Distribution and biogeography of Central American howling monkeys (Alouatta pigra and A. palliata)

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DISTRIBUTION AND BIOGEOGRAPHY OF CENTRAL AMERICAN HOWLING MONKEYS (*ALOUATTA PIGRA* AND *A. PALLIATA*)

A Thesis

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Master in Science

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Amrei Baumgarten
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# TABLE OF CONTENTS

ACKNOWLEDGMENTS........................................................................................................... ii

ABSTRACT ............................................................................................................................... iv

CHAPTER
1 INTRODUCTION ................................................................................................................ 1

2 DISTRIBUTION OF THE BLACK HOWLING (*ALOUATTA PIGRA*) AND THE
MANTLED HOWLING (*A. PALLIATA*) MONKEY IN THEIR CONTACT ZONE IN
EASTERN GUATEMALA. ........................................................................................................... 3
   Introduction ......................................................................................................................... 3
   Methods .............................................................................................................................. 4
   Study Area ......................................................................................................................... 4
   Methods .............................................................................................................................. 5
   Statistical Analyses ........................................................................................................... 6
   Results .............................................................................................................................. 6
   Discussion ......................................................................................................................... 11

3 THE DISTRIBUTION OF CENTRAL AMERICAN HOWLING MONKEYS
(*ALOUATTA SP.*) AND BIOGEOGRAPHIC IMPLICATIONS............................................... 16
   Introduction ......................................................................................................................... 16
   Methods .............................................................................................................................. 17
   Results .............................................................................................................................. 17
   Discussion ......................................................................................................................... 21
   Historical Biogeography ................................................................................................... 22

4 CONCLUSIONS .................................................................................................................. 25

REFERENCES ....................................................................................................................... 27

APPENDIX
1 DESCRIPTION OF SURVEY SITES IN EASTERN GUATEMALA ................................. 33

2 LIST BY COUNTRY OF REFERENCES USED FOR LOCALITY DATA ............................... 35

VITA........................................................................................................................................ 37
ABSTRACT

Central America has two howling monkey species: the widespread mantled howling monkey (*Alouatta palliata*) and the endemic and endangered black howling monkey (*A. pigra*) limited to southeastern Mexico, northern Guatemala and Belize. Studies that verify the distribution of these species are needed, especially in their contact zones where sympatry is reported. Their evolutionary history remains controversial. My study examines their distribution at a local scale in a potential contact zone in eastern Guatemala through direct observations and interviews and at a regional scale across the entire isthmus using data from museum specimen localities, study sites, historic records and field surveys. Using GIS I analyzed the distributions against geographic and ecological features to infer current barriers between both species and explore the possibility of their role in the initial speciation. I found no evidence for current sympatry in eastern Guatemala; instead parapatry is maintained by a riverine barrier and by ecological adaptation, as only *A. pigra* occurs in the cold montane habitats further inland. My study reveals broader elevational and vegetational tolerances by *A. pigra* than previously reported. My results suggest differences in elevation and cold tolerances by the two species which I consider an important ecological barrier separating them at present. I identified the highland massif of northern Central America and their associated coniferous and subalpine vegetation as a geographic barrier. In contrast to other studies, I propose that both species ranges are not adjacent throughout, but separated by these mountains and only coming into contact in a broad sympatry zone in the lowlands north of the highland massif in Mexico and in the narrow parapatry zone in Guatemala. I present an alternative biogeographic hypothesis that proposes an initial split by the northern Central American highland massif during cold periods that resulted in the isolation of the *A. pigra* lineage in the Yucatan peninsula and in the further divergence in cold tolerance.
CHAPTER 1
INTRODUCTION

Two species of howling monkeys of the family Atelidae occur in Central America, the mantled howling monkey (*Alouatta palliata*) and the black howling monkey (*A. pigra*). *A. palliata* is widespread, extending from southern Mexico to Ecuador; whereas *A. pigra* is an endemic species, confined to Belize, northern Guatemala and southeastern Mexico. *A. pigra* is categorized as endangered in the IUCN Red List of Threatened Species (Cuarón et al. 2003) and studies on their distribution and status in the wild are necessary (Rodríguez-Luna et al. 1996; Matamoros et al. 1997; Estrada and Mandujano 2003). Of particular importance are potential contact zones with *A. palliata* at the northwest and southeast range limits, where sympatry has been reported, respectively, in Tabasco, Mexico (Smith 1970; Cortés-Ortiz et al. 2003) and in eastern Guatemala (Horwich and Johnson 1986; Curdts 1993). These records are surprising since other howling monkey species usually have allopatric distributions throughout their ranges (Crockett 1998). Contact zones are important for the study of speciation as they may reveal factors that are involved both in the formation and maintenance of species (Jiggins et al. 1996). Unlike most *Alouatta* species where driving forces of their speciation are strong physical barriers that inhibit gene flow, no clear biogeographic factors have been discovered that might account for the *pigra/palliata* speciation (Cortés-Ortiz et al. 2003).

Chapter 2 describes the geographic distribution of *Alouatta pigra* and *A. palliata* in their potential contact zone in eastern Guatemala at the southeastern range limit of *A. pigra*. Previous studies have resulted in ambiguous definition of both species’ ranges in the region and in different description of the degree of sympatry. Among factors that influence the distribution of howling monkeys are topographic barriers, habitat types, anthropogenic activities and presence of potential primate competitors. I analyze if the presence of the howling monkeys is associated
with vegetation type, elevation, presence of the spider monkey (*Ateles geoffroyi*), hunting activities and protection status of the survey sites and I hope to identify geographic barriers that might affect both species’ distributions.

Results in Chapter 2 suggest that *Alouatta pigra* occurs commonly at high elevations and in sites where temperatures fall below 0°C, whereas *A. palliata* seems not to occur at such extremes. I was interested to see if the differences in elevation and cold tolerances between both species are a pattern throughout their ranges. Tolerance of higher elevations and colder temperatures by *A. pigra* may be an important consequence of its historical isolation from *A. palliata*. Therefore, Chapter 3 focuses on comparing extensive distribution data of *A. pigra* and *A. palliata* with geographic and ecological features to identify distributional patterns, current barriers and ecological preferences throughout their ranges in Central America.

Two basic biogeographic hypotheses for the presence of the two species of *Alouatta* in Central America have been suggested: an invasion in separate waves by two different species (Smith 1970; Ford 2005) or a single invasion with a speciation event in Central America (Smith 1970). I evaluate my findings of current geographic and ecological barriers between *A. pigra* and *A. palliata* with these hypotheses and explore a modified scenario that accounts for the present distribution pattern and differences in elevation and cold tolerances.
CHAPTER 2

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

INTRODUCTION

The black howling 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).

The presumed 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), while other areas of Mexico and Guatemala need similar detailed studies (Estrada and Mandujano 2003). Of particular importance are potential contact zones with the mantled howling monkey, *A. palliata*, at the northwest and southeast range limits, where sympatry has been reported, respectively, in Tabasco, Mexico (Smith 1970; Cortés-Ortiz et al. 2003) and 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).

Furthermore, 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 howling monkeys 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 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 I 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 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. 2.1). 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 asl (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. 2.1).

Continuous tracts of tropical forests are mainly restricted 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).
Methods

Following Brockelman and Ali (1987), I conducted a distributional field survey during the dry season, February to April, of 2005. Cartographic maps (1:25000), vegetation maps and a Landsat TM satellite image (2003) were used to identify suitable monkey habitat, access ways 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 by vehicle, boat, mule or foot. At each survey site geographic location and altitude were recorded with a Garmin GPS 72.

Howling 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 howling monkey vocal activity, in order to locate monkeys 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 howlers 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**

I used tests for homogeneity of proportions with a logistic analysis approach to detect habitat-specific distributional patterns. Specifically, I 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 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. 2.1; Appendix 1); interviews were conducted at 47 sites and direct observations at 23 sites. I 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 only useful to identify *A. palliata*, as interviewees clearly distinguished the calls. In contrast, at *A. pigra* sites, interviewees could not distinguish species’ calls.

Overall, *Alouatta pigra* was found at 26 sites: 7 through both interviews and direct observations, 7 through observations only and 12 sites through interviews only (Appendix 1). *A.
Figure 2.1: 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.
*palliata* was found at 12 sites: 5 through interviews and direct observation, 3 through observations only and 4 through interviews only (Appendix 1).

*Alouatta pigra* were 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.2.1). *A. palliata* were verified along the Atlantic coast south of the Río Dulce and inland along the Río Motagua valley and in Sierra Caral (Fig. 2.1).

Of five potential vegetation types, *A. pigra* was found in four and *A. palliata* in three (Table 2.1). 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. *A. palliata* was most often in “agroproductive systems with significant portions of broad-leaved forest”, although there was no statistically significant association (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 2500m asl (Table 2.2). *A. pigra* was found in all altitudinal ranges (Table 2.2) 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 (>2000m) were all occupied by *A. pigra*, the highest being 2705 m in Sierra de las Minas. On the contrary, *A. palliata* occurred significantly more in lowland sites and was not recorded at elevations higher than 1000m (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 howling monkey populations: *Alouatta pigra* was found in 6 and *A. palliata* in 2 (Appendix 1). Of the total survey
sites, 32 sites (55%) where in protected areas with enforcement and 26 sites (45%) were located outside protected areas or in protected areas without vigilance. Howling monkey occurrence was not associated with the protection status of the survey site (test of independence $G^2=0.33$, df=1, $p=0.59$).

Table 2.1: Vegetation types (UNESCO classifications following INAB, 2001) of the survey sites and number of sites with presence/absence records for each species.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>#sites</th>
<th>#sites with $A.\text{pigra}$</th>
<th>#sites with $A.\text{palliata}$</th>
<th># sites with both spp</th>
<th># sites without howlers</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Tropical evergreen broad-leaved periodically flooded forest</td>
<td>13</td>
<td>10</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2. Tropical evergreen and semievergreen broad-leaved forest</td>
<td>21</td>
<td>9</td>
<td>3</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>3. Tropical evergreen and semievergreen mixed forest¹</td>
<td>6</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>4. Seasonal evergreen shrubland with mixed forest¹</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>5. Agroproductive systems with significant portions of broad-leaved forest</td>
<td>15</td>
<td>3</td>
<td>6</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>58</strong></td>
<td><strong>26</strong></td>
<td><strong>12</strong></td>
<td><strong>0</strong></td>
<td><strong>20</strong></td>
</tr>
</tbody>
</table>

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

Of 97 interviewees, 76% denied hunting or never heard of anyone hunting howling monkeys. Most (19 of 22) of the remaining 24% responded that they had only heard of other persons killing howling monkeys and didn’t consider them a valuable bush meat; two respondents used howling monkeys as bait for river shrimp and one hunted howling monkey for meat and medicine. (Howling monkey broth was used as treatment for respiratory illness.) Howling monkeys kept as pets were rare. The reports on hunting activity were spread across the survey sites, unrelated to ethnic group of interviewees or geographic region.
Table 2.2: Altitudinal ranges (following INAB, 2001) of the survey sites and number of sites with presence/absence records for each species.

<table>
<thead>
<tr>
<th>Altitudinal descriptor</th>
<th>Elevation (meters)</th>
<th>#sites</th>
<th>#sites with A. pigra</th>
<th>#sites with A. palliata</th>
<th># sites with both spp</th>
<th># sites without howlers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lowland</td>
<td>0-499</td>
<td>39</td>
<td>18</td>
<td>10</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Sub-montane</td>
<td>500-999</td>
<td>8</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Lower montane</td>
<td>1000-1499</td>
<td>5</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Upper montane</td>
<td>1500-2000</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Altimontane</td>
<td>&gt;2000</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>58</td>
<td>26</td>
<td>12</td>
<td>0</td>
<td>0</td>
<td>20</td>
</tr>
</tbody>
</table>

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 that for *Alouatta* species (34% and 40% of interview sites, respectively), and its range overlapped with both *A. palliata* and *A. pigra* (Appendix 1). *Ateles* occurred in sites with and without howling 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. 2.1). The southeastern range limit is not associated with any barrier. I 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. 2.1).
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 howling monkey, *Alouatta pigra*, in its southern geographic range in topographically and ecologically heterogeneous eastern Guatemala, providing needed information on detailed occurrence localities (Matamoros et al. 1997; Rodríguez-Luna et al. 1996) and new reports of its ecological tolerances. It also contributes to the limited knowledge of the status and distribution of the mantled howling 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. My 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. These results contrast with the reports that *A. pigra* is restricted to elevations below 400 m, 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 southshore 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 by
A. palliata to survive in fragmented habitats is widely recognized by other authors (e.g. Silva Lopez et al. 1988; Estrada and Coates-Estrada 1984; 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) and north of Lake Izabal. The species was present in some disturbed sites, which is 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 protective status and extensive forest cover with other wildlife, including the spider monkey. The premontane and montane elevations at the sites may act as a limiting factor for the species. Other studies have also found that A. palliata is absent from elevations above 700m asl 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 asl but only at lower latitudes in Central America (Timm et al. 1989). The red howling monkey, Alouatta seniculus, occurs at high elevations in the Colombian Andes (Gaulin and Gaulin 1982; Hernández-Camacho and Cooper 1976).

I found little evidence for hunting pressure on howling monkeys and no association between hunting and the distribution of the two species. Hunting of howling monkeys is also limited in Belize (Horwich and Johnson 1984) but more common in Mexico (Horwich and Johnson 1984; Silva López et al. 1988; Estrada and Coates-Estrada 1984). 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). I found
no evidence for 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; Rodriguez-Luna 1987; Silva López et al. 1988).

The study region has a high potential for the conservation of the endangered black howling monkey *A. pigra*, since six of its protected areas harbor the species (Table 3), 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 howling monkey conservation in Belize and Mexico (Horwich 1998). The occupied habitats in the study area are ecologically heterogeneous in comparison with the species range in the Yucatán Peninsula, which is predominantly lowland rainforest (Watts et al. 1986; Horwich and Johnson 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 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 howling *A. palliata* at risk in eastern Guatemala. These are the most northerly populations of the subspecies *A. palliata palliata*, which stresses the importance for conservation actions 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. I 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 highlands of Baja Verapaz, Alta Verapaz and Sierra de las Minas (Curdts 1993). In the northwestern part of the putative contact zone, the Rio Dulce acts as a physical barrier separating both species. Curdts (1993) also reported the species on opposite banks 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 only historic records place *A. pigra* here. Further east in the lower Motagua valley I 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, which may be explained by ecological differences. My results suggest that *A. palliata* is associated with forests found at low elevations, precluding its expansion into wet and cold habitats of Sierra de las Minas, where *A. pigra* is found. Habitat preferences seem to act as a barrier between howling monkey species in other cases of near sympatry (Crockett 1998) as reported for *A. fusca* and *A. caraya* in northern Argentina (Di Bitteti et al. 1994) and *A. seniculus* and *A. caraya* in southwestern Amazonia (Iwanaga and Ferrari 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 howlers in the area (Cortés-Ortiz et al. 2003).
CHAPTER 3
THE DISTRIBUTION OF CENTRAL AMERICAN HOWLING MONKEYS
(ALOUATTA SP.) AND BIOGEOGRAPHIC IMPLICATIONS

INTRODUCTION

In Central America there are two species of howling monkeys of the family Atelidae, the mantled howling monkey (Alouatta palliata) and the black howling monkey (A. pigra). Some authors add a third species, A. coibensis, confined to Coiba Island and Azuero Peninsula of Panama (Rylands et al. 1997), but a recent phylogenetic study recognizes only A. palliata and A. pigra at the species level (Cortés-Ortiz et al. 2003). A. pigra is an endemic species, confined to Belize, northern Guatemala and southeastern Mexico, whereas A. palliata is widespread, occurring west and south of the Yucatan peninsula and extending south throughout Central America into the Pacific plain of Colombia and Ecuador.

Alouatta palliata and A. pigra are sister species that split ~3 mya. They belong to the trans-Andean clade that separated from the South American cis-Andean clade about 6.8 mya with the formation of the Northern Andes (Cortés-Ortiz et al. 2003). The evolutionary history of the two species remains controversial and several scenarios for their speciation and colonization of Central America have been proposed (Smith 1970; Cortés-Ortiz et al. 2003; Ford 2005).

Here I compare extensive distribution data of the Central American howling monkeys with geographic and ecological features to identify distributional patterns, current barriers and ecological preferences throughout their ranges and in their contact zones. I evaluate my findings with the existing models for the origin and biogeography of both species and develop a modified hypothesis based on my proposal of geographic and ecological barriers.
METHODS

To determine the distribution of *Alouatta palliata* and *A. pigra* I used museum specimen records from collection databases and catalogues of the major National History Museums in North America and Europe (references), study sites and historic records described in the scientific literature (Appendix 2) as well as distributional surveys (Horwich and Johnson 1986; Watts et al. 1986; Serio-Silva et al. 2005; previous chapter).

I assigned geographic coordinates for the museum specimen collection localities using gazetteers from the GEOnet Names Server of the National Geospatial-Intelligence Agency and the US Board on Geographic Names for foreign places and verifying localities with country maps provided by the Louisiana State University Cartographic Information Center. For discrepant museum records either I or curators verified the identity of specimens by measuring the skulls and examining the skins.

I used a Geographic Information System (ArcView Version 3.3) to overlay the distribution data with digital maps of ecosystems and elevations of Mesoamerica (Puebla, Mexico to Panama) (CCAD 2003a, b) and obtain joined attribute tables. This allowed me to see if the distributions are coincident with ecological or geographic barriers and detect patterns that could be related to biogeographic events responsible for speciation. I also explored the literature for ecological preferences and behavior in the species’ contact zones, as these may reveal factors that are maintaining the species and that were possibly involved in the initial speciation (Jiggins et al. 1996). I created a range map based on broad regions of correspondence between distributional data and permissive ecosystems and elevations.

RESULTS

My analysis of the distribution of *Alouatta palliata* and *A. pigra* at the elevation and ecosystem scale revealed new features of the ecological tolerance of these species. Both historic
collections and field data support a broad elevational tolerance by *A. pigra*, with sites varying from sea level up to 3350 m. High elevation occurrences from 1800 to 3350 m were found in western Guatemala (LACM specimen # 53664) and in eastern Guatemala (Salvin and Godman 1879; Curdts 1993; previous chapter; FMNH specimen #64590). The localities above 2500 m freeze some days of the year (MAGA 2001), implying cold tolerance by *A. pigra*. In contrast, *Alouatta palliata* did not occur above 2000 m and most of its montane localities are at lower latitudes in Central America, where minimum temperatures do not reach freezing; for example at 1500 m in Monteverde, Costa Rica, the absolute minimum temperature is 9°C (Clark et al. 2000).

Furthermore, I found that both, *Alouatta palliata* and *A. pigra* have broad vegetational tolerances, as they occurred over a variety of vegetation types that included evergreen and semievergreen broad-leaved forests, evergreen and semievergreen mixed forests, deciduous and semideciduous broad-leaved forests, mangroves and swamps. Based on my records, both species occupied the same forest types in their respective parapatric ranges.

My study identified an important geographic barrier separating the two species: the highland massif of northern Central America, including Sierra Madre de Chiapas, Mexico, central highlands of Guatemala and Honduras (Fig. 3.1). The region is characterized by montane coniferous forests, subalpine forests and semiarid inland valleys, all unsuitable habitats for *Alouatta*. Therefore, the continuous highland belt in Mexico and Guatemala seems to be a barrier between the species and it defines the southern limit of the range of *Alouatta pigra*. *A. palliata* borders these mountains in Mexico at lower elevations in Tabasco, Veracruz and the Isthmus of Tehuantepec (Fig. 3.1). It probably bordered the same massif along its Pacific side as indicated by historical records in Mexico (Estrada and Coates-Estrada 1984), Guatemala (Handley 1950) and El Salvador (Daugherty 1972; USNM specimens # 282795, # 282850). The
Figure 3.1.: The distribution of *Alouatta palliata* (lines) and *A. pigra* (points) in Central America. Elevation ranges are: grey (525-1700 m), dark grey (1700-2400 m), black (>2400 m). Black dots (*A. palliata*) and squares (*A. pigra*) are collection localities of museum specimens, study sites and selected survey sites from previous chapter, Serio-Silva et al. (2005), Horwich and Johnson (1986), Watts et al. (1986). Range limits were created considering these localities, historic accounts and permissive primate habitat.
range of *A. palliata* in El Salvador continues south to Nicaragua and most probably north into Honduras along a narrow strip at the Guatemala/Honduras border (Fig. 3.1). A second region without howling monkey records are the lowlands of eastern Nicaragua, which is probably a collection artifact as suitable howler habitat is present throughout much of the region, with exception of some areas of pine savanna.

My distribution map shows only two potential contact zones between the species: (1) a very broad area of sympatry, north of the highland massif in Mexico and (2) a narrow contact zone in eastern Guatemala where the highlands almost reach the Caribbean Sea (Fig. 3.1). No evidence was found for adjacent ranges in Chiapas, Mexico or central Guatemala. In Mexico, range overlap extends over the lowlands of the states of Tabasco and Campeche. Sympatric localities are around Macuspana, Tabasco (Smith 1970 based on KU specimens; Horwich and Johnson 1986) and in northern end of Laguna de Térmínos in Campeche (Serio-Silva et al. 2005). I found an area of proximity around Zapata, Tabasco (formerly called Monte Cristo) while mapping collection localities of USNM #100518 (*A. palliata*) and AMNH #14521 (*A. pigra*). No current geographic or ecological barrier between the species was evident as both occurred in the same ecosystems and on both sides of the Usumacinta river. Limited hybridization has been reported in this region (Cortés-Ortiz et al. 2003).

In the second contact zone in eastern Guatemala, the two species are narrowly parapatric, separated by a deep river basin, as well as by habitat preferences (previous chapter). *Alouatta palliata* is found south of the Rio Dulce-Lake Izabal basin and *A. pigra* to the north and west. Interestingly, southwest of the basin *A. pigra* does occur in the highlands of the Sierra de las Minas but is not found in the lowlands occupied by *A. palliata* which is not found in the humid and cold montane forests of the Sierra. However, the intervening area may have had some range overlap, based on historical records (Alston 1879; USNM #238704), although the area is now
intensive agriculture devoid of both species. No area of sympatry was recorded after recent extensive on site investigations (previous chapter).

**DISCUSSION**

Overall my results confirm much of the previously published data on distributions of *Alouatta palliata* and *A. pigra* in Central America, but I have flushed out two important new features, one with regard to the broader ecological tolerances of *A. pigra* than previously reported and the other with regard to the barriers between both species.

My results on the high elevation occurrences of *Alouatta pigra* in the southern parts of their geographic range is contrary to works of Horwich and Johnson (1986) and Reid (1997) who stated that the distribution of *A. pigra* was limited to areas below 500m with mean annual temperature above 25 °C. Furthermore, I found that *A. palliata* does not occur above 2000m, which is in contrast to Reid’s (1997) report that the species occurs up to 2500 m. My findings that both species have broad vegetational tolerances is in contrast to earlier publications that presumed *A. pigra* was limited to aseasonal forests and *A. palliata* alone presented tolerance to dry seasonal forests (Smith 1970). Actually, the presence of *A. pigra* in swamps, mangroves and dry deciduous forests has been reported by other authors (Watts et al. 1986; Serio-Silva et al. 2005).

I consider that the differences in elevation and cold tolerances are an important ecological barrier, presently separating the species. This was especially evident in their contact zone in eastern Guatemala, where *Alouatta palliata* does not enter the mountains of Sierra de las Minas, and where *A. pigra* was found up to 2705m (previous chapter).

Anatomical differences between the two species support the evolution of cold tolerance in *Alouatta pigra*. Its body size is 30% larger than *A. palliata* (mean weights of 8893 g and 6250 g respectively (Ford and Davis 1992)). An increase in mammalian body size is normally
adaptive when it results in lower external surface area which reduces relative heat loss, thereby improving metabolic efficiency in cold environments (Clutton-Brock and Harvey 1983; Schmidt-Nielsen 1984). Large plathyrrhines are protected by their higher body mass/area ratio against cold temperatures (Ford and Corrucine 1985). Also, *A. pigra* shows longer, thicker and denser fur than *A. palliata* (Lawrence 1933; Hill 1962), thereby providing better surface insulation for heat retention and protection in cold temperatures (Schmidt-Nielsen 1984). It has been suggested that dense fur may function in conserving heat in *Lagothrix* which ranges into high altitudes and may suffer periodic cold stress (Ford and Davis 1992).

Lastly I suspect that the highland massif of northern Central America with its associated coniferous and subalpine vegetation is an important barrier between the species. Together with the Rio Dulce-Lake Izabal drainage barrier, which is a geologically old river gorge, it separates the two *Alouatta* species. My distribution map differs from that of other authors (Smith 1970; Hall 1981; Ford 2005) in that the ranges of *A. palliata* and *A. pigra* are not adjacent throughout, but mainly separated by the highland massif in Chiapas and Guatemala where neither species occurs. Furthermore, my map suggests that in the recent past *A. palliata* populations from Mexico may have bordered the highlands, connecting to populations from Honduras and El Salvador through the lowland tropical forests of the Pacific Coast of Mexico and Guatemala before they were cleared (Daugherty 1972; Rzedowski 1981; Wallace 1997) but not through the mountains of Chiapas and Guatemala as suggested in other distribution maps (e.g. Hall 1981).

**Historical Biogeography**

Given the current ecological barriers (differential elevation and cold tolerances) and geographical barriers (mountains in Chiapas and Guatemala and the Rio Dulce-Lake Izabal drainage), I can ask whether these may have been key factors in *Alouatta* speciation. Smith’s (1970) hypothesis of a single invasion of the ancestral lineage dispersing into Central America
and diverging into *palliata* and *pigra* failed to identify a suitable barrier to gene flow that could have been responsible for initial isolation. However, my data suggest that the ancestral *Alouatta* could have been split by the north Central American highland massif, especially during colder periods, leaving an isolated subpopulation in the Yucatan peninsula and another subpopulation in the lowlands to the south. The onset of cooling at 2.7 mya (Hooghiemstra and Ran 1994) roughly coincides with the estimated time of split between *A. palliata* and *A. pigra* of 3 mya (Cortés-Ortiz et al. 2003). Sea level rises at around 2 mya (Cortés-Ortiz et al. 2003) could have provided additional separation of the subpopulations, as coastal regions became inaccessible (Ford 2005).

Under this scenario, I can hypothesize that the isolated subpopulation in the Yucatan evolved cold tolerance allowing it to survive the climatic conditions during glacial periods, which were significant as suggested by a tree line depression of up to 1000 m (Leyden 1987), glaciations in the bordering Sierra de Cuchumatanes (Weyl 1980) and expansion of temperate oak forests into the Petén lowlands (Leyden et al. 1994; Leyden 2002). Persistence was perhaps aided by the proposed late Tertiary and Quaternary glacial refuges of current warm-moist-forest species in northern foothills in south Mexico, Belize and Guatemala (Toledo 1982; Wendt 1989). Meanwhile, the remainder of the species retracted south to warmer lowlands, perhaps even to regions of Costa Rica and Panama where lowland rainforest persisted during glaciations (Bush and Colínvaux 1990; Colínvaux 1997).

During warmer interglacial periods, the diverging *Alouatta palliata* lineage probably expanded northward where it may have had contact with the divergent *A. pigra* lineage in the lowland edges of the latter’s range. In the current inter-glacial, both species are in secondary contact in two different situations: in the lowlands of the western Yucatán both species are sympatric with limited hybridization (Cortés-Ortiz et al. 2003) and in eastern Guatemala
parapatry is maintained by a riverine barrier and by ecological adaptation. Perhaps behavioral premating isolation mechanisms such as call recognition or troop impermeability further impede genetic introgression.

The alternative explanation for the presence of two species of *Alouatta* in Central America requires the invasion by two different species. This “double invasion” hypothesis states that an initial dispersal by the ancestral lineage from South America became *A. pigra*, followed by a second invasion by *A. palliata* derived from the same lineage. Smith (1970) originally suggested the first invasion was along emergent islands or small corridors before closure of the isthmus and the second invasion occurred at the time of the closure. Armed with molecular clock data, Cortés-Ortiz et al. (2003) and Ford (2005) argued for a first invasion after isthmus closure around 3 mya, followed by gene flow interruption by an increase in sea level, resulting in the arrival of *A. palliata* in a second wave after 2 mya.

An important requirement for any double invasion hypotheses is the posterior expansion of *Alouatta palliata*, concurrent with a range reduction of *A. pigra*. Such competitive superiority has been postulated based on the greater ecological tolerances of *A. palliata* in forest types (Smith 1970) or in elevation (Ford 2005, citing Reid 1997), but my data negate both those differences. Also arguing against differential dispersal or competitive abilities are the species similarities in diet and resource exploitation (Silver et al. 1997), similar home range sizes (Crockett and Eisenberg 1987) and ability to thrive in small forest fragments (Crockett 1998). In contrast, a speciation event around the present ranges of both species in the northern Central American highlands does not need to explain major changes in ranges for either species or postulate competitive superiority of *A. palliata*. 
CHAPTER 4

CONCLUSIONS

Overall, my thesis contributes to the knowledge of the geographic distribution and habitats of the endangered black howling monkey *Alouatta pigra*, and proposes ecologic and geographic barriers that may be important in maintaining the two species of Central American howling monkeys and that were possibly involved in their initial speciation.

In my study of the geographic distribution of *A. pigra* and *A. palliata* in their potential contact zone in eastern Guatemala (Chapter 2), I found no evidence for current range overlap or sympatry. Instead, their distributions are clearly separated by a riverine barrier and by unsuitable dry shrubland. Further, ecological preferences seem to reinforce parapatry, as only *A. pigra* occurs in the high elevations and cold habitats further inland. I also found that the distribution of both howling monkey species in the study area was unaffected by the presence of the spider monkey (*Ateles geoffroyi*), by the protection status of the survey site or by hunting activities.

In the study region of eastern Guatemala *A. pigra* was widespread and occupied several different habitat types across altitudinal ranges from sea level up to 2705 m. *A. palliata* did not occur at the higher elevations. The occurrence of *A. pigra* in several diverse protected ecosystems and low hunting pressure gives the region a high potential for the conservation of this endangered species. My data also 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.

The distribution of *A. pigra* has been considered to be limited to areas below 500m (Horwich and Johnson 1986; Watts et al. 1986; Reid 1997), but my results (Chapters 2 and 3) show that in the southern parts of its geographic range the species occurs at high elevations from 1800m to 3350m. Locales above 2500m reach temperatures below 0°C some days of the year,
which implies cold tolerance by *A. pigra*. My results on the distribution of *A. palliata* (chapter 2 and 3) however suggest that this species is present only at elevations below 2000m and in montane localities that do not reach freezing. Anatomical differences in body size and fur between both species further support differences in cold tolerance.

These ecological differences seem to separate the species at present, which becomes evident in their contact zones: in eastern Guatemala *A. palliata* does not enter the cold montane habitats of *A. pigra* and both species occur in parapatry (chapter 2). In contrast, in the lowlands of western Yucatan, the ranges overlap over a broad area (chapter 3) and the species occur in sympatry with occasional hybridization (Cortés-Ortiz et al., 2003).

Besides this ecological barrier, my results (chapter 3) reveal the highland massif of northern Central America and their associated coniferous and subalpine vegetation as a geographic barrier between both species. In contrast to previous maps, I propose that both species ranges are not adjacent throughout Chiapas, Mexico and central Guatemala, but separated by these mountains.

Based on the identification of current barriers between the species in Central America, I present a modified biogeographic hypothesis (Chapter 3) that proposes an initial split by the northern highland massif during cold periods that resulted in isolation of the *A. pigra* lineage in the Yucatan peninsula and in the further divergence in cold tolerance. This scenario supports Smith’s (1970) proposal of a single invasion of the ancestral lineage into Central America and offers a missing mechanism for interruption of gene flow accountable for the *pigra/palliata* speciation.
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MUSEUM DATABASES USED

AMNH-American Museum of Natural History New York

BMNH-British Museum of Natural History (Natural History Museum London)
CAS-Mammal Collection of California Academy of Sciences
FLMNH-Florida Museum of Natural History
FMNH-Chicago Field Museum of Natural History
KU-University of Kansas Biodiversity Research Center
LACM-Los Angeles County Museum of Natural History
LSUMZ-Louisiana State University Museum of Natural Science
MCZ-Museum of Comparative Zoology Harvard University
MSU-Michigan State University Museum
MVZ-Museum of Vertebrate Zoology University of California Berkeley
NMS-Royal Scottish Museum (National Museums of Scotland)
NMW-Naturhistorisches Museum Wien
ROM-Royal Ontario Museum
UMMZ-University of Michigan Museum of Zoology
UMNH-Utah Museum of Natural History
USNM-Smithsonian Institution National Museum of Natural History
YPM-Peabody Museum Yale University
# APPENDIX 1

DESCRIPTION OF SURVEY SITES IN EASTERN GUATEMALA

<table>
<thead>
<tr>
<th>Site Nr</th>
<th>Locality</th>
<th>Geographic reference (latitude, longitude)</th>
<th>Protection status (^a)</th>
<th>Detection method</th>
<th>Alouatta sp.</th>
<th>Atel... geo... (^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Chelema I village</td>
<td>15°23'N 90°03'W</td>
<td>Private reserve</td>
<td>sighting, interview</td>
<td><em>A. pigra</em></td>
<td>No</td>
</tr>
<tr>
<td>2</td>
<td>Lowland south of Chichipate village(^1)</td>
<td>15°29'N 89°27'W</td>
<td>None</td>
<td>sighting, interview</td>
<td><em>A. pigra</em></td>
<td>No</td>
</tr>
<tr>
<td>3</td>
<td>Highlands north of Chichipate village</td>
<td>15° 27'N 89°27'W</td>
<td>None</td>
<td>interview</td>
<td>none</td>
<td>Yes</td>
</tr>
<tr>
<td>4</td>
<td>Selich village</td>
<td>15°32'N 89°29'W</td>
<td>None</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>Yes</td>
</tr>
<tr>
<td>5</td>
<td>Nimlabenque village</td>
<td>15°35'N 89°17'W</td>
<td>None</td>
<td>interview</td>
<td>none</td>
<td>No</td>
</tr>
<tr>
<td>6</td>
<td>Secacar village</td>
<td>15°34'N 89°17'W</td>
<td>None</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>No</td>
</tr>
<tr>
<td>7</td>
<td>Boquerón park</td>
<td>15°33'N 89°17'W</td>
<td>None</td>
<td>sighting</td>
<td><em>A. pigra</em></td>
<td>n/a</td>
</tr>
<tr>
<td>8</td>
<td>Sakitzul finca</td>
<td>15°50'N 89°21'W</td>
<td>Proposed private reserve</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
</tr>
<tr>
<td>9</td>
<td>Guitarra village</td>
<td>15°50'N 89°16'W</td>
<td>None</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
</tr>
<tr>
<td>10</td>
<td>Sahilá village(^2)</td>
<td>15°45'N 89°07'W</td>
<td>None</td>
<td>interview</td>
<td>none</td>
<td>no</td>
</tr>
<tr>
<td>11</td>
<td>Highlands west of Sahilá village</td>
<td>15°43'N 89°08'W</td>
<td>None</td>
<td>interview</td>
<td>none</td>
<td>no</td>
</tr>
<tr>
<td>12</td>
<td>La Laguna finca</td>
<td>15°36'N 89°05'W</td>
<td>None</td>
<td>interview</td>
<td>none</td>
<td>no</td>
</tr>
<tr>
<td>13</td>
<td>Tijax finca</td>
<td>15°40'N 89°00'W</td>
<td>None</td>
<td>interview</td>
<td>none</td>
<td>no</td>
</tr>
<tr>
<td>14</td>
<td>Calajá village</td>
<td>15°51'N 89°04'W</td>
<td>None</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
</tr>
<tr>
<td>15</td>
<td>Río Sarstún</td>
<td>15°54'N 89°05'W</td>
<td>Río Sarstún Multiple Use Area</td>
<td>sighting</td>
<td><em>A. pigra</em></td>
<td>n/a</td>
</tr>
<tr>
<td>16</td>
<td>Río Sarstún shores Guatemala side</td>
<td>15°55'N 89°03'W</td>
<td>Río Sarstún Multiple Use Area</td>
<td>sighting</td>
<td><em>A. pigra</em></td>
<td>n/a</td>
</tr>
<tr>
<td>17</td>
<td>Río Sarstún shores Belize side</td>
<td>15°54'N 88°59'W</td>
<td>Sarsto... Temash Reserve</td>
<td>sighting</td>
<td><em>A. pigra</em></td>
<td>n/a</td>
</tr>
<tr>
<td>18</td>
<td>Sarstún village</td>
<td>15°53'N 88°56'W</td>
<td>Río Sarstún Multiple Use Area</td>
<td>sighting, interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
</tr>
<tr>
<td>19</td>
<td>Calix -Black creek finca</td>
<td>15°48'N 88°53'W</td>
<td>None</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
</tr>
<tr>
<td>20</td>
<td>Chocón-Machacas biological station</td>
<td>15°47'N 88°50'W</td>
<td>Chocón Machacas Manatee Biot...</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
</tr>
<tr>
<td>21</td>
<td>Mario Dary scientific station</td>
<td>15°12'N 90°13'W</td>
<td>Mario Dary Quetzal Biot...</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
</tr>
<tr>
<td>22</td>
<td>Las Cabañas scientific station</td>
<td>15°05'N 89°56'W</td>
<td>Sierra de las Minas BR – core area</td>
<td>sighting, interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
</tr>
<tr>
<td>23</td>
<td>Albores village</td>
<td>15°03'N 89°57'W</td>
<td>Sierra de las Minas BR – buffer zone</td>
<td>interview</td>
<td>none</td>
<td>no</td>
</tr>
<tr>
<td>24</td>
<td>trail to Volcán Las Palomas</td>
<td>15°09'N 89°37'W</td>
<td>Sierra de las Minas BR – core area</td>
<td>sighting</td>
<td><em>A. pigra</em></td>
<td>n/a</td>
</tr>
<tr>
<td>25</td>
<td>Alejandría finca</td>
<td>15°08'N 89°36'W</td>
<td>Sierra de las Minas BR-multiple use zone</td>
<td>sighting, interview</td>
<td><em>A. pigra</em></td>
<td>no</td>
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<td>26</td>
<td>Los Angeles village</td>
<td>15°14'N 89°47'W</td>
<td>Sierra de las Minas BR – buffer zone</td>
<td>interview</td>
<td><em>A. pigra</em></td>
<td>yes</td>
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Appendix 1 continued
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<tr>
<th>No.</th>
<th>Site Name</th>
<th>Latitude/Longitude</th>
<th>Protected Area</th>
<th>Activity</th>
<th>Species</th>
<th>Presence</th>
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<td>27</td>
<td>San Vicente II village</td>
<td>15° 14′N 89° 48′W</td>
<td>Sierra de las Minas BR – buffer zone</td>
<td>interview</td>
<td>A. pigra</td>
<td>yes</td>
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<tr>
<td>28</td>
<td>Manguitos II lowlands¹</td>
<td>15° 21′N 89° 83′W</td>
<td>None</td>
<td>interview</td>
<td>A. pigra</td>
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<td>29</td>
<td>Highlands south of Manguitos village</td>
<td>15° 17′N 89° 30′W</td>
<td>Sierra de las Minas BR – buffer zone</td>
<td>interview</td>
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<td>30</td>
<td>Semuy II lowlands¹</td>
<td>15° 20′N 89° 25′W</td>
<td>Bocas Polochic Wildlife Reserve</td>
<td>interview</td>
<td>A. pigra</td>
<td>no</td>
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<td>31</td>
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<td>15° 18′N 89° 25′W</td>
<td>Sierra de las Minas BR – buffer zone</td>
<td>interview</td>
<td>A. pigra</td>
<td>yes</td>
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<td>32</td>
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<td>sighting, interview</td>
<td>A. pigra</td>
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<td>33</td>
<td>Río Osuro</td>
<td>15° 21′N 89° 60′W</td>
<td>Bocas Polochic Wildlife Reserve</td>
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<td>A. pigra</td>
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<td>34</td>
<td>Lake Izabal shore and Polochic</td>
<td>15° 22′N 89° 57′W</td>
<td>Bocas Polochic Wildlife Reserve</td>
<td>sighting</td>
<td>A. pigra</td>
<td>n/a</td>
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<td>35</td>
<td>Naranjal Yaxte village</td>
<td>15° 20′N 89° 20′W</td>
<td>None</td>
<td>interview</td>
<td>A. pigra</td>
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<td>36</td>
<td>Izabal village</td>
<td>15° 24′N 89° 08′W</td>
<td>None</td>
<td>interview</td>
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<td>no</td>
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<td>37</td>
<td>Morán village</td>
<td>15° 09′N 89° 29′W</td>
<td>Sierra de las Minas BR – buffer zone</td>
<td>interview</td>
<td>A. pigra</td>
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<td>38</td>
<td>Highlands north of Morán village</td>
<td>15° 12′N 89° 29′W</td>
<td>Sierra de las Minas BR – core area</td>
<td>forest survey</td>
<td>none</td>
<td>n/a</td>
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<td>39</td>
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<td>15° 17′N 89° 11′W</td>
<td>Sierra de las Minas BR – buffer zone</td>
<td>interview</td>
<td>none</td>
<td>yes</td>
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<td>40</td>
<td>Montaña Chiclera regional park</td>
<td>15° 30′N 88° 51′W</td>
<td>Municipal Reserve</td>
<td>interview</td>
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<td>no</td>
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<td>41</td>
<td>Juan Vicente Creek</td>
<td>15° 40′N 88° 50′W</td>
<td>Rio Dulce National Park - none</td>
<td>sighting, interview</td>
<td>A. palliata</td>
<td>no</td>
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<td>42</td>
<td>Casa Guatemala</td>
<td>15° 41′N 88° 57′W</td>
<td>Rio Dulce National Park – none</td>
<td>sighting, interview</td>
<td>A. palliata</td>
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<td>43</td>
<td>Río Frío lowland¹</td>
<td>15° 39′N 88° 55′W</td>
<td>None</td>
<td>interview</td>
<td>A. palliata</td>
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<td>44</td>
<td>Highland east of Río Frío village</td>
<td>15° 40′N 88° 51′W</td>
<td>Cerro San Gil Reserve</td>
<td>interview</td>
<td>none</td>
<td>yes</td>
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<td>45</td>
<td>Cayo Piedra finca</td>
<td>15° 41′N 88° 54′W</td>
<td>Rio Dulce National Park - none</td>
<td>interview</td>
<td>none</td>
<td>no</td>
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<td>46</td>
<td>Cayo Quemado village</td>
<td>15° 46′N 88° 50′W</td>
<td>Rio Dulce National Park – none</td>
<td>interview</td>
<td>none</td>
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<td>47</td>
<td>Tameja village¹</td>
<td>15° 44′N 88° 48′W</td>
<td>None</td>
<td>interview</td>
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<td>48</td>
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<td>Cerro San Gil Reserve</td>
<td>interview</td>
<td>none</td>
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<td>49</td>
<td>San Gil biological station</td>
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<td>interview</td>
<td>none</td>
<td>yes</td>
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<td>50</td>
<td>Laguna Santa Isabel</td>
<td>15° 50′N 88° 28′W</td>
<td>Punta Manabique Wildlife Reserve</td>
<td>sighting</td>
<td>A. palliata</td>
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<td>51</td>
<td>Estero Lagarto village</td>
<td>15° 55′N 88° 36′W</td>
<td>Punta Manabique Wildlife Reserve</td>
<td>sighting, interview</td>
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<td>52</td>
<td>Cabo Tres Puntas village</td>
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<td>Punta Manabique Wildlife Reserve</td>
<td>sighting, interview</td>
<td>A. palliata</td>
<td>yes</td>
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<td>53</td>
<td>San Vicente Paul village¹</td>
<td>15° 24′N 88° 47′W</td>
<td>None</td>
<td>interview</td>
<td>A. palliata</td>
<td>no</td>
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<td>54</td>
<td>Highlands south of San Vicente Paul</td>
<td>15° 23′N 88° 44′W</td>
<td>Proposed Sierra Caral reserve - none</td>
<td>interview</td>
<td>A. palliata</td>
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<td>55</td>
<td>Animas village¹</td>
<td>15° 27′N 88° 42′W</td>
<td>None</td>
<td>interview</td>
<td>A. palliata</td>
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<td>56</td>
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<td>15° 26′N 88° 41′W</td>
<td>Proposed Sierra Caral reserve - none</td>
<td>interview</td>
<td>A. palliata</td>
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<td>57</td>
<td>Champas finca</td>
<td>15° 32′N 88° 28′W</td>
<td>Proposed Sierra Caral reserve - none</td>
<td>sighting, interview</td>
<td>A. palliata</td>
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<td>58</td>
<td>Cacao village</td>
<td>15° 35′N 88° 25′W</td>
<td>None</td>
<td>sighting</td>
<td>A. palliata</td>
<td>n/a</td>
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</table>

¹Denotes site at foothills, interviewees at these sites gave information for both lowland and highland

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*a Name and category of protected area of SIGAP (Sistema Guatemalteco de Areas Protegidas); none: outside protected area or in protected area without vigilance

*b Presence as reported in interviews
APPENDIX 2

LIST BY COUNTRY OF REFERENCES USED FOR LOCALITY DATA

**Mexico**


Gonzalez-Kirchner, J.P. 1998. Group size and population density of the black howler monkey (*Alouatta pigra*) in Muchukux Forest, Quintana Roo, Mexico. Folia Primatol 69:260-265.


Silva-Lopez, G., F. García-Orduña and E. Rodríguez-Luna. 1988. The status of *Ateles geoffroyi* and *Alouatta palliata* in disturbed forest areas of Sierra de Santa Marta, Mexico. 9 (Dic):53-61


**Guatemala**


Appendix 2 continued
<table>
<thead>
<tr>
<th>Location</th>
<th>Reference</th>
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VITA

Amrei Baumgarten was born in Guatemala City, Guatemala, to Jan Baumgarten and Elisabeth Helene Peter. She is married to Pablo Granados-Dieseldorff and is the mother of Matthias. She studied biology in the Universidad de San Carlos de Guatemala, where she graduated with honors and received the School of Chemical Sciences and Pharmacy faculty award for best thesis. She worked for two years in the same university as a lecturer in statistics and as a researcher in a mammal monitoring project. Amrei received a scholarship from the Fulbright faculty development program Central America to pursue her Master in Science degree in the United States. She started her graduate studies in January 2004 in Louisiana State University under the guidance of Dr. Bruce Williamson. During her last year at LSU she taught biology laboratory classes for majors.