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Source: Neotropical Primates, 14(1) : 11-18

Published By: Conservation International

URL: <https://doi.org/10.1896/044.014.0103>

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DISTRIBUTION OF THE BLACK HOWLER MONKEY (*ALOUATTA PIGRA*) AND THE MANTLED HOWLER MONKEY (*A. PALLIATA*) IN THEIR CONTACT ZONE IN EASTERN GUATEMALA

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Abstract

We studied the geographic distribution of the endangered black howler monkey, *Alouatta pigra*, in its southeastern range in eastern Guatemala along its putative contact zone with the mantled howler monkey, *A. palliata*. A distributional survey of both species was conducted through direct observations and interviews, and the data analyzed with GIS to detect potentially limiting geographic and ecological factors. *Alouatta pigra* was not associated with any specific vegetation type or altitudinal range, as it occurred in many forest types from the lowlands up to elevations of 2705 m a.s.l., in contrast to prior reports of it being restricted to elevations below 400 m a.s.l. and having a strong affinity for riverine forests. *Alouatta palliata* did not occur at the higher elevations. Distribution of both howler monkey species was unaffected by the presence of *Ateles*, by protection status of the survey site, or by hunting activities. Deforestation appears to have restricted both species in some areas. Throughout the southeastern range of *A. pigra*, we found no evidence for current sympatry with *A. palliata*, as their distributions are separated by a river barrier and unsuitable dry shrubland. Ecological preferences also seem to reinforce allopatry, with only *A. pigra* occurring in wet and cold montane forests of the Sierra de las Minas. Our data indicate that highland habitats in Mexico and Guatemala, previously considered unsuitable for *A. pigra*, may need to be evaluated for distribution assessments and management plans. Populations of *A. pigra* in the diverse protected ecosystems in eastern Guatemala may be an important component for conservation of the species.

Key Words: *Alouatta pigra*, *A. palliata*, geographic distribution, allopatry, eastern Guatemala

Resumen

Se estudió la distribución geográfica del mono aullador negro, *Alouatta pigra*, y el mono aullador de manto, *A. palliata*, en el este de Guatemala, en donde reportes previos proponen traslape de rangos. Esta región constituye el límite sureste del rango de *A. pigra*, especie en peligro de extinción y endémica del sur de México, Belice y Guatemala. La distribución de ambas especies se determinó mediante observaciones directas y encuestas. Los datos fueron analizados con SIG para detectar posibles factores limitantes, tanto ecológicos como geográficos. La presencia de *A. pigra* no estuvo asociada con ningún tipo de vegetación particular o rango altitudinal, encontrándose la especie en varios tipos de bosque desde los 0 hasta los 2705 msnm. Estos datos no coinciden con estudios previos que describen a *A. pigra* como una especie restringida a elevaciones por debajo de los 400 msnm y con alta afinidad por bosques ribereños. *Alouatta palliata* no se registró en altitudes elevadas. La distribución de ambas especies de monos no se vio afectada por la presencia de *Ateles*, por el estado de protección del sitio de muestreo, ni por actividades de cacería. En algunas áreas las especies se ven restringidas por la deforestación. No se encontró evidencia de simpatría ni traslape de rangos. Los rangos de ambas especies se separan por un río y por hábitat inadecuado de bosque seco. Además, preferencias ecológicas parecen reforzar la alopatría, puesto que únicamente *A. pigra* ocurre en los bosques húmedos y fríos de la Sierra de las Minas. Nuestros datos sugieren que hábitats montañosos en México y Guatemala previamente categorizados no aptos para *A. pigra*, necesitarían considerarse en evaluaciones de distribución y planes de manejo. Las poblaciones de *A. pigra* en los diversos ecosistemas protegidos en el este de Guatemala podrían ser importantes componentes en la conservación de la especie.

Palabras Clave: *Alouatta pigra*, *A. palliata*, distribución geográfica, alopatría, oriente de Guatemala

Introduction

The black howler monkey, *Alouatta pigra*, is endemic to Guatemala, Belize and southern Mexico. Recently, it was categorized as endangered in the IUCN Red List of Threatened Species due to population size reduction based on habitat decline (Cuarón *et al.*, 2003). Conservation

assessments and action plans for the species mandate updating distribution maps and describing the status of wild populations (Rodríguez-Luna *et al.*, 1996; Matamoros *et al.*, 1997).

Limited knowledge of the geographic distribution of *A. pigra* is based on museum specimens (Smith, 1970;

Hall, 1981) and broad field studies done in Belize and Mexico (Horwich and Johnson, 1986; Watts *et al.*, 1986) and Guatemala (Curdts, 1993). Recent fieldwork in the Yucatán peninsula detailed the species' distribution and habitat preferences (Navarro *et al.*, 2003; Serio-Silva *et al.*, 2006), but other areas of Mexico and Guatemala need similar detailed studies. Of particular importance are potential contact zones with the mantled howler monkey, *A. palliata*, at the northwest and southeast range limits, where sympatry has been reported in Tabasco, Mexico (Smith, 1970; Cortés-Ortiz *et al.*, 2003) and suspected in eastern Guatemala (Horwich and Johnson, 1986; Curdts, 1993). Contact zones are important for the preservation of primate biodiversity (Jones and Bicca-Marques, 2004) and essential for the study of genetics and ecology of speciation (Jiggins *et al.*, 1996).

The studies in southern Belize and eastern Guatemala have resulted in ambiguous and inconclusive definition of ranges for the two species. For example, Horwich and Johnson (1986) identified sympatry at the Belize-Guatemala border around the Sarstún River, based on suggestions of *palliata*-like individuals on the Guatemala side of the river, where only *A. pigra* was expected. Curdts (1993) proposed large areas of sympatry in the mountains of Baja and Alta Verapaz and Sierra de las Minas, Guatemala, but provided no empirical evidence. The objective of the present study was to define the geographic distribution of *A. pigra* and *A. palliata* in their contact zone in eastern Guatemala at the southeastern range limit of *A. pigra*. In addition we hoped to identify ecological factors and geographic barriers that might affect both species' distributions.

Methods

Study area

The contact zone and putative area of sympatry of *A. pigra* and *A. palliata* lies within 88°–90° W longitude and 15°–16° N latitude, encompassing the eastern part of Guatemala, bounded by Belize, Honduras and the Atlantic Ocean (Fig. 1). Five Guatemalan departments are partly or totally within the area: Alta Verapaz, Baja Verapaz, Izabal, Zacapa and El Progreso. The area is topographically and ecologically heterogeneous with elevations ranging from sea level to 3,000 m a.s.l. (CONAP, 2005) and ecosystems varying from flooded coastal forest to montane cloud forest. The region is transversed by several mountain ranges and large rivers (Fig. 1). Continuous tracts of tropical forests are restricted primarily to protected areas. Forest conversion by traditional slash-and-burn maize cultivation is combined with intensive socioeconomic activities: coffee and cardamom plantations in the highlands, and cattle ranching, banana, African palm and rubber plantations in the lowlands. The Department of Izabal, which occupies a large part of the study area, has 20% of its total area in cattle pastures and crop monocultures (INAB, 2001).

Surveys

Following Brockelman and Ali (1987), we conducted a distributional field survey during the dry season, February to April 2005. Cartographic maps (1:25000), vegetation maps, and a Landsat TM satellite image (2003) were used to identify suitable monkey habitat, access routes, and survey sites. Survey sites were selected to test potential geographic barriers and to cover the altitudinal ranges and vegetation types of the region. Additionally, site selection was dependent on the presence of suitable forest cover and existence of key persons who would facilitate entrance to villages, contact appropriate interviewees, and serve as translators in K'ekchi villages. Survey sites were accessed using vehicle, boat, mule or by foot. At each survey site geographic location and altitude were recorded with a Garmin GPS 72.

Howler monkey occurrences were detected by two methods: interviews (Pinto and Rylands, 1997; Iwanaga and Ferrari, 2002) and broad forest surveys along trails and rivers (Brockelman and Ali, 1987). Interviews consisted of non-leading questioning about the primates in the area, as well as other questions related to the interviewee's occupation, residence time in the area, and hunting activities. Additionally, interviewees were asked to recognize photographs of possible local primate species (*Alouatta*, *Ateles*, *Cebus*) and South American *Alouatta* species, as well as playbacks of loud calls of *A. pigra* and *A. palliata*. People interviewed were mainly subsistence hunters, town elders with knowledge of the forest, park rangers, landowners, and field biologists. Forest surveys were made during 3-day visits to key sites in early mornings and late afternoons during peak hours of howler monkey vocal activity, in order to locate individuals and make visual and/or auditory identification.

Species presence/absence records obtained from valid interviews and/or direct observations at each site were incorporated into a Geographic Information System (ArcView version 3.3). Digital maps of the vegetation types of Guatemala (INAB, 2001; CCAD-WB, 2003), protected areas, and elevation curves were overlaid with the geographical coordinates of sites to create joined attribute tables and allow analyses of the distribution of howler monkeys in relation to physical and ecological features. Information collected through interviews on hunting pressure and on the occurrence of the spider monkey, *Ateles geoffroyi*, was also related to the presence/absence records of the howler monkeys. A search of collection databases of 18 natural history museums in North America and Europe and a review of literature were made to obtain any historic records of the occurrence of *A. pigra* and *A. palliata* in the region.

Statistical analyses

We used tests for homogeneity of proportions with a logistic analysis approach to detect habitat-specific distributional patterns. Specifically, we used a nominal model to test if vegetation type had an effect on the probability of occurrence of each species and an ordinal model to test for

a trend in probability of occurrence along an altitudinal gradient. Also, tests of independence were used to assess howler monkey association with (a) the presence of *Ateles* and (b) the protection status of the site. All statistical tests were performed with SAS version 9.0.

Results

A total of 58 sites were visited (Fig. 1); interviews were conducted at 47 sites and direct observations at 23 sites. We conducted 97 interviews, 59% with ladino and 41% with K'ekchi interviewees. Five interviews were classified as invalid due to inconsistencies in descriptions or identifications of photographs. Playbacks proved useful only to identify *A. palliata*, as interviewees clearly distinguished the calls. In contrast, at *A. pigra* sites, interviewees could not distinguish between the two species' calls. Overall, *Alouatta pigra* was found at 26 sites: seven through both interviews and direct observations, seven through observations only, and 12 sites through interviews only (Table 1). *Alouatta palliata* was found at 12 sites: five through interviews and direct observation, three through observations only, and four through interviews only (Table 2).

Alouatta pigra was verified along both banks of the Río Sarstún, the Atlantic coast, the north shore of Lake Izabal-Río Dulce, both banks of the Río Polochic and inland in the Purulhá mountains, Sierra Yalijux, Sierra Santa Cruz, and Sierra de las Minas (Fig. 1, Table 1). *Alouatta palliata* was verified along the Atlantic coast south of the Río Dulce and inland along the Río Motagua valley and in Sierra Caral (Fig. 1, Table 2).

Of five potential vegetation types, *A. pigra* was found in four and *A. palliata* in three (Table 3). Neither species occurred in "seasonal evergreen shrubland with mixed forest". Only *A. pigra* occurred in "tropical evergreen and semievergreen mixed forest" typical of cloud forest. *Alouatta palliata* was most often in "agroproductive systems with significant portions of broad-leaved forest", although the association was not statistically significant (test of homogeneity of proportions $\chi^2 = 7.6$, $df = 4$, $p = 0.10$). In contrast, *A. pigra* was less frequent in this disturbed vegetation type and more commonly associated with flooded forests, mixed forests and broad-leaved forest (test of homogeneity of proportions $\chi^2 = 14.41$, $df = 4$, $p < 0.01$). Survey sites were distributed across elevations from sea level to more than

Table 1. Localities where *Alouatta pigra* occurs (see Fig. 1), protection status, and detection method.

Site No.	Locality	Protection status	Method
1	Chelemá	private reserve	sighting, interview
2	Lowland south of Chichipate village	None	sighting, interview
4	Selich village	None	interview
6	Secacar village	None	interview
7	Boquerón	None	sighting
8	Sakitzul finca	proposed private reserve	interview
9	Guitarra village	None	interview
14	Calajá village	None	interview
15	Río Sarstún, Belize side	Sarstoon Temash Reserve	sighting
16	Río Sarstún, Guatemala side	Río Sarstún Multiple Use Area	sighting
17	Río Sarstún, Belize side	Sarstoon Temash Reserve	sighting
18	Sarstún village	Río Sarstún Multiple Use Area	sighting, interview
19	Calix – Black creek finca	None	interview
20	Chocón-Machacas scientific station	Chocón Machacas Biotope	interview
21	Mario Dary Biotope	Mario Dary Biotope	interview
22	Las Cabañas scientific station	core area SM BR ¹	sighting, interview
24	trail to Volcán Las Palomas	core area SM BR ¹	sighting
25	Alejandría finca	multiple use zone SM BR ¹	sighting, interview
26	Los Angeles village	buffer zone SM BR ¹	interview
27	San Vicente II village	buffer zone SM BR ¹	interview
28	Manguitos II village lowlands	None	interview
30	Semuy II village lowlands	Bocas Polochic Wildlife Reserve	interview
32	Selempín biological station	Bocas Polochic Wildlife Reserve	sighting, interview
33	Río Oscuro	Bocas Polochic Wildlife Reserve	sighting
34	Lake Izabal shore	Bocas Polochic Wildlife Reserve	sighting
35	Naranjal Yaxte village	None	sighting, interview

¹ SM BR: Sierra de las Minas Biosphere Reserve.

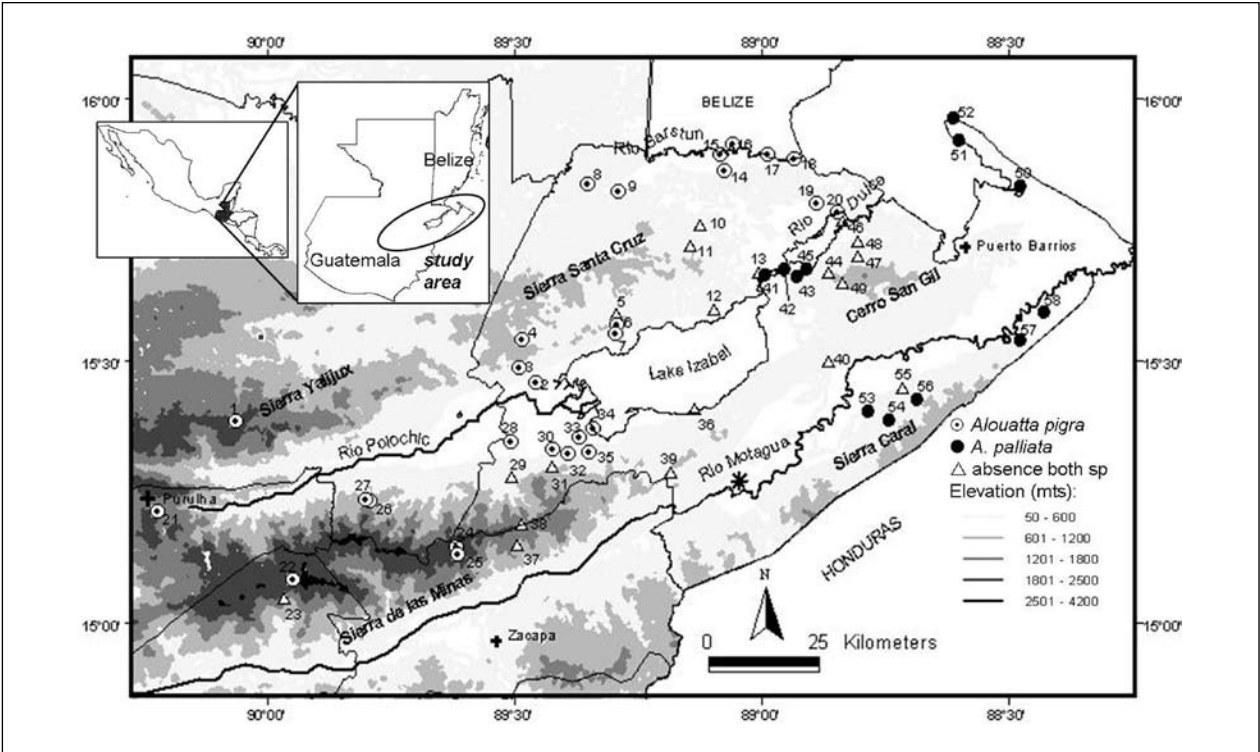


Figure 1. The study area in eastern Guatemala, showing the location of the survey sites, mountains, major rivers, and department limits. Asterisk shows the historic location of *A. pigra* in Quiriguá, Izabal.

Table 2. Localities where *Alouatta palliata* occurs (see Fig. 1), protection status, and detection method.

Site No.	Locality	Protection Status	Method
41	Juan Vicente Creek	Río Dulce National Park – none	sighting, interview
42	Casa Guatemala	Río Dulce National Park – none	sighting, interview
43	Río Frío lowland	None	interview
45	Cayo Piedra fina	Río Dulce National Park – none	sighting
50	Laguna Santa Isabel shore	Punta Manabique Wildlife Reserve	sighting
51	Estero Lagarto village	Punta Manabique Wildlife Reserve	sighting, interview
52	Cabo Tres Puntas village	Punta Manabique Wildlife Reserve	sighting, interview
53	San Vicente Paul village	None	interview
54	San Vicente Paul highlands	proposed Sierra Caral reserve – none	interview
56	Animas village highlands	proposed Sierra Caral reserve – none	interview
57	Champas finca lowlands	None	sighting, interview
58	Cacao village	None	sighting

Table 3. Vegetation types (UNESCO classifications following INAB, 2001) of the survey sites and number of sites with presence/absence records for each species.

Vegetation type	No. of sites	No. of sites with <i>A. pigra</i>	No. of sites with <i>A. palliata</i>	No. of sites with both spp.	No. of sites without howler monkeys
1. Tropical evergreen broad- leaved periodically flooded forest	13	10	3	0	0
2. Tropical evergreen and semievergreen broad-leaved forest	21	9	3	0	9
3. Tropical evergreen and semievergreen mixed forest ¹	6	4	0	0	2
4. Seasonal evergreen shrubland with mixed forest ¹	3	0	0	0	3
5. Agroproductive systems with significant portions of Broad-leaved forest	15	3	6	0	6
Total	58	26	12	0	20

¹Mixed forest = broad-leaved and needle-leaved forest

Table 4. Altitudinal ranges (following INAB, 2001) of the survey sites and number of sites with presence/absence records for each species.

Altitudinal descriptor	Elevation (m)	Number of sites	No. of sites with <i>A. pigra</i>	No. of sites with <i>A. palliata</i>	No. of sites with both spp.	No. of sites without howler monkeys
Lowland	0–499	39	18	10	0	11
Sub-montane	500–999	8	1	2	0	5
Lower montane	1000–1499	5	2	0	0	3
Upper montane	1500–2000	3	2	0	0	1
Altimontane	>2000	3	3	0	0	0
Totals		58	26	12	0	20

2500 m a.s.l. (Table 4). *Alouatta pigra* was found in all altitudinal ranges (Table 4) and no ordinal association was detected (test of homogeneity of proportions, ordinal model $\chi^2 = 1.61$, $df = 1$, $p = 0.20$). The altimontane survey sites (> 2000 m a.s.l.) were all occupied by *A. pigra*, the highest being 2705 m a.s.l. in Sierra de las Minas. In contrast, *A. palliata* occurred significantly more frequently in lowland sites and was not recorded at elevations higher than 1000 m a.s.l. (test of homogeneity of proportions, ordinal model $\chi^2 = 4.07$, $df = 1$, $p < 0.05$).

Of the 10 major protected natural areas surveyed, 80% sustained howler monkey populations: *Alouatta pigra* was found in six and *A. palliata* in two (Tables 1 and 2). Of the total survey sites, 32 sites (55%) were in protected areas with enforcement and 26 sites (45%) were located outside protected areas or in protected areas without vigilance. Occurrence of howler monkeys was not associated with the protection status of the survey site (test of independence $G^2 = 0.33$, $df = 1$, $p = 0.59$).

Of 97 interviewees, 76% denied hunting or ever hearing of anyone hunting howler monkeys. Most (19 of 22) of the remaining 24% responded that they had only heard of other people killing howler monkeys and did not consider them a valuable bush meat; two respondents used howler monkeys as bait for river shrimp, and one hunted these primates for meat and medicine (howler monkey broth was used as treatment for respiratory illness). Howler monkeys kept as pets were rare. The reports on hunting activity were distributed across the survey sites, unrelated to ethnic group of interviewees or geographic region. The only other primate species in the area reported in the interviews was the spider monkey *Ateles geoffroyi*. The white-faced capuchin monkey, *Cebus capucinus*, was not known to locals and probably does not extend into Guatemala. Records for *Ateles geoffroyi* presence were slightly lower than those for *Alouatta* species (34% and 40% of interview sites, respectively), and its range overlapped with both *A. palliata* and *A. pigra*. *Ateles* occurred in sites with and without howler monkeys and there was no evidence of association or dissociation with *Alouatta* (test of independence $G^2 = 0.11$, $df = 1$, $p = 0.76$).

No evidence was found for a current zone of sympatry between *Alouatta pigra* and *A. palliata*. Only one interviewee claimed to have seen both species in mixed troops, but this was disputed by other interviewees at the same site (site 19) and it conflicted with records from surrounding sites as well. The identified range limits for *A. pigra* are: Lake Izabal and Río Dulce in the east, unsuitable habitat of pine forest west of Purulhá in Baja Verapaz in the southwest and pine forest and dry shrubland in foothills of Sierra de las Minas in the south (Fig. 1). The southeastern range limit is not associated with any barrier. We found the most southeasterly populations of *A. pigra* in the tip of Sierra de las Minas (site 35), and historical records place the species farther east in Quiriguá in the middle Motagua valley (Salvin and Goodman, 1879; museum specimen in the Smithsonian National Museum of Natural History, USNM 238704) (Fig. 1). The western range limit of *A. palliata* is dry deciduous shrubland. The heavily disturbed area to the south of Lake Izabal in the lower Motagua valley is the northwest limit and the Río Dulce the north limit.

Discussion

This study reports the distribution of the endangered black howler monkey, *Alouatta pigra*, in its southern geographic range in topographically and ecologically heterogeneous eastern Guatemala, providing needed information on detailed occurrence localities (Rodríguez-Luna *et al.*, 1996; Matamoros *et al.*, 1997) and new reports of its ecological tolerances. It also contributes to the limited knowledge of the status and distribution of the mantled howler monkey, *A. palliata*, in Guatemala. *Alouatta pigra* was widespread and occupied several different habitat types across altitudinal ranges from sea level up to 2705 m. Our results show no evidence of significant association with a specific vegetation type or altitude. In his preliminary study in Guatemala, Curdts (1993) also found *A. pigra* at high elevations above 2000 m a.s.l. These results contrast with the reports that *A. pigra* is restricted to elevations below 400 m a.s.l., with a strong affinity for riverine forest (Horwich and Johnson, 1986; Watts *et al.*, 1986; Ostro *et al.*, 2000). Models of the species' current range based on preference for lowland forests (Luecke, 2004) need to consider potential

premontane and montane habitats to avoid underestimation of actual range.

Forest disturbance by humans influences the distribution patterns of *A. palliata* and *A. pigra* in the region mainly by eliminating suitable monkey habitat. This is especially the case along the Río Motagua Valley and south shores of Lake Izabal and Río Dulce. Here extensive monocultures and cattle pastures have replaced the original tropical forest (INAB, 2001), which may account for the high frequencies of *A. palliata* in disturbed vegetation types. The ability of *A. palliata* to survive in fragmented habitats is widely recognized by other authors (e.g., Estrada and Coates-Estrada, 1984; Silva López *et al.*, 1988; Clarke *et al.*, 2002). Deforestation in the range of *A. pigra* occurs mainly in the upper and middle Río Polochic valley, where the species was once very common (Salvin and Godman, 1879), as well as north of Lake Izabal. The species was present in some disturbed sites, in accordance with other reports of *A. pigra* thriving in forest fragments (Horwich and Johnson, 1984; Baumgarten, 2000; Estrada *et al.*, 2002).

The absence of *A. palliata* from the Cerro San Gil area (sites 44, 47, 48, 49) was unexpected, since the area has protected status and extensive forest cover with other wildlife, including the spider monkey. The premontane and montane elevations at these sites may act as a limiting factor for the species. Other studies have also found that *A. palliata* is absent from elevations above 700 m a.s.l. in mountainous ranges in Mexico (Silva López *et al.*, 1988; Estrada and Coates-Estrada, 1996). The species is present at elevations up to 1500 m a.s.l., but only at lower latitudes in Central America (Timm *et al.*, 1989). The red howler monkey, *Alouatta seniculus*, occurs at high elevations in the Colombian Andes (Hernández-Camacho and Cooper, 1976; Gaulin and Gaulin, 1982).

We found little evidence for hunting pressure on howler monkeys and no association between hunting and the distribution of the two species. Hunting of howler monkeys is also limited in Belize (Horwich and Johnson, 1984) but more common in Mexico (Estrada and Coates-Estrada, 1984; Horwich and Johnson, 1984; Silva López *et al.*, 1988). In contrast, subsistence hunting has accounted for local extinctions of *Alouatta* in localities in the Brazilian Amazon (Peres, 1990) and the Peruvian and Bolivian Amazon (Freese *et al.*, 1982). *Alouatta* occurrence may be influenced by competition with other primates in some habitats (Eisenberg, 1979), although not always (Peres, 1997; Iwanaga and Ferrari, 2002). We found no evidence for competitive exclusion between *Ateles* and *Alouatta* species. In Mexico the spider monkey *Ateles* is more widespread than *Alouatta* and sympatric with it in only a few places (Watts *et al.*, 1986; Rodríguez-Luna *et al.*, 1987; Silva López *et al.*, 1988).

The study region has a high potential for the conservation of the endangered black howler monkey, *A. pigra*, since six

of its protected areas harbor the species (Table 1), the largest being the Sierra de las Minas Biosphere Reserve (246,803 ha) (CONAP, 2005). Furthermore, the low hunting pressure and the occurrence of the species outside protected areas provides the opportunity for community-based conservation projects and sustainable resource programs, which have proven effective for howler monkey conservation in Belize and Mexico (Horwich, 1998). The occupied habitats are ecologically heterogeneous in comparison with the species' range in the Yucatán Peninsula, which is predominantly lowland rainforest (Horwich and Johnson, 1986; Watts *et al.*, 1986; Navarro *et al.*, 2003). The populations of *A. pigra* living in cloud forests at high elevations are an important component in conserving the species variability and its gene pool. Previously considered to be unsuitable habitats, highlands will have to be considered in distribution assessments and management plans for the species. The severe deforestation south of Lake Izabal-Río Dulce puts the populations of the mantled howler monkey *A. palliata* at risk in Guatemala. These are the most northerly populations of the subspecies *A. palliata palliata*. Important conservation actions here include conservation in the protected areas without enforcement, the legal declaration of the proposed Sierra Caral protected area, and the establishment of the Mesoamerican Biological Corridor project that connects Punta de Manabique Wildlife Reserve with protected areas in Honduras.

The results of this study are relevant to clarifying the distribution of *Alouatta pigra* and *A. palliata* in their contact zone in eastern Guatemala. We found no evidence for current range overlap or sympatry as well as no support for the previous proposed sympatric areas around Río Sarstun (Horwich and Johnson, 1986) or in the highlands of Baja Verapaz, Alta Verapaz, and Sierra de las Minas (Curdts, 1993). In the northwestern part of the putative contact zone, the Río Dulce acts as a physical barrier separating both species. Curdts (1993) also reported *A. pigra* on the north bank and *A. palliata* on the south bank of this river. River boundaries are often limiting factors for the distribution of primates (Ayres and Clutton-Brock, 1992; Wallace *et al.*, 1996). In the eastern part of the contact zone, *A. pigra* occurs on the southwest side of Lake Izabal and tip of Sierra de las Minas. South of Lake Izabal suitable monkey habitat has been removed and *A. pigra* is known only from historic records. Further east in the lower Motagua Valley we registered exclusively *A. palliata*. It is possible that a narrow sympatry existed south of the lake before forest loss. Further range overlap is not evident, probably explained by ecological differences. Our results suggest that *A. palliata* is associated with forests found at low elevations, precluding its expansion into the wet and cold habitats of Sierra de las Minas where *A. pigra* is found. Habitat preferences seem to act as a barrier between howler monkey species in other cases of near sympatry (Crockett, 1998) as reported for *A. fusca* and *A. caraya* in northern Argentina (Di Bitetti *et al.*, 1994) and *A. seniculus* and *A. caraya* in southwestern Amazonia (Iwanaga and Fer-

rari, 2002). Further, *A. pigra*'s lack of wide expansion into *A. palliata*'s range in the lowlands may perhaps involve assortative mating or hybrid inviability.

In the extreme south of the potential contact zone, the ranges of both species are interrupted by dry deciduous shrubland south of the Sierra de las Minas. The semidesert characteristics of this vegetation clearly constitute an effective ecological barrier between the species. In contrast to the scenario in Guatemala, *A. pigra* and *A. palliata* in Mexico have a broad sympatric area that extends over the lowlands of the states of Tabasco and Campeche. Nevertheless, species introgression seems to be limited as Smith (1970) found no evidence for hybridization based on museum specimens from the same localities, although occasional interbreeding may occur in mixed troops of howler monkeys in the area (Cortés-Ortiz *et al.*, 2003).

Acknowledgments

This study was supported by two Louisiana Governor's Office of Environmental Education Research Grants. We are grateful to FUNDAECO, Fundación Defensores de la Naturaleza, FUNDARY, CECON-USAC, Parroquia El Estor, Finca Tijax, Finca Cáliz and Finca Champas for technical support and research permission. Special thanks to all interviewees and enthusiastic guides and to Daniel Tenes, Carlos Avendaño, Haroldo García and José Moreira for assistance in the field. We thank Kellen Gilbert for comments on this manuscript. This study was carried out with the required permits from the Consejo Nacional de Areas Protegidas-Guatemala. The senior author was supported by a grant from the Fulbright Faculty Development Program Central America.

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