

Geographical Distribution of the Black Howler (*Alouatta pigra*) in Central America

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ABSTRACT. The geographic range of the black howler, *Alouatta pigra* in Mexico, Guatemala, and Belize was investigated by travelling through and visiting 65 locations within or close to the expected range. The existence of the species was noted through first hand observations or was documented by talking with residents and knowledgeable people in the area. Observations were made on captive animals as well. All sites and probable sites of *A. pigra* were noted to be under 1,300 ft in altitude and in areas with a mean annual temperature above 25°C and a mean annual rainfall over 1,000 mm per year. This area coincides with tropical rain forest areas, including both tropical evergreen and semi-evergreen rain forests. *A. pigra* was most plentiful in riverine areas which showed flooding for some part of the year. Two areas of possible sympatry with *A. palliata* were noted. In all cases, the troop sizes of *A. pigra* were extremely small, under ten individuals, and infants could easily be sexed, in contrast to *A. palliata* which is known to occur in troops of 15-18 and is difficult to sex at an early age. Finally, a very gross method for population estimation from searching time emerged from the study.

Key Words: Howlers; Geographic distribution; Speciation; Central America.

INTRODUCTION

SMITH (1970) in an anatomical study of *Alouatta palliata*, observed a case of sympatry in two supposed subspecies of *A. palliata* in Mexico. His study of the skulls, dentition, and pelage differences of the two forms led him to conclude that the differences were distinct enough to rate species status. The two forms in the Macuspana, Tabasco area of Mexico showed (1) different cranial and body sizes, (2) different skull shapes, (3) differences in upper molar dentition, and (4) color and texture differences in pelage. Judging from differences in the hyoid bone, he thought male vocalizations might also differ.

Behavioral studies of *Alouatta pigra* in Belize have subsequently supported the species distinction with additional differences noted as well. While it is difficult to tell the sexes in young *A. palliata* (GLANDER, 1980), *A. pigra* males as early as 2 months of age exhibit descended white testes (HORWICH, 1983). A second feature in variation is with troop sizes: *A. palliata* troop sizes generally range between 15-20 or higher, while *A. pigra* troops average between 4-6. Lastly, perhaps related to the other factors, *A. pigra* shows a tendency toward one-male groups and perhaps a tendency toward monogamy (BOLIN, 1981).

These differences solidifying the species status, the distribution and the general conservation status of *A. pigra* were virtually unknown (IUCN RED DATA BOOK, 1978). It had been noted that habitat destruction and hunting were contributing to the species' decline (IUCN RED DATA BOOK, 1978), and habitat alteration was thought to allow *A. palliata* to displace *A. pigra* within the areas of sympatry (SMITH, 1970). Thus, we set out to survey the general range of *A. pigra* and the overlap areas with *A. palliata*, as well as to gather information on habitat destruction, troop sizes, sexual dimorphism, and vocalizations in the populations observed.

METHODS

We travelled by truck throughout the range of *A. pigra* in Mexico, Belize, and Guatemala from mid-January through mid-April 1983, specifically investigating areas reported to contain howlers. Figure 1a shows the route we took, often doubling back in certain areas, covering about 6,000 miles within the range of *A. pigra*. We attempted to make first hand sightings but often additionally questioned people in the areas travelled, on the occurrence of the howlers, hair color, types of howlers observed, and the roaring.

We differentiated personal observations on wild and captive howlers, reliable secondary sources, and secondary sources whose reliability was uncertain. Reliability was based on (1) our observation that the habitat was intact and could support howlers, and (2) how well and what we knew about our informants (knowledge of the local fauna, type of work they did, etc.) especially if we had only one informant for the site, and whether we had more than one informant for a site.

We also observed individuals of *A. palliata mexicana* in "Los Tuxtlas," Vera Cruz and two free-ranging troops in zoos at Parque La Venta, Villahermosa, Tabasco and Tuxtla Gutierrez, Chiapas to have a basis for comparison.

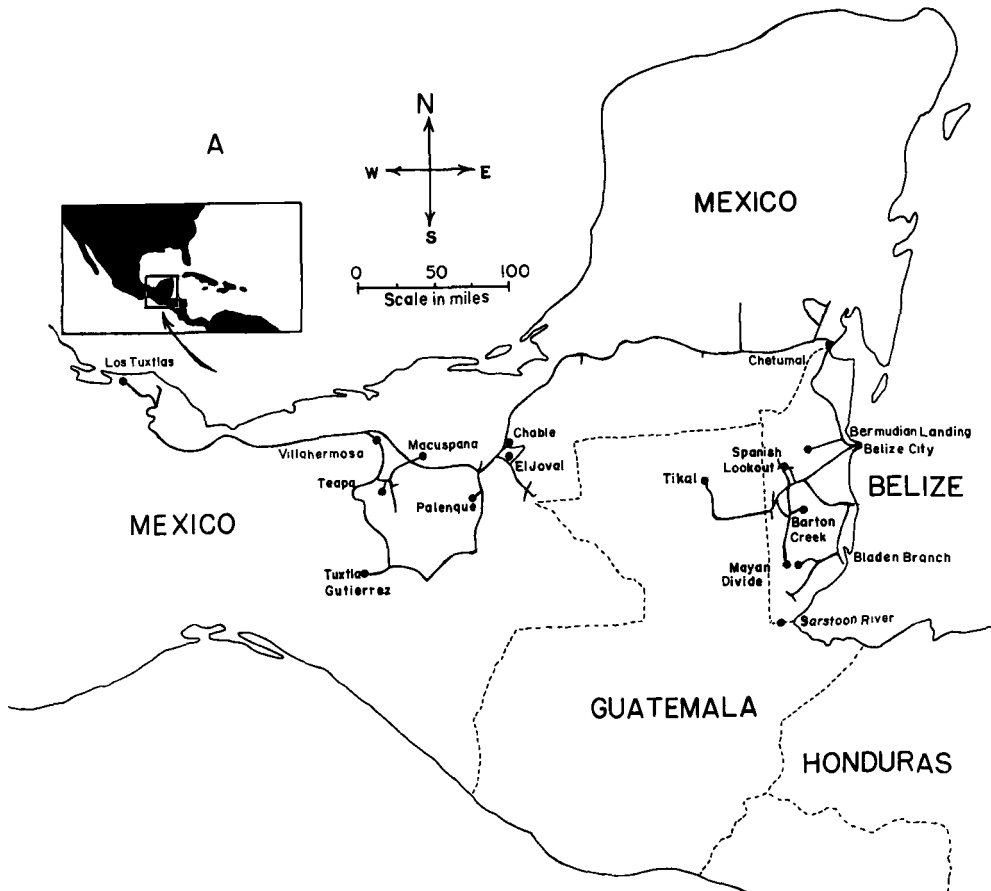


Fig. 1a. Map indicating route travelled in search of *A. pigra*.

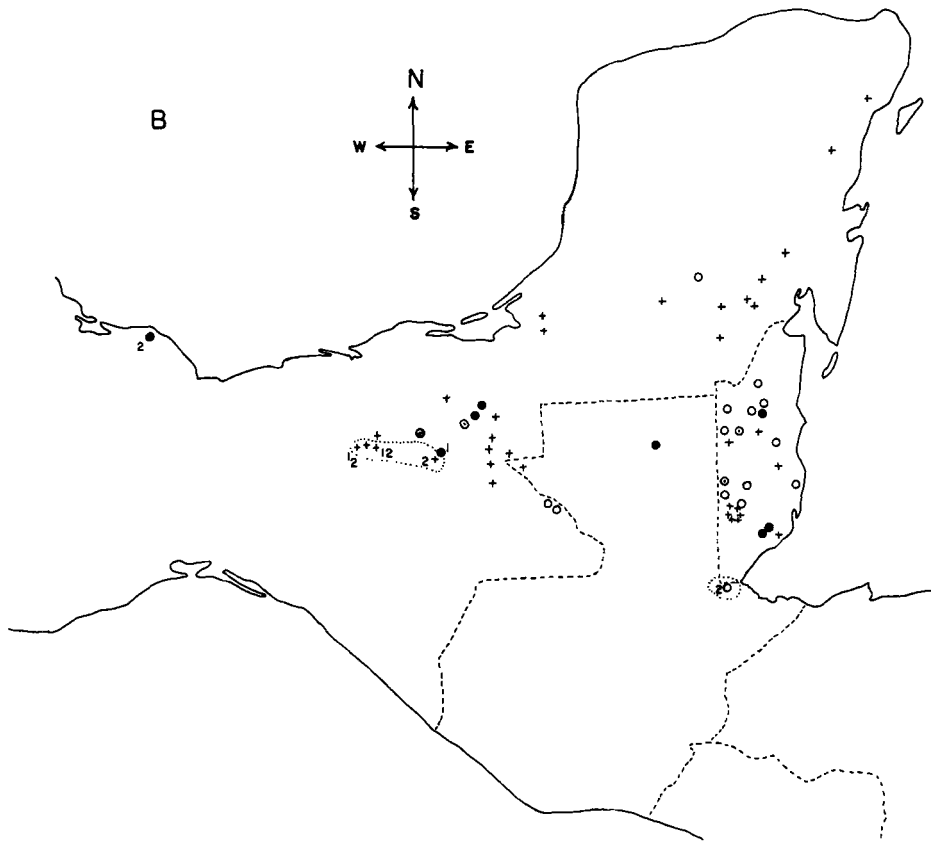


Fig. 1b. Map indicating actual and possible locations of *A. pigra* and *A. palliata*. 1: *A. pigra*; 2: *A. palliata*. ●: Actual sightings; ◎: captive individuals seen; ○: trusted secondary sources; +: other secondary sources; ⊙: probable overlap zones of *A. pigra* and *A. palliata*.

While searching for howlers, we noted approximate walking time and the number of troops located, to give a relative idea of density. On encountering a troop, we usually spent about an hour counting the number, sex, and age of the troop members and recorded sounds when possible. From this information we devised a crude population estimating technique to compare the number of troops in unknown areas with areas of known populations.

We also made habitat descriptions noting where cutting or lack of forests was evident. We then mapped our route, definite and probable howler sites, captive animals noted, and compared these locations with vegetation, altitude, temperature, rainfall, and other geographic factors. We additionally compared troop sizes from our census and other studies, using the Mann-Whitney U test.

RESULTS

Figure 1b indicates definite sites where we observed howlers, possible sites noted by informants, and information from captive animals seen. All information concerns *A. pigra* except for observations on Los Tuxtlas and two potential overlap areas.



Fig 1c. Map indicating areas over 1,000 ft in altitude (drawn from Government of Belize topographical maps).

Our investigations of the Macuspana area of sympatry indicated a lack of habitat or howlers in the area noted by SMITH (1970) with indication of an overlap zone of the two species about 25 miles southwest of Macuspana near Teapa, Tabasco. Although we never saw either species, our careful non-leading questioning of informants indicates a distinct possibility of the two species occurring together in the hills outside of Teapa.

A second area of possible sympatry may exist, based on one Belizean informant who had specifically seen howlers with buff colored sides (*A. palliata*?) on the Guatemala side of the Sarstoon river on the southern Belize-Guatemala border. He originally thought they were "monkeys" (the local word for non-howler monkeys) but realized that they were "baboons" (local name for howlers) when he heard them call. The prevalence of *A. pigra* close to the border and its occurrence in SMITH's (1970) map leads us to suspect that the area may be one of sympatry as well.

Finally, with the factors used to compile Figures 1b-d, and our notes on population areas, habitats, and habitat destruction, we constructed an estimated range of *A. pigra* (Fig. 1e). Generally we feel our map is too optimistic, and that the range is more probably a series of isolated populations. The two largest areas in Figure 1e are probably not continuous but are represented as such since we have no specific information within them.

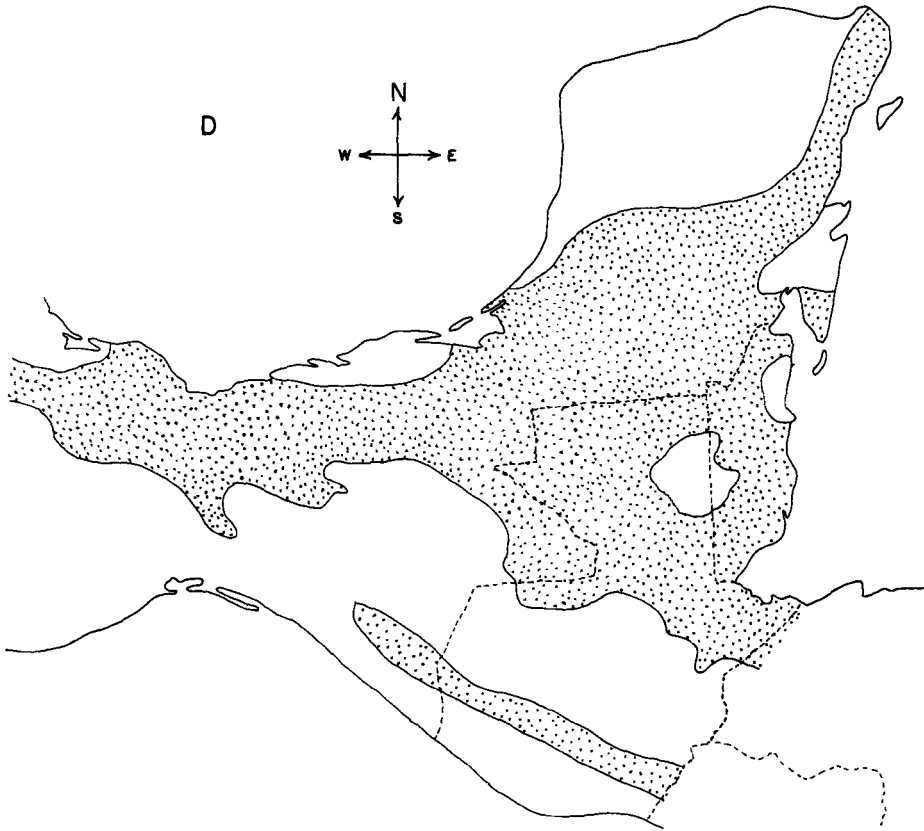


Fig. 1d. Map indicating the areas of tropical rain forest in Mexico, Guatemala, and Belize (drawn from RZEDOWSKI, 1978; TOLEDO, 1982; PENNINGTON & SARUKHAN, 1968).

Although troop size is not a very reliable species identification characteristic, we feel the large troop size difference between the two species is worthy of note. We feel it plays a significant role and is involved with the immature sexual dimorphism or the lack of it and the tendency toward one-male groups in *A. pigra*. In comparing *A. palliata* and *A. pigra* with regard to troop size, using available censuses, we graphed the number of troops against the number of individuals per troop (Fig. 2) and calculated some basic population statistics. As can be seen, there is little overlap between the two species with *A. palliata mexicana* falling between the two. When comparing the two populations using the Mann-Whitney U test, the two species are highly significant at the .00003 level as was *A. p. mexicana* from the rest of the species, indicating they are acting like different populations in regard to troop size. When comparing troop statistics certain trends are evident. *A. pigra* has very small groups with a marked one-male tendency with an adult male to female ratio close to one. Indeed, BOLIN (1981) even suggests that *A. pigra* shows a tendency toward monogamy which these figures support, although individual troops do not always show it. *A. p. mexicana*, although it has a relatively small troop size, maintains a definite multi-male trend with a similar close to equal adult sex ratio. The other difference between it and other *A. palliata* is with the approximate 1:2 adult male to female ratio in *A. p. palliata*. For comparison, *A. fusca* and *A. seniculus* both show smaller troop sizes, a lesser tendency toward uni-male groups and a close

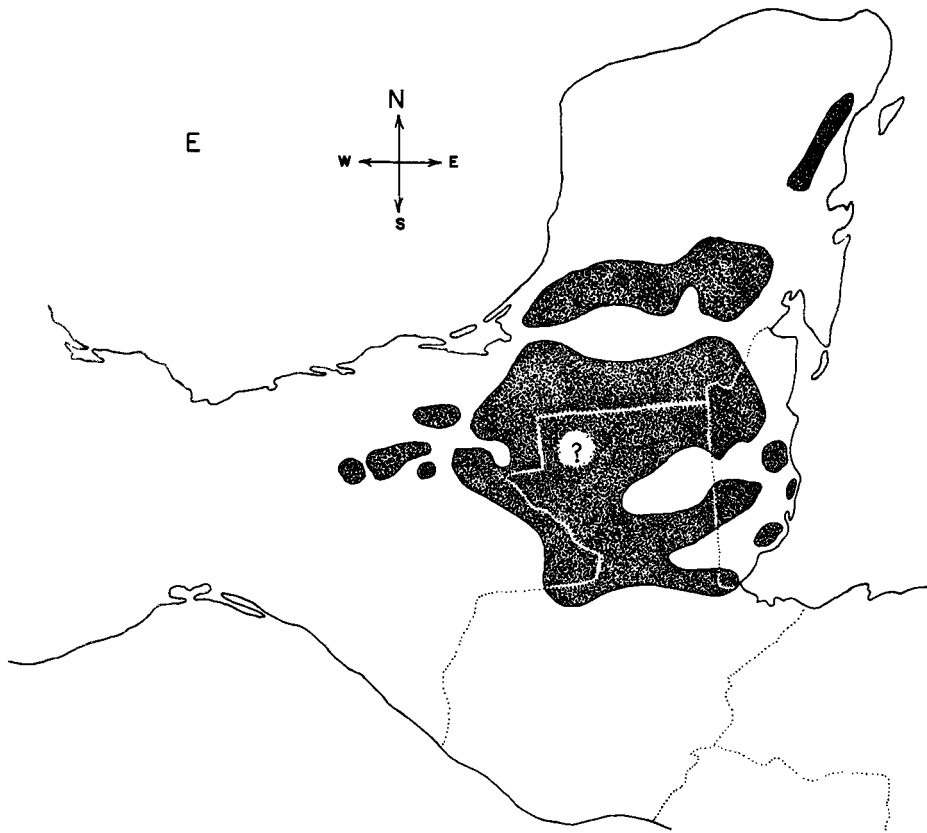


Fig. 1c. Map indicating the probable present range of *A. pigra*. The largest area was unexplored and thus questionable but all the large areas are probably series of small "island" populations.

to even adult sex ratio (CORDEIRA DA SILVA, 1981; BRAZA et al., 1981; NEVILLE, 1972; RUDRAN, 1979). CLARKE and GLANDER (1983—presented paper) specifically noted the very high male mortality which occurs in *A. p. palliata* perhaps accounting for the much lower male to female sex ratios.

Table 2 shows an indication of density of howlers per area explored. Using the number of troops seen per hour compared with known or accurate area estimates, we obtained a gross factor between 11–15. This, when multiplied by the number of troops per searching hour gives a relative estimate of the population. Using 12 as our estimation factor (Table 2), there are two areas of over estimation: the Tuxtla Gutierrez Zoo in which the area of searching (zoo confines) was limited and very easy to get around in, and in the El Joval-Chable samples in which we had guides and easily found troops in a very short time and never searched other areas. Thus the El Joval-Chable are over estimates and do not have as many troops as Bermudian Landing. At Bermudian Landing one can almost constantly hear sounds during much of the day. We did not hear this much activity in any other area visited.

DISCUSSION

The survey confirms SMITH's (1970) speciation of *A. palliata* and *A. pigra* with a similar

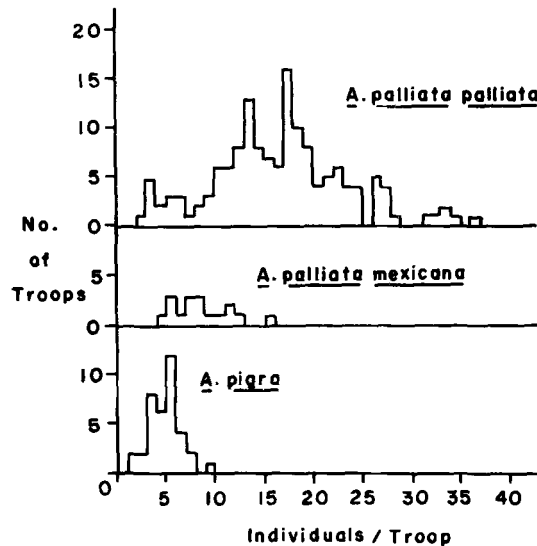


Fig. 2. The number of troops plotted against the number of individuals in each troop for *A. pigra*, *A. palliata palliata*, and *A. palliata mexicana* using the following censuses: *A. pigra*: BOLIN, 1981; COELHO et al., 1976; HORWICH & GEBHARD, 1983; present study (Table 1); *A. p. palliata*: BALDWIN & BALDWIN, 1972; CARPENTER, 1934, 1962; CHIVERS, 1969; GLANDER, 1980; MITTERMEIER, 1973; *A. p. mexicana*: ESTRADA, 1982.

Table 1. Troop censuses of *Alouatta pigra* in 1983.

Area	Troop	Adult		Subadult		Juvenile		Infant		Total
		Male	Female	Male	Female	Male	Female	Male	Female	
Belize:										
Bermudian Landing	Fig tree	1	2	—	—	—	1	—	—	4
	Cashew	1	2	1	—	—	2	—	1	7
	Upriver	2	2	—	—	—	2	—	—	6
	New upriver	1	2	—	—	2	1	—	—	6
	Pasture	—	3	1	—	3	—	1	—	8
	On river	5		—	—	1	—	1	—	7
Mexico:										
El Joval	First	1	2	—	1	1	—	—	—	5
	Second	1	2	—	—	1	—	—	—	4
Chable		1	2	—	—	1	1	—	—	5
Guatemala:										
Tikal	Temple 4	1	2	—	—	—	—	2	—	5
	Temple 13	1	2	—	—	—	1	1	—	5

range for *A. pigra*. The zone of sympatry noted by SMITH was similar except that much of the area is no longer viable howler habitat. However, nearby areas are probable overlap areas.

In general, the habitat and range of *A. pigra* is shrinking radically, especially in Mexico where there are few extended ranges of forest except in Chiapas along the Usumacinta River on the Guatemala border. This is the largest tract of evergreen tropical rain forest in Mexico (ESTRADA, 1982).

Figure 1d shows the distribution of the tropical rain forest constructed from TOLEDO (1982) and RZEDOWSKI (1981). Almost all howler locations fit into that vegetation distribution. The main problem of fit comes from the area on the Guatemala-Belize border which accord-

Table 2. Number of troops found per time searched in various areas of Mexico and Belize.

Area (Species)	Hours searched	No. of troops found	Troops per hour	Search factor ¹⁾	Estimated population using 12 as factor	Known or accurate population estimate
Mexico:						
Los Tuxtlas (<i>A. palliata</i>)	8.5	2	.35	11.4	4.2	4
Palenque (<i>A. pigra</i>)	10	1	.10	10?	1.2	1?
Teapa (<i>A. palliata</i> ; <i>A. pigra</i>)	6	0	0	—	0	(+)?
Tuxtla G. zoo (<i>A. palliata</i>)	5.5	1	.18	5.6	2.2	1
El Joval (<i>A. pigra</i>)	1	2	2	—	24?	(+)
Chable (<i>A. pigra</i>)	.5	1	2	—	24?	(+)
Belize:						
Barton Creek (<i>A. pigra</i>)	8	0	0	—	0?	1?
Bermudian Landing (<i>A. pigra</i>)	8.25	9	1.1	15	13.2	15-18
Spanish Lookout (<i>A. pigra</i>)	3	0	0	—	0	?
Mayan Divide (?)	18	0	0	—	0	(-)?
Bladen Branch (?)	18	0	0	—	0	(-)?

1) Accurate estimate/troops per hour.

ing to TOLEDO (1982) is oak-pine forest. Based on Belizean government vegetation maps, it appears as though TOLEDO's placement of that area is slightly incorrect.

Two other climatic factors describe the area designated as tropical rain forest. From the southern border of the rain forest (Fig. 1d), the mean annual temperature lines indicating temperatures above 25°C closely follows the limits of Figure 1d (ATLAS OF MEXICO, 1975; ATLAS CLIMATOLOGICO DE GUATEMALA, 1964). This area is also described, though not quite as uniformly by the mean annual rainfall. All points within the howler range are defined by 1,000 mm of rain per year or more (ATLAS OF MEXICO, 1975; ATLAS CLIMATOLOGICO DE GUATEMALA, 1964; FURLEY & CROSBIE, 1974).

These temperature and rain figures define a number of climatic areas as described by KOPPÉN (GARCÍA, 1973). Although they show variation, they are all described as tropical rain climates with no cool season. They differ locally as to the prevalence of a dry season and when it occurs (ATLAS OF MEXICO, 1975; RZEDOWSKI, 1978; GARCÍA, 1973). The whole range includes what has been termed tropical semi-evergreen and tropical evergreen forest as noted by PENNINGTON and SARUKHAN (1968). Roughly, the southern area, including the main isthmus of Mexico as well as the Peten of Guatemala and much of Belize, is composed of evergreen rain forests while the main part of the Yucatan peninsula is semi-evergreen forest.

The habitat differences of the two species are not clear but we differ with SMITH (1970) that habitat destruction may be allowing *A. palliata* to displace *A. pigra*. Habitat destruction is reducing any habitable areas for either species. From our survey it seems that altitude may be a limiting factor for *A. pigra*. In all cases, the known and possible sites of *A. pigra* were under 1,300 ft in altitude. Local Belizean informants noted that on the southern region of the Mayan mountains, the howlers were only found in the lower areas while other monkeys were found in the higher elevations. *A. pigra* may be limited from expanding its range and isolated on the peninsular areas of Mexico, Guatemala, and Belize by the mountain areas of Chiapas (Mexico), Guatemala, and Honduras, which curve around below Belize (ATLAS OF CENTRAL AMERICA, 1979), whereas *A. palliata* is found in areas considerably higher than 1,000 ft in Mexico (ESTRADA, pers. comm.) and Costa Rica (GLANDER, pers. comm.; CONRAD, pers. comm.). It may be this feature which separates the two species. Although *A. pigra* is tied to evergreen and semi-evergreen areas, the fact that it does not occur in comparable habitats

below the mountain regions of southern Mexico (Fig. 1c) also suggests that altitude is limiting.

Finally, the two areas of greatest abundance of *A. pigra* were in riverine areas of Mexico and Belize. These are areas which show some seasonal flooding and at Bermudian Landing, some areas which are swampy most of the year. This suggests that these riverine areas which are somewhat like the "Canacoital" areas noted by PENNINGTON and SARUKHAN (1968) are specifically good habitat for *A. pigra*. Part of the reason may be the existence of a number of fig species which favor this habitat. Since these areas are not particularly good for human use, they may allow for possible preservable habitats for *A. pigra*.

CONCLUSIONS

1. *Alouatta pigra* shows enough different characteristics to be considered a different species from *A. palliata*.
2. The geographic range of *A. pigra* has been shrinking rapidly into smaller isolated areas with reproductively isolated populations, especially in Mexico due to habitat destruction and hunting.
3. The geographic range of *A. pigra* follows the range of the tropical evergreen and semi-evergreen rain forest in Mexico, Guatemala, and Belize.
4. The geographic range of *A. pigra* is distributed in areas under 1,000–1,300 ft in altitude and in areas in which the mean annual temperature is above 25°C and the mean annual rainfall is over 1,000 mm per year.
5. The optimum habitat of *A. pigra* seems to be in riverine areas in which some seasonal flooding occurs.

Acknowledgements. We would like to thank the many Mexican and Belizean residents for their help in locating sites and possible sites of howlers. We also especially thank Drs. ALEJANDRO ESTRADA, SILVESTRE ORTEGA DOMINGUEZ, GILBERTO LOPEZ, MIGUEL ALVEREZ DEL TORO, JEREMY DAHL, and DORA WEYER for their help. Thanks also to FRANK PANTON and the National Meteorological Service of Belize for meteorological records. Additional thanks to Dr. ALEJANDRO ESTRADA for reading and critiquing the manuscript. This study was sponsored by World Wildlife Fund, U.S.A.

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—Received October 18, 1985; Accepted December 4, 1985

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