the ruins of the site have been excavated, the rest are covered by rain forest vegetation, and vestiges of buildings can be easily observed amidst the vegetation or roots of trees. Several of the Mayan structures were built at the top of the many hills, while the majority of the largest

buildings and plazas are found close to the edge of the Río Usumacinta (Figs. 1, 2).

### Primate surveys

Primate surveys were conducted in November 2001 and in April 2002 in a 100 ha area around the Mayan ruins of Yaxchilán. We triangulated early morning (0500 hrs) choruses to determine the presence and location of howler monkey troops. Vocalizations emitted by spider monkeys were also recorded for the same purpose. An existing system of trails was used to gain access to different parts of the 100 ha area. To triangulate monkey vocalizations in the early morning, we climbed to the top of the tallest (50 m)

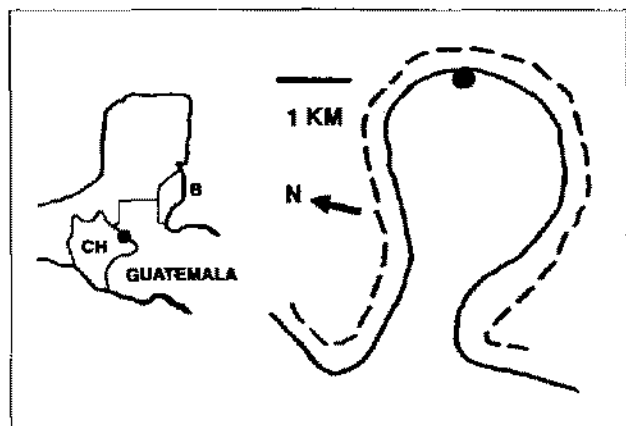


Figure 1. Location of Yaxchilán by the Río Usumacinta demarcating the international boundary between Mexico and Guatemala. The omega-shaped area comprises the protected forest of the Mayan site, about 1100 ha, with an additional 1600 ha inland. The black dot is the area where the ruins are located. The dotted line around the omega shape shows the route followed during the river survey of howler and spider monkeys. CH = Chiapas, B = Belize.

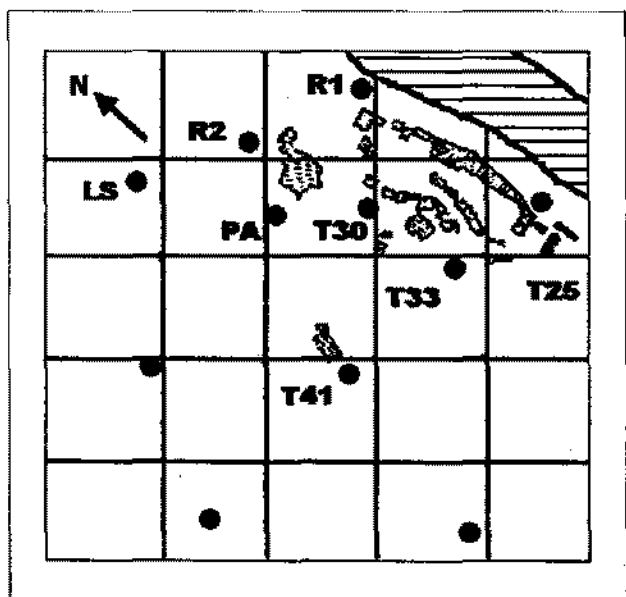


Figure 2. Study area (100 ha) where the Mayan ruins of Yaxchilán are located. The shaded area in the upper right corner is the Río Usumacinta. Codes refer to howler monkey troops detected. The three dots without code are three troops that were heard howling, but could not be located. Grid cells are 200 x 200 m.

Mayan structures (Temples 39, 40 and 41) from which we could monitor vocal exchanges between troops in the 100 ha area. The direction from which vocalizations were heard were determined with a compass and plotted on a detailed map of the site.

Two teams searched for the monkeys. An average of  $8.0 \pm 2.0$  hrs/day was spent exploring different sections of the study area by walking slowly (1.0 km/hr) through the forest or along the existing system of trails. When a troop of howler monkeys or a subgroup of spider monkeys was sighted we noted its location on a detailed map of the archeological buildings. A GPS (Garmin GPS III, Kansas, USA) was used to obtain precise georeference points. We completed 200 man/hours and walked 62.3 km surveying howler and spider monkeys in the study area.

Contacted howler and spider monkey groups were followed for several hours and repeatedly counted by each team to confirm identification and age and sex composition. Individuals were classified as adults, juveniles and dependant infants. Accurate identification of the sex was only possible for the adults and juveniles. All groups detected were found and followed on consecutive days, further aiding in confirmation of their size and composition and identity. We carefully examined consistency in the age and sex composition of each group, their location in relation to the trail system and topographical and archaeological features of the terrain, and their relative location with other troops. Trees in which howler and spider monkeys were sighted were measured (height and diameter at breast height - dbh). Average weights of *A. pigra* and *A. geoffroyi* available in the literature (Coelho *et al.*, 1976) were used to estimate the biomass (kg/ha) represented by the monkeys in the study area.

Two additional surveys of howler and spider monkeys were conducted from a boat by navigating 13.7 km along the Río Usumacinta, following the contour of the omega-shaped area where the site of Yaxchilán is located (Fig. 1). They started at 0530 hrs and were conducted down river (S-N direction) with the outboard motor off, allowing for a gentle and silent flow of the boat. Vocalizations and sightings were located using the GPS. A GPS reading was taken every 500 m to obtain an estimate of the length and width of the omega-shaped study area.

## Results

### Howler monkeys

Vocalization surveys resulted in the detection of 11 troops of howler monkeys in the 100 ha area surrounding the Mayan buildings. Eight were in the forest and repeatedly counted on consecutive days, yielding a total 54 howler monkeys and one solitary male. The other three troops could not be found, but were heard howling on other days in the same general location (W-SW of the ruins) (Fig. 2).

Forty-one percent of the individuals counted were adult males, 30% were adult females, 8% were juvenile males,

6% were juvenile females and 15% were infants (Table 1). Average troop size was  $6.6 \pm 2.1$  individuals, ranging from 4 to 10. Troops had an average of  $2.8 \pm 1.6$  adult males,  $2.0 \pm 0.5$  adult females,  $0.8 \pm 0.4$  juvenile males,  $1.0 \pm 0.0$  juvenile females and  $1.3 \pm 0.5$  infants (Table 1).

Adult male to adult female ratio was 1:0.73, and in juveniles the sex ratio was 1:0.75. Adult to non-adult ratio was 1:0.40, and adult female to immature ratio was 1:0.97 (Table 1). Using the average troop size calculated for the eight counted, and the total number of troops detected, howler monkey density in the 100 ha study area was estimated at 0.72 ind/ha or 72.6 ind/km<sup>2</sup>. Total biomass represented by the eight troops and the solitary male was estimated at 367 kg, and mean biomass per troop was  $44.8 \pm 15.0$  kg. Using this last figure, we estimated howler monkey biomass at 492.8 kg/km<sup>2</sup> or 4.9 kg/ha.

### Spider monkeys

We confirmed the existence of three subgroups of spider monkeys in the 100 ha study area with a total of 17 individuals. They were observed several times in different locations, and sometimes in the same trees as howler monkeys. Their identity was confirmed by the size of the subgroup and by its age and sex composition. Adult males accounted for 35.3% of individuals counted, adult females

for 29.4%, juvenile males for 5.9%, juvenile females for 11.8% and infants for 17.6% (Table 1).

Mean subgroup size was  $5.67 \pm 3.06$  individuals, and mean sex and age composition of these subgroups was  $2.00 \pm 1.00$  adult males,  $1.67 \pm 1.15$  adult females,  $1.50 \pm 0.71$  juveniles and  $1.50 \pm 0.71$  infants. The adult male to adult female sex ratio was 1:0.83 and in juveniles it was 1:2.0; the adult female to immature ratio was 1:1.20. Density was estimated at 0.17 ind/ha or 17 ind/km<sup>2</sup> and spider monkey biomass at 106.45 kg/km<sup>2</sup> or 1.06 kg/ha (Table 1).

### Vegetation types used by howler and spider monkeys

All sightings of howler and spider monkeys were in tall evergreen rain forest. The mean height and dbh of trees used by howler monkeys were  $11.07 \pm 6.9$  m (range 4-30 m) and  $63.4 \pm 28.5$  cm (range 45-120 cm), respectively. In the case of spider monkeys, mean height and dbh of trees used were  $19.6 \pm 7.3$  m (range 4-30 m) and  $78.7 \pm 28.3$  cm (range 45-120 cm), respectively. Spider monkeys preferred taller trees than howler monkeys (U test,  $P < 0.01$ ) (Fig. 2).

### River survey

The survey down the Río Usumacinta along the contour of the omega-shaped study area resulted in the auditory detection of 17 troops of howler monkeys and one subgroup

Table 1. Results of the survey of howler and spider monkeys in a 100 ha area around the Mayan site of Yaxchilán, Chiapas, Mexico, located at the edge of the Río Usumacinta.

	Howler		Spider		Infants	Total
	Males	Females	Males	Females		
<i>Alouatta pigra</i>						
T25	5	2	0	1	2	10
T33	3	2	1	1	2	9
T30	2	2	1		1	6
R1	1	2		1		4
R2	5	2			1	8
PA	2	1	1		1	5
T41	1	3			1	5
LSTRIP	3	2	1			6
Total	22	16	4	3	8	53
Mean	2.8	2.0	0.8	1.0	1.3	6.6
+ sd	1.6	0.5	0.4	0.0	0.5	2.1
Solitary males	1					1
Total howler monkeys						54
<i>Ateles geoffroyi</i>						
Subgroup						
1	1	1			1	3
2	3	1	1			5
3	2	3		2	2	9
Total spider monkeys	6	5	1	2	3	17
Mean	2.00	1.67	1.00	2.00	1.50	5.67
± sd	1.00	1.15	0.00	0.00	0.71	3.06

of spider monkeys, along a stretch of 13.7 km. Sixty-five percent of the howler monkey troops ( $n = 11$ ) and the single spider monkey subgroup were detected on the Mexican side of the river. Howler monkey troops were detected at a rate of 0.80 troops/km surveyed on the Mexican side and 0.48 troops/km surveyed on the Guatemalan side.

## Discussion

The results of the primate surveys presented here should be viewed as preliminary. Further field work will provide information on the consistency and variability of the demographic traits we have observed for *A. pigra* and *A. geoffroyi* at Yaxchilán. Our surveys showed that howler troops and *Ateles* subgroups were detected at a rate of 0.18 troops/km and 0.048 subgroups/km surveyed, respectively, confirming that *A. pigra* is more numerous than *A. geoffroyi* at Yaxchilán. The 13.7 km river survey along the edges of the omega shape area in which Yaxchilán is located, also showed a predominance of howler monkeys, with spider monkeys present in lower numbers.

### Howler monkeys

The density of 72.6 individuals/km<sup>2</sup> we estimated for *A. pigra* in Yaxchilán is significantly higher than those reported for this species in other large rain forest tracts in Mexico, such as Muchukux, Quintana Roo (15.1 ind/km<sup>2</sup>; González-Kirchner, 1998) and Calakmul and Palenque, Chiapas (15.2 ind/km<sup>2</sup> and 23 ind/km<sup>2</sup>, respectively; Estrada *et al.*, 2002, in prep.). Coelho *et al.* (1976) and Schlichte (1978) reported a density of 5-9 individuals/km<sup>2</sup> (1978) at Tikal, Guatemala.

High densities of *A. pigra* have been reported from Belize, ranging from 47-178 individuals/km<sup>2</sup> in fragmented strips of riparian vegetation and small forest patches, which

authors have indicated may be due to overcrowding (Silver *et al.*, 1999; Ostro *et al.*, 1999, 2000; Horwich *et al.*, 2001). However, the high densities found in Yaxchilán and in other large tracts of rain forest such as Calakmul, Campeche (Estrada *et al.*, in prep.), Palenque, Chiapas (Estrada *et al.*, 2002), and in Muchukux, Quintana Roo (González-Kirchner, 1998), seem to contradict such an assumption.

Mean troop size in Yaxchilán ( $6.6 \pm 2.1$  individuals) compares to troop sizes reported for *A. pigra* in Calakmul, Campeche ( $7.5 \pm 2.3$  individuals; Estrada *et al.*, in prep.) and Palenque, Chiapas ( $7.0 \pm 2.8$  individuals; Estrada *et al.*, 2002), but they are higher than those reported in Belize and Guatemala, where mean troop size varies from 4.4 to 6.3 individuals (Coelho *et al.*, 1978; Bolin, 1981; Horwich and Gebhard, 1983; Ostro *et al.*, 1999), and the small troops averaging 3.16 individuals reported for *A. pigra* in central Quintana Roo, Mexico (González-Kirchner, 1998).

Seventy-five percent of the troops detected in Yaxchilán had more than one adult male, as was found in Palenque, Chiapas, and in Calakmul, Campeche, where 75% and 60% of the troops, respectively, were multimale (Estrada *et al.*, 2002, in prep.). However, at Tikal, Guatemala, troop surveys by different authors consistently reported unimale troops (Coelho *et al.*, 1976; Schlichte, 1978; Horwich and Johnson, 1986). In Yaxchilán, Calakmul, and in Palenque the overall adult sex ratio was 1:0.73 to 1:0.90 (Estrada *et al.*, 2002, in prep.). Data from Belize showed most recorded troops to be unimale, and the adult sex ratio was 1:1 to 1:1.63 (Bolin, 1981; Ostro *et al.*, 1999; Horwich *et al.*, 2001).

### Spider monkeys

The density (17 ind/km<sup>2</sup>) we report for *A. geoffroyi* in Yaxchilán falls within the range reported for the species in other extensive tracts of rain forest in Quintana Roo, Mexico, such as Najil Tucha (14.5 ind/km<sup>2</sup>) and Muchukux (27.1 ind/km<sup>2</sup>) (González-Kirchner, 1999), and in Calakmul (25 ind/km<sup>2</sup>), Campeche, Mexico (Estrada *et al.*, in prep.). In Tikal, Guatemala, densities for *A. geoffroyi* were found to range from 26 to 45 ind/km<sup>2</sup> (Coelho *et al.*, 1976; Cant, 1978), while in Costa Rica population densities ranged from 6-9 ind/km<sup>2</sup> (Freese, 1976; Chapman, 1988). In fragmented landscapes in Los Tuxtlas, Mexico, *A. geoffroyi* is found at densities of 0.22 ind/km<sup>2</sup> (Estrada and Coates-Estrada, 1996), but in more extensive forest in the same region, the density was reported at 0.66 ind/km<sup>2</sup> (Silva-López and Jimenez-Huerta, 2000).

Spider monkey subgroup size ( $5.6 \pm 3.06$  individuals) in Yaxchilán is similar to that reported for *A. geoffroyi* in Calakmul, Campeche (6.6 individuals) (Estrada *et al.*, in prep.), in Chiapas, Mexico (5.0 individuals) (Eisenberg, 1966) and in Los Tuxtlas, Veracruz at 0.66-6.2 individuals (Silva-López *et al.*, 1988, 2000). It is higher than that reported for the Muchukux and Najil Tucha forests in Quintana Roo, where subgroup sizes averaged 4.5 and 3.8 individuals, respectively (González-Kirchner, 1999), as

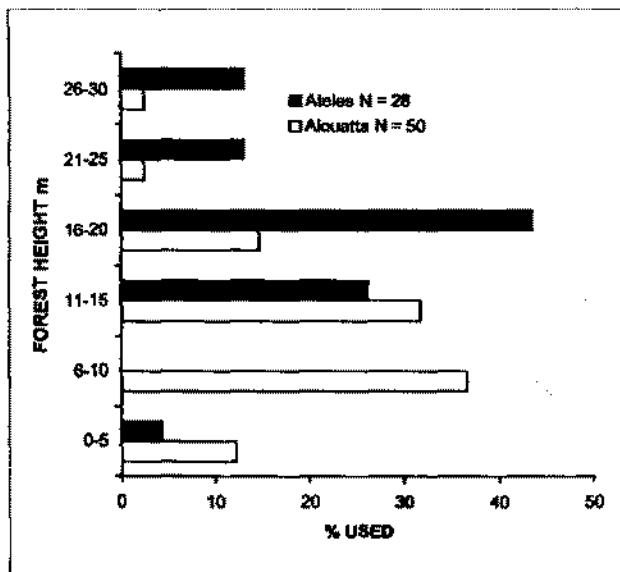


Figure 3. Distribution of heights of trees used by spider and howler monkeys at the site of Yaxchilán. Note the preference by spider monkeys for tall trees (>10 m), whereas howler monkeys preferred trees >4 and <25 m).

well as in Belize and Guatemala (4.5 and 2.6 individuals, respectively) (Coelho *et al.*, 1976; Cant, 1978, 1990),

The adult sex ratio detected in Yaxchilán (1:0.83) strongly favoring adult males, contrasts with the ratio reported for the same species in Calakmul (1:1.96) (Estrada *et al.*, in prep.) and in Muchukux and Najil Tucha forests in Quintana Roo (1:1.26) (González-Kirchner, 1999). A sex ratio of 1:1.56 was reported for spider monkeys in disturbed forest areas in Los Tuxtlas, Veracruz (Silva-López *et al.*, 1988), while a ratio of 1:3.25 was reported for a population of spider monkeys in an undisturbed forest site in the same region (Silva-López and Jiménez-Huerta, 2000). The adult sex ratio for *A. geoffroyi* reported in Tikal, Guatemala was 1:2.23 (Coelho *et al.*, 1976). The 1:1.20 adult female to immature ratio in Yaxchilán suggests a population with a capacity to sustain itself and grow (Clarke *et al.*, 2002).

Spider monkeys in Yaxchilán preferred the tall trees of the upper canopy (70% used were 16- > 30 m in height), as has been noted in other localities in Mexico, such as Quintana Roo (González-Kirchner, 1999) and Calakmul (Estrada *et al.*, in prep.), besides other Neotropical sites (Van Roosmalen and Klein, 1988; Symington, 1988; Yoneda, 1990). They can, however, be seen at all levels of the forest when traveling and will often forage in low trees bearing ripe fruit. The howler monkeys in Yaxchilán preferred lower strata than spider monkeys, spending much more time in the middle and lower canopy. This was similar to our observations in Calakmul (Estrada *et al.*, in prep.).

#### General comments

The differences in population parameters for *A. pigra* and *A. geoffroyi* between Yaxchilán and other sites, may be within the natural variation in their populations, due to hunting or to the lack of data on both species in Mexico, Belize and Guatemala. Clearly, more sites need to be surveyed to document the range of variation in density, group size and other demographics for *A. pigra* and *A. geoffroyi* within the range of their current geographic distribution in northern Mesoamerica.

In this vein of thinking, it has been indicated that *A. pigra* is typically found in riparian forests at elevations below 400 m, and that the population in Tikal, Guatemala (Ostro *et al.*, 2000) is exceptional. However, our survey in Yaxchilán showed no concentration of howler troops along the Río Usumacinta; the majority of the troops detected were distributed inland. In Palenque, Chiapas and Calakmul, Campeche in Mexico, *A. pigra* populations are common in the non-riparian habitats dominating these sites, and in Palenque they occur in forests at 500 m above sea level (Estrada *et al.*, 2002; Estrada *et al.*, in prep.).

While discriminating separate howler monkey groups is relatively easy, it is more difficult for spider monkeys. The members of relatively large groups or communities travel in small temporary subgroups of unstable composition (Van

Roosmalen and Klein, 1988; Kinzey, 1996). Because of the fission-fusion nature of their social organization it is rare to see all members of the community together, and group sizes are difficult to estimate (Coelho *et al.*, 1976; Klein and Klein, 1977). The surveys conducted along the Río Usumacinta in Yaxchilán detected more howler and spider monkeys on the Mexican side than on the Guatemalan side of the river. During our surveys we noted much deforestation (slash and burn), as well as hunting (rifle shots heard several times) on the Guatemalan side. Although preliminary, these observations suggest the need for further surveys to better assess and monitor the status of *A. pigra* and *A. geoffroyi* along the international border formed by the Río Usumacinta.

The presence of the important Mayan ruins at Yaxchilán has resulted in the permanent protection of the surrounding rain forest, and its populations of *A. pigra* and *A. geoffroyi*. Yaxchilán. This is also true of sites such as Palenque (Estrada *et al.*, 2002) and Calakmul (Estrada *et al.*, in prep.), and together they constitute important foci for the conservation of *A. pigra* and *A. geoffroyi* in this area of Mesoamerica.

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## A POSSIBLE EXAMPLE OF COERCIVE MATING IN MANTLED HOWLING MONKEYS (*ALOUATTA PALLIATA*) RELATED TO SPERM COMPETITION

Clara B. Jones

### Introduction

If females with internal fertilization mate more than once during a reproductive cycle, the potential exists for sperm from more than one male to compete for access to eggs inside her reproductive tract. This phenomenon, termed "sperm competition," has received increasing attention in the mammalian, including primate, literature in recent years (e.g., Harcourt, 1997; Gomendio *et al.*, 1998; Dixson, 1998). Several studies have demonstrated that coercive mating ("coercive copulations," "forced copulations," "rape") may be associated with multiple mating by female insects (Moller, 1998), and Smith (1984; also see Thornhill and Palmer, 2000) suggested that human rape might have evolved as an adaptation to sperm competition, although there is no necessary or sufficient relationship between rape and sperm competition. The present short communication describes an apparent case of coercive mating in the context of sperm competition for mantled howling monkeys (*Alouatta palliata*), a species in which coercive mating has not been reported. Attempts to force copulations by male mantled howlers are generally rebuffed successfully by females with a bared-teeth, open-mouth display, sometimes accompanied by vocalizations (Jones, 1985). Such behavior

### Results

On 5 March 1977 (late dry season), the focal animal was male R, the third and lowest-ranking male in the study group. He was observed to lie and rest in a tree along the Rio Corobici with female PY who demonstrated evidence of estrus -2 (a few days subsequent to "peak" estrus [see Jones, 1985]). A sub-adult/young adult male who had not yet joined the male hierarchy rested approximately 50 feet downriver, and several adult females and young were nearby. No other adult males were sighted. Male R vocalized continuously with high intensity guttural barks to female PY, the young male, and/or (an)other individual(s). While the functions of vocalizations in mantled howlers have not been investigated, these barks have been interpreted to communicate motivation (Jones, 2000).

At 1:04 pm, male R initiated the stereotyped lingual gesture (tongue moving rapidly in and out of mouth, a sexual signal characteristic of the genus *Alouatta* [Carpenter, 1934]) with female PY, who responded in kind. Reciprocal lingual gesturing continued for 3 min. Male R subsequently lay rear-present to female PY, a posture that has been interpreted as submissive (Jones, 2000). At 1:20 pm, male R sat up and mounted female PY, thrusting 40 times in 37 sec with an ejaculatory pause. Subsequent to copulation, the pair rested. During the resting period, male R occasionally emitted high guttural barks.

At 2:21 pm, female PY initiated lingual gesturing with male R. The male, lying on a branch with the female, failed to reciprocate the female's lingual gestures and shifted posture in apparent vigilance. At 2:30 p.m., male R initiated lingual gestures with female PY and subsequently sat up, looking downriver in the direction of the young male. At 2:33 pm, female PY moved 30 ft upriver past male R, sitting rear-present to the male. Male R moved towards the female and sat 10 ft behind her. Female PY continued to move upriver. Male R continuously vocalized at low intensity.

At 2:37 pm., male G, the second-ranked male of Group 5, moved rapidly upriver past male R, mounted female PY without preliminaries to copulation, and thrustured approximately 37 times with an ejaculatory pause. The