

EVIDENCE TO SUPPORT THE SUCCESSFUL REINTRODUCTION OF *ALOUATTA*
PIGRA TO THE NAHÁ REGION OF CHIAPAS, MEXICO

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CHAPTER I

INTRODUCTION

Ethnoprimateology

In the majority of anthropology departments within the United States, primatology is considered a specialization within biological anthropology. Primatology is a fairly young discipline in this country, as anthropologists only began to study primates in the 1950s (Strum and Fedigan 2000). The primary impetus for the development of primatology within anthropology was belief that knowledge of our closest living relatives could help us understand the origins and evolution of human behavior. Although this belief forged a link between biological and cultural anthropology, few anthropologists currently ascribe to this notion. Today we study primates as members of natural communities of plants and animals, and strategic models are used to explain the evolutionary and ecological processes that affect their behavior and ecology. Recently, however, the methodologies and perspectives of a new approach within primatology, called ethnoprimateology, have provided a link between biological and cultural anthropology (Riley 2006 and Loudon *et al.* 2006).

Leslie Sponsel (1997) was the first anthropologist to describe ethnoprimateology and also coined the term. Sponsel (1997) argued that, despite what would seem to be scientists' implied acceptance of the Linnaean designation of humans as primate, few biological or social scientists ever actually considered humans as primates within an

ecosystem and in relation to other faunal species in a natural community. Instead, when scientists, including primatologists, did consider *Homo sapiens*, it was generally in a conservation context and it was primarily as an unnatural and destructive element in the environment (Sponsel 1997). However, humans have always been a part of, not apart from nature, and humans and primates likely have lived in relationships throughout human history and pre-history (Fuentes 2006 and Riley 2006).

The intersection of human and primate ecologies can drive research in primatology, and Sponsel (1997) suggests six areas of topical interest in ethnoprimateology. All six topics incorporate human ecology with primate ecology. The first area, comparative ecology, Sponsel (1997) defines as the similarities and differences in human and nonhuman primate ecologies within their environments, either as sympatric or as allopatric species. Ethnoprimateologists investigate the predator–prey relationship between humans in indigenous societies and the primates that they hunt for subsistence purposes under the topic area of predation ecology (Sponsel 1997). Symbiotic ecology is the third area Sponsel (1997) suggests, and encompasses the relationships between humans and primates in the same environments. As a fourth area, Sponsel (1997) recommends cultural ecology: the role of primates within the human cultural systems. Ethnoecology is the fifth area, and Sponsel (1997) describes this area as the human knowledge, beliefs and values ascribed to primates. The last topical area Sponsel (1997) identifies is conservation ecology, in which the ethnoprimateologist seeks to identify the positive and the negative impacts on primate populations resulting from human use of that primate. Primatologists can use both cultural and biological methodologies in each of these topic areas. Examples of the ethnoprimateological approach can be found in

Cormier's (2006) study of primates as a means of subsistence and as symbols in South America, in Hardin and Remis' (2006) research on gorillas in a forest reserve in the Central Africa Republic, and in Louden *et al.*'s (2006) field study in Bali, Indonesia.

I approached my study of the Central American black howler monkey (*Alouatta pigra*) from an ethnoprimateological perspective. While my first question considered the presence or absence of howlers in the Lacandon rainforest surrounding Nahá, I also thought it important to consider not only howler ecology, but also Lacandon Maya ecology in Nahá and in the surrounding forest. Whether or not howlers and humans intersect, and the extent to and manner in which they do, is pertinent to howler conservation. The status of howlers is affected by the actions of humans, and if howlers are currently present in the Lacandon rainforest, then they must share resources with humans. In addition to shared resources, human predation of howlers is a necessary consideration. If howlers have recently returned to the Nahá region, hunting could quickly decimate small populations that have yet to become fully established. If forest conditions are less than optimal, even low levels of hunting would further exacerbate ecological pressures for howlers.

My study consisted of three parts: census walks, botanical analysis and interviews with local Lacandon Maya. I expected that by conducting census walks, I would be able to determine whether or not *A. pigra* had returned to the Nahá forests and, in addition, be able to estimate population density. If howlers had returned to the forests, I would also expect that there would be food resources present. However, the future success of any new populations of howlers would require that not only would appropriate plant species

be available, but that these species would also be of sufficient size and be present at adequate densities to maintain healthy *A. pigra* populations.

If howlers had recently returned to the Nahá region, the current population density would potentially increase over time as long as conditions were favorable. Long-term access to food is one of the obvious conditions that would allow for an increase in the number of animals that the forest could support. Therefore, I established a primary botanical plot to determine potential resource availability for current and future howler troops. Moreover, I established a second botanical plot and used it, in conjunction with the first, to determine whether or not there were trees of sufficient size to allow howlers to travel through the forest and to access resources.

A second condition important to the potential success of howlers in an area where they are sympatric with humans is that the prevailing perceptions and practices of humans must allow for the coexistence of howlers and humans within a common ecosystem. My goal was to determine current Lacandon resource use to elucidate the extent to which howlers and humans in this region rely on similar resources and, furthermore, to ascertain current levels of Lacandon predation of howlers. In addition, I wanted to find out what were the local people's perceptions of howlers and if their ideas about the presence of howlers in their forest had changed over time. I examined the perceptions and practices of the local villagers across generations by selecting for my interviews individuals who represented varying age categories.

Human ecology and howler ecology need to be compatible if humans and howlers are to have a successful sympatric relationship. In other words, both species' survival requirements have to be met. It is possible that *Alouatta pigra* could return to the forest

surrounding Nahá and subsequently experience levels of stress that are not conducive to maintaining healthy populations, either due to an inadequate environment or to hunting pressures. By utilizing an ethnoprimateological approach, I hope to elucidate the extent to which a sympatric relationship is possible between humans and *A. pigra* in the Nahá forest region.

Alouatta pigra

Alouatta pigra is one of six generally identified species within the *Alouatta* genus (*Alouatta belezebul*, *Alouatta caraya*, *Alouatta fusca*, *Alouatta palliata*, *Alouatta pigra* and *Alouatta seniculus*), though there are disputably one or more additional species (Kinzey 1997, Crockett 1998 and Horwich 1998). The genus dates as far back as the Pleistocene (McKenna 1980) and today ranges from southern Mexico to northern Argentina and southeastern Brazil, making it the New World monkey with the broadest distribution (Moynihan 1976 and Kinzey 1997). In addition, species within *Alouatta* are also typically among the largest New World primates, weighing on average 6.4 kilograms (Moynihan 1976, Kinzey 1997 and Horwich 1998). Howlers are arboreal, preferring the middle and upper canopies, and quadrupedal (Milton 1980), with two distinguishing morphological features: an enlarged hyoid that allows for their characteristic calls and a prehensile tail that acts as a fifth limb (Moynihan 1976, Kinzey 1997 and Milton 1980).

Alouatta species tend to be allopatric, though areas of sympatry have been noted primarily between *A. palliata* and *A. pigra*, *A. palliata* and *A. seniculus*, and *A. caraya* and *A. fusca* (Moynihan 1976, Kinzey 1997 and Crockett 1998). While *Alouatta* species are allopatric to each other, they are often, but not always, sympatric with other primate

species, including humans (Kinzey 1997). Howler species are present in varying habitat types within the Neotropics and at altitudes ranging from sea level to more than 3,200 meters (Crockett 1998). Habitat types range from swamp, evergreen and mangrove forests to gallery, deciduous and semi-deciduous forests (Kinzey 1997 and Crockett 1998). Importantly, howlers can be found in forest fragments and in disturbed habitats, though success depends at least in part on hunting pressures (Estrada and Coates-Estrada 1984, Crockett 1998, Estrada *et al.* 2002b and Muñoz *et al.* 2006).

While the general distribution of *Alouatta* is wide, the distribution of some of the species within the genus is not. *Alouatta pigra* currently exists only within Central America in Belize, Guatemala and southeast Mexico (Crockett 1998, Horwich 1998 and Pavelka and Behie 2005). As noted above, *A. pigra* is sympatric with *A. palliata* in limited areas within southern Tobasco and southern Compeche, both in Mexico (Smith 1970 and Estrada and Coates-Estrada 1984). The elevation range for *A. pigra* seems to fall within the parameters of sea level and 1,300 meters (Horwich and Johnson 1986). Like other species of *Alouatta*, *A. pigra* can be found in fragmented and disturbed forests (Estrada and Coates-Estrada 1984 and Estrada *et al.* 2002b).

Group size for *Alouatta pigra* is smaller than that of other species within the genus—including the species' closest relative, *A. palliata*—with numbers ranging anywhere from 2 to 11 individuals (Horwich and Johnson 1986, Horwich *et al.* 2001b and Pavelka 2003). *Alouatta pigra* are among the more sexually dimorphic howler species (Kinzey 1997), and both sexes disperse from birth groups upon maturation (Kinzey 1997 and Ostro *et al.* 2001). Group composition for *A. pigra* varies, with previous studies reporting both multimale and single-male groups, as well as male–

female pairs. Howlers are feeding generalists, consuming both leaves and fruit, and exhibiting dietary flexibility (Milton 1980, Kinzey 1997 and Silver *et al.* 1998).

La Selva

The Selva Lacandona is the largest remaining tropical forest area, covering approximately 1.9 million hectares, within the state of Chiapas (O'Brien 1998a and 1998b). The Selva Lacandona is situated in the eastern sector of the state, to the west of the Ucumacinta River and north of the border with Guatemala (O'Brien 1998a and see Figure 1.1). The region is composed of sections of intact forest, along with significant areas of disturbance (Medellin 1994, O'Brien 1998a and 1998b). The remaining forested areas are typically tropical lowland forests; however, forest coverage declined dramatically from the previously existing 1.9 million hectares to the approximately 500,000 hectares documented in the early 1990s (Medellin 1994). While the Selva contains a diverse array of floral and faunal species (Goodnight and Goodnight 1956, Medellin 1994, Alvarez *et al.* 2003 and ParksWatch 2004b), this range of diversity has been threatened for the past several decades due to intense levels of deforestation by humans (O'Brien 1998a, 1998b and Alvarez *et al.* 2003).

Within the Selva Lacandona are the Montes Azules Biosphere Reserve and the Lacantún Biosphere Reserve (see Figure 1.2), adjacent regions of protected land that encompass 331,200 hectares and 61,873 hectares respectively, with altitudes ranging from 120 meters to 1,500 meters across the two reserves (ParksWatch 2004a and 2004b). Average temperatures in the lowlands of the Lacantún Biosphere Reserve are generally

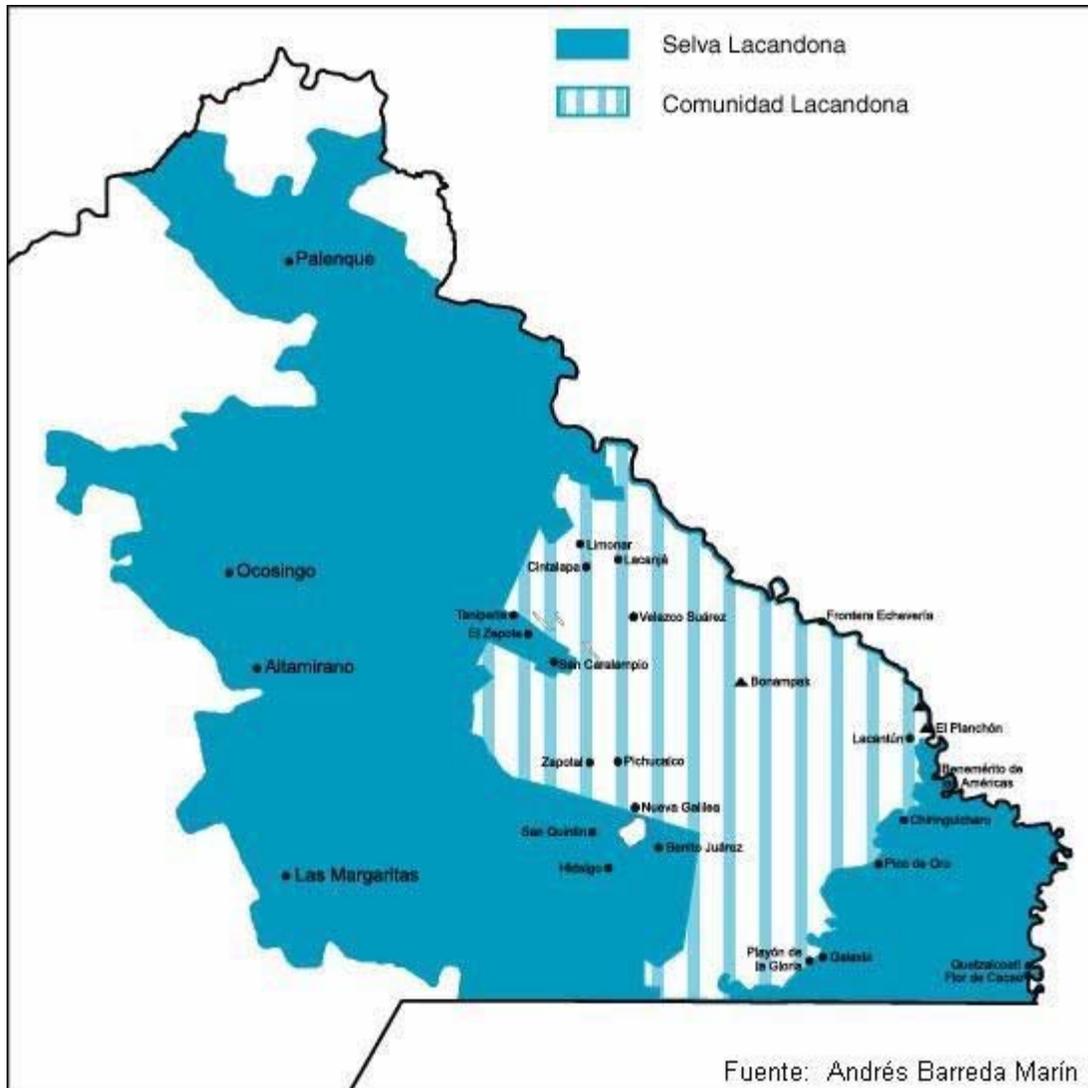


Figure 1.1: Map of the Selva Lacandona and Area of the Comunidad Lacandona.

This map is from the Centro de Investigaciones Económicas y Políticas de Acción Comunitaria (CIEPAC) website:

<http://www.ciepac.org/archivo/images/maps/selcomlac.jpg>.

between 26 and 28° Celsius, while in the higher elevations found in the Montes Azules Biosphere Reserve, the average temperatures vary between 24 and 25° Celsius (ParksWatch 2004a and 2004b). Annual rainfall within the entire region is between 2,500 millimeters and 3,000 millimeters. The Comunidad Lacandona owns the Lacantún



Figure 1.2: Map of Protected Areas in Chiapas and Surrounding Areas.

This map is part of a larger map of protected areas from the ParksWatch website: www.parkswatch.org.

Biosphere Reserve and part of the Montes Azules Biosphere Reserve (O'Brien 1998a and ParksWatch 2004a). Both regions are protected lands and centers of biodiversity within Mexico; however, both areas are critically threatened despite the protection they are supposed to receive from the Mexican government (Mendoza and Dirzo 1999, ParksWatch 2004a and 2004b).

As with other remaining forest areas in Mexico, these two biosphere reserves face threats from deforestation, political strife surrounding land ownership, encroachment and wildlife trafficking (O'Brien 1998a and ParksWatch 2004a and 2004b). Land ownership has long been an issue in Chiapas, and especially in the Selva Lacandona. In the latter half of the 19th century, Selva Lacandona land was primarily in the hands of timber companies, foreign investors and speculators (O'Brien 1998a). Extensive colonization of

the Selva Lacandona did not begin until the 20th century, following the Mexican Revolution (O'Brien 1998a). The government implemented land and agrarian reforms that, in the end, placed large parcels of land into the hands of the Lacandon Maya (O'Brien 1998a). O'Brien (1998a) provides a thorough and extensive discussion on the historical and political activities in the Selva Lacandona that have led to current conditions.

Aside from the Lacandon proprietorship of the Lacantún Biosphere Reserve, the Comunidad Lacandon also own approximately 10,000 hectares of land surrounding Nahá (Kashanipour and McGee 2004). The Lacandon Maya village of Nahá is located at approximately 820 meters (Kashanipour and McGee 2004); though recent Google Earth Satellite (GES) information indicates that peak elevations in the immediate area reach elevations of slightly more than 1,200 meters. Nahá is situated northwest of the Lacantún and Montes Azules Biosphere Reserves (see Figure 1.2). According to the ParksWatch website (www.parkswatch.org), nearly 4,000 hectares of the land around Nahá are protected under the designation of a Flora and Fauna Protected Area. At this time, despite the designation as a protected area, the Lacandon Maya in Nahá face threats to the stability of their forest similar to the threats to the Lacantún and Montes Azules Biospheres Reserves. The areas surrounding the Nahá forest are *ejidos* owned by non-Lacandon Maya (O'Brien 1998a). The residents of these areas are rapidly clearing previously forested areas in order to establish grazing land for cattle and large scale agricultural plots (O'Brien 1998a and see Figures 1.3-1.5).

The Nahá region consists of montane rain forest, excluding the 60 meters of upper canopy generally found in tropical rain forest environments (Kashanipour and McGee



Figure 1.3: Nahá Region: 1990 Deforestation Conditions.

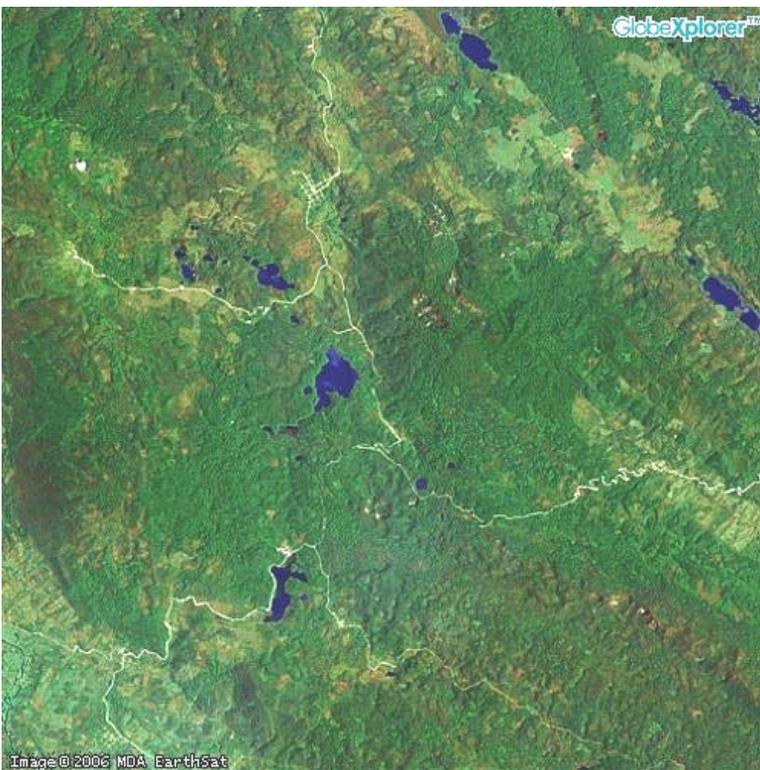


Figure 1.4: Nahá Region: 1999 Deforestation Conditions.



Figure 1.5: Nahá Region: 2006 Deforestation Conditions.

2004). Average rainfall would be in the range found for the region as a whole: 2,500 millimeters to 3,000 millimeters. Average temperatures specific to this area are, to my knowledge, unavailable. However, since elevations fall within the range given for Montes Azules Biosphere Reserve, it is possible to infer that average temperatures for Nahá would be similar to average temperatures in the Montes Azules Biosphere Reserve (24 to 25° Celsius).

In the 1930s and 1940s, non-Lacandon Maya—the Chol, Tzotzil and Tzeltal—began settling the Selva Lacandon through small land grants given by the government as a result of agrarian reforms (O’Brien 1998a and McGee 2002). The forest was cleared for farming and cattle as the human population inhabiting the Selva Lacandona continued to grow (O’Brien 1998a). Cattle ranches began to invade the Selva Lacandona at an increasing pace during the 1970s with the influx of an even greater number of people

migrating into the region (O'Brien 1998a). Some of the land was initially cleared for agricultural production, and then subsequently converted to pasture lands, a less expensive endeavor (O'Brien 1998a). The pressure cattle grazing places on the land, however, is detrimental, and as the land quickly becomes incapable of any substantial growth, even more land is cleared to maintain large herds of cattle (McGee 2002). From my own personal observations of the region, large scale agricultural plots still exist immediately outside of the Nahá forest. Therefore, a combination of pastures and agriculture fields has been pushing in on the boundaries of the Nahá forest. This can be clearly seen in Figures 1.3-1.5. The three satellite images span a period of only 16 years, and yet the increasing levels of deforestation are evident. Encroachment appears most severe from the northeast and southwest; however, in the northwest region, deforestation from the other two directions appears to be closing in. The region to the southeast currently appears less critical, though the potential exists for ongoing deforestation that will eventually lead to forest islands.

Lacandon Maya

The Lacandon Maya established a permanent settlement in Nahá in 1972, a condition of land title grants allocated by the Mexican government (O'Brien 1998a and Nigh 2002). Prior to this time, the Lacandon Maya lived in dispersed settlements that consisted of family members rather than larger communities of both related and unrelated families (McGee 2002 and Nigh 2002). The Lacandon were required to live in stable communities as a condition of the land grants, which gave 66 heads of households a total of 614,321 hectares of land (O'Brien 1998a, McGee 2002, and Nigh 2002). Concurrently,

the Mexican government also established protected areas of forest in an effort to curb deforestation (O'Brien 1998a and McGee 2002). The designated protected areas overlapped the land given to the Lacandon. While the government encouraged the Lacandon to settle within the protected areas and granted them proprietorship of these areas, the government also relocated approximately 6,000 Chol and Tzeltal Maya outside of the newly designated protected lands (O'Brien 1998a and McGee 2002).

As a result of government decisions regarding land usage and land tenure, tensions between the Lacandon and non-Lacandon Maya arose and continue into the present (O'Brien 1998a and McGee 2002). The Chol, Tzeltal and Tzotzil Maya groups living in the *ejidos* surrounding Nahá resent the land given to the Lacandon and frequently file formal disputes over legal land tenure (O'Brien 1998a). Part of the issue arises from the fact that the government initially formed *ejidos*, which encouraged relocation into the Selva Lacandona, and then subsequently reallocated that land to the Lacandon (O'Brien 1998a). Additional disputes arise after new colonizers invade and clear forest lands (O'Brien 1998a). In casual conversation with one of the Lacandon men, I was told that the villagers frequently file complaints with the government against non-Lacandon that sneak onto their land and clear large tracts of forest. It is often the case that the encroachment is discovered accidentally and too late to save the forest.

The Mexican government gave the Lacandon Maya land in the Selva because of purported ancestral ties to the ancient Maya from that region (O'Brien 1998a). In reality, it appears that the land grants initially gave the government access to the forest for logging (O'Brien 1998a and McGee 2002). The Lacandon received gifts in the form of clothing and medicine, as well as royalties (though as much as 70 percent of these

royalties were controlled by the Nacional Financiera, S.A., or NAFINSA) in return for access to the forest for logging purposes (O'Brien 1998a). In another casual conversation with a Lacandon man, the villager stated that the community "woke up" one day and realized that their forest was disappearing and that all of the animals were also gone. Furthermore, he indicated that the community decided to improve the conditions of their forest. These same sentiments were re-iterated during interviews with some of the local villagers (see Chapter IV for further discussion).

A change in the economic structure within Nahá potentially allows a greater possibility for forest regeneration in spite of decreasing amounts of available land. The Lacandon have traditionally cultivated farming plots, known in Mayan as *milpas*, in a form of subsistence that is referred to as swidden agriculture (Diemont *et al.* 2006). *Milpa* cultivation, as practiced by the Lacandon, utilizes the natural environment without depleting it (McGee 2002 and Diemont *et al.* 2006). Historically, the Lacandon concurrently planted several types of crops in their *milpas* and rotated *milpas* such that each went through a fallow period where the forest and soil were allowed to regenerate (Hammond and Miksicek 1981, McGee 2002 and Diemont *et al.* 2006). The entire cycle of the *milpa* moves through three stages: the *milpa* stage, which can last up to five years; the shrub tree phase, averaging around seven years; and the short tree, or secondary forest, stage, which is typically cleared after 15-20 years (Hammond and Miksicek 1981 and Diemont *et al.* 2006). The Lacandon supplemented the diet from their *milpas* by hunting wild game, including howler and spider monkeys (McGee 2002).

An increase in tourism has led to a subsequent decrease in swidden agricultural practices (McGee 2002). In the 1980s, an unpaved road was constructed that connected

Nahá to Palenque, easing access both into and out of the Lacandon forest. The Lacandon in Nahá then began to devote more time in creating crafts for sale to tourists in Palenque. As the Lacandon devoted more time making goods and more time in Palenque selling their goods, less time was available for agricultural practices. In addition, the tourist industry led to a cash-based economy, which in turn meant that the Lacandon could purchase subsistence items that they previously were required to grow. McGee (2002) concludes that agricultural practices have been adapted to the changing economy; the Lacandon now frequently have fewer *milpas* and hire Tzeltal Maya to work their *milpas* for at least part of the season. While conservation of the forest might benefit from this changing economy, a cash-based economy is not self-sustaining, and the long term costs and benefits to the Lacandon are not predictable nor are they consistent.

CHAPTER II

ALOUATTA PIGRA POPULATION CENSUS

Introduction

The genus *Alouatta* is broadly distributed throughout a large portion of Central and South America, and in varying environmental types (Kinzey 1986 and Silver *et al.* 1998); however, the species *Alouatta pigra* is found only in southeastern Mexico, northern Guatemala, and Belize (Horwich *et al.* 2001a and Estrada *et al.* 2002a and 2002b). Prior to the year 2003, *Alouatta pigra* had been listed on the IUCN Redlist of Threatened Species in the category of Least Concern (IUCN 2006 Redlist website: <http://www.iucnredlist.org>). In 2003, due to an increase in available information for black howlers and the subsequent knowledge that the species' numbers had declined appreciably and that deforestation had dramatically reduced their habitat, *Alouatta pigra* was moved to the Endangered Species category (IUCN 2006 Redlist website: <http://www.iucnredlist.org>). This means that the status of the black howler has gone directly from Least Concern in 2000 to Endangered in 2003, without ever receiving the intermediate designation of Vulnerable. Therefore, it is imperative that broader geographical research is conducted to determine population densities for this species across its geographic region.

To date, the major study sites for *Alouatta pigra* have been at a protected site, the Baboon Sanctuary, in Belize and at archaeological sites in Guatemala and Mexico.

Studies conducted on black howlers have primarily been on the behavior and ecology of this species. However, some census data for howler populations have been collected in these regions, providing information on group size, home range size and group structure. Even so, census data is limited and sporadic, with few long range studies that track changes in population density across generations of *A. pigra*. This is reflective of the general lack of data for this species (Gómez-Marin *et al.* 2001 and Estrada *et al.* 2004). There does seem to be an increase in the amount of research conducted on black howlers in more recent years, including an increasing number of census surveys, though there do not appear to be any censuses from regions outside of the aforementioned areas.

In 1934, C. R. Carpenter (Collias and Southwick 1952) conducted perhaps the first census of the genus *Alouatta* (*Alouatta palliata aequatorialis*) on Barro Colorado Island, Panama. Collias and Southwick (1952) conducted a subsequent census of the same species almost 20 years later, noting a population decrease by half during this time period. Outside of Panama, population censuses for *A. pigra* seem to have first occurred in the late 1970s and in the early 1980s. Estrada (1984) conducted a simple preliminary survey to ascertain black howler presence and distribution (versus establishing population density estimates) on the Yucatan Peninsula, and Horwich and Johnson (1986) conducted a broad survey in Belize, Guatemala and Mexico of *Alouatta pigra* in order to begin to establish a broad geographic distribution for the species. One challenge in locating and determining census studies for *Alouatta pigra* in the literature is in the species history. During the years prior to 1970, the black howler was considered a subspecies of *Alouatta palliata*, and in the years following 1970, there was still conflict and confusion regarding the species status of *A. pigra* (Horwich 1983).

The Community Baboon Sanctuary in Belize was established in 1985 (Horwich *et al.* 2001b) in order to conserve the black howler, and it has been the major research site for this species for more than 18 years (Ostro *et al.* 2001). Researchers have conducted long-term studies at the sanctuary that include documentation of density changes in the black howler populations, from the earliest studies conducted in the 1980s to recent surveys (e.g. Horwich *et al.* 2001a and 2001b) from various villages within the sanctuary boundaries (Ostro *et al.* 2001). An additional source of surveys in Belize comes from researchers at the Cockscomb Basin Wildlife Sanctuary, a region that contains only howlers that have been translocated and their offspring (Ostro *et al.* 2001). Pavelka (2003) and Pavelka *et al.* (2005) provide systematic census data from one other region in Belize, the Monkey River, a protected area in the south of the country. Work by Pavelka *et al.* (2005) is of particular interest in terms of conservation as they document population density and structure changes following a natural disaster, Hurricane Iris, which struck Belize in October 2001. The populations at Monkey River experienced a period of troop disorganization that lasted approximately three months, spent more time on the ground and at lower levels in the trees due to complete canopy loss, and survived for several weeks on deadfall and new leaves (Pavelka *et al.* 2005). Interestingly, the howlers at Monkey River also exhibited reduced vocalizations following the loss of 42 percent of the total population in the hurricane (Pavelka *et al.* 2005).

In Guatemala, population densities have only been determined at the archaeological site of Tikal (Estrada *et al.* 2004). In the early 1970s, Coelho *et al.* (Estrada *et al.* 2004) conducted the first census of the howler population at Tikal. There

appear to have been no further censuses of this area until 2002 when Estrada *et al.* (2004) conducted a population survey of black howlers at the Tikal site.

Within Mexico, systematic census data have only been recently collected. Estrada and colleagues have provided the majority of census data for *Alouatta pigra* on the Yucatan Peninsula, and all of this data is from archaeological sites. In 2001 and 2002, Estrada *et al.* (2002a and 2004) surveyed the howler populations at the Mayan archaeological sites of Yaxchilán, located on the Río Usumacinta, the boundary between Mexico and Guatemala, and Calakmul, located in Campeche. Their surveys provide the first estimates of population density at these two sites. During the winter of 2001 and the spring of 2002, Estrada *et al.* (2002b) conducted a survey at another Mayan archaeological site: Palenque. The team's research of this region is important, and relevant to my research in Nahá, in that the forests surrounding Palenque consist of a number of fragmented sections rather than one continuous forest region (Estrada *et al.* 2002b). Subsequent research at Palenque, and in other regions where forest fragments exist, would provide valuable information on the ability of black howlers to maintain genetically healthy populations in forest fragments and on the rate of ongoing deforestation in the region.

Nahá is situated southeast of Palenque and northwest of Yaxchilán. Both Palenque and Yaxchilán represent national parks with ancient Mayan ruins that are in close proximity to Nahá. Although the nearby village of Mensábak contains classic Mayan ruins, it is not a national park, and Nahá and the surrounding forest do not contain any ancient Mayan ruins. As such, past research (e.g. Estrada *et al.* 2002b) that has focused on howlers located at ancient archaeological sites—quite possibly due to the

protected status of these areas—has not covered the Nahá forest. While research conducted at archaeological sites provide valuable information on howler populations, these sites cannot be considered representative of all environments in which howlers live. My study is an attempt to begin broadening our understanding of howler populations beyond archaeological sites. I purposefully chose a region in which *A. pigra* are sympatric with humans, as there are few situations in which this is not the case and the conservation of howlers depends on more complete information regarding howler populations in these areas.

Methodology

Census Walks

The forest surrounding Nahá contains a network of existing trails utilized by the Lacandon to gain access to their *milpas* and to access the forest to harvest building materials, to cut firewood, and to collect wild plant, fruit and berry sources. These trails had previously been the only way in and out of the village; therefore, some of the major trails lead to other villages. I used the existing trail system for census walks as the rugged terrain and the density of secondary undergrowth were prohibitive in creating new trails. Furthermore, the Lacandon own the forest (O'Brien 1998a) and are reluctant to cut forest growth unnecessarily.

Prior to conducting census walks, volunteers and I measured and flagged trails in 25 meter increments. At each 25 meter point, we read a compass bearing to the next 25 meter point. I also used a Magellan Meridian™ Gold handheld GPS device to record waypoints for all points at which the GPS had satellite contact. Trails were labeled A-R,

with lengths measuring from 50 meters for the shortest trail to 1,700 meters for the longest. The entire system consisted of 8,355 meters of trails.

The male members within *A. pigra* troops typically engage in a morning chorus (Collias and Southwick 1952, Estrada *et al.* 2002b, Estrada *et al.* 2002a and Kitchen 2004); however, in Nahá, this behavior was not observed. The howlers were heard at random times during the day, though primarily in the middle of the afternoon, and for unknown reasons. The call of one howler was heard as late as ten o'clock at night.

Additionally, I heard no howler calls between June 21, 2006 and July 12, 2006.

Although I could detect the presence of howlers through occasional vocalizations, I observed no patterns in the time or in the location of calls. Therefore, I determined that census walks would be conducted on a systematic and rotating basis, with different trails walked in the morning and in the afternoon.

There were three major trails in different sections of the forest, with shorter trails leading off of the primary, longer trails. I utilized the primary trails as the starting point for census walks and determined the rotation of walks between these three trails. There were twelve morning census walks and ten afternoon census walks between June 19, 2006 and July 18, 2006, for a total of 49,168 meters walked at an average of 2,235 meters per walk. The pace of census walks was approximately 1 kilometer per hour. Visibility through the forest varied throughout, with a range from less than five meters in areas with dense secondary undergrowth to 50 meters in the most open sections of forest.

Point Sampling Surveys

I received information from some of the Lacandon villagers that they often saw howlers in very specific locations. One villager reported that *A. pigra* troops frequently visited the banana trees in his house garden. I received reports from others that howlers regularly came to the edges of their *milpas* to feed. Given this information, I opted to conduct point sampling surveys from four *milpas* in three separate sections of the forest, as well as from a vantage point above the house garden with the banana trees.

Over the course of the study period, I conducted a total of sixteen point samples in the four *milpas* and above the one house garden. For the *milpa* samples, I observed from the center of the *milpa* and rotated in a circular direction, using a pair of Zeiss (15 x 45) binoculars, in order to observe all directions. In conducting point samples of the house garden, I stood on a trail that overlooked the entire house garden and the area of the forest at the edge of the garden. Given that the howlers had been heard vocalizing at different times throughout the day, I conducted point samples at varying times throughout the day for an average of 30 minutes per sample.

Results

Census Walks

On June 20, 2006, while conducting my second census walk, I heard the vocalizations of one or two males from my position on trail A. The calling lasted approximately ten minutes. I took a compass bearing perpendicular to the direction of the vocalizations; however, the undergrowth was too dense to allow for a visual sighting. In addition, the density of the undergrowth prevented me from leaving the trail. I

followed two other trails that headed in the general direction from which I had heard the calls, though I was not able to obtain a visual sighting of the howlers nor did I hear any other sounds that would indicate the presence of howlers in close proximity.

As previously stated, I did not hear the howlers vocalize between June 21, 2006 and July 12, 2006. On July 13, 2006, however, I again heard the howlers vocalize. Two assistants and I first heard the vocalizations on our way to the trailhead where we were to begin an afternoon census walk. We heard the howler calls for approximately thirty minutes, though the calls ceased as we neared the general area from which the vocalizations seemed to originate. As with the previous incident during which I heard the howlers call, the terrain and undergrowth density prevented a visual sighting of the howlers, and again it was not conducive to leave the trail and our attempt to do so was unsuccessful. The howlers were not heard again during the remainder of the census walk.

While I was able to ascertain the presence of howlers through their vocalizations during two of my census walks, the census walks yielded no visual sightings of *Alouatta pigra*.

Point Sampling Surveys

During the point sampling surveys, I did not hear or see any *Alouatta pigra* in the various *milpas* or the house garden. Nearly all of the point sample surveys were conducted from June 21, 2006 through July 12, 2006 when no howler vocalizations were heard at any point during the day and when no howlers were seen on census walks.

Population Density

I was able to establish the presence of *Alouatta pigra* from their vocalizations during the set-up period of this study from June 10, 2006 through June 18, 2006. It was during that time span that I heard the majority of vocalizations. By the time I had begun conducting census walks, the calls had generally subsided, with only two subsequent incidences. Thus, I was not able to determine a population density estimate for *Alouatta pigra* in the forest surrounding Nahá.

Discussion

While I was unable to determine an estimate of population density for *Alouatta pigra* in the Nahá rain forest, I did establish their presence. I heard more howler vocalizations during the set-up period of my project than I did at any other time. By the time I began conducting census walks, the vocalizations had ceased. As such, it was not possible to determine prior to conducting my walks the general area in which the howlers were located on a daily basis, significantly decreasing the odds that I would come across a troop during censuses. There are two possible explanations for the sudden cessation of howler calls: seasonal changes in foraging patterns and changes in the levels of human activity in the forest.

Prior to beginning to feed in the mornings, howlers typically engage in a morning, or dawn, chorus, which presumably serves as a means by which to notify other troops of the group's location (Milton 1980). These calls seem to function as a mechanism with which to avoid interaction and conflict between troops, thereby conserving the energy that would otherwise be expended in an inter-group conflict (Milton 1980 and Kitchen

2004). For the afternoon or evening feeding, howler troops move to a different location and, upon entering a new area, male howlers frequently vocalize, again notifying nearby troops of the group's location change (Milton 1980).

As I noted earlier, the howlers around Nahá did not seem to engage in regular vocalizations, quite possibly because there was no need to do so. If the number of troops living in the area is small, and each troop generally has a large enough home range that the likelihood of encountering another troop is also small, then it is quite possible that the howlers around Nahá would not have the need to vocalize on a regular basis. While vocalizations are less expensive energetically than conflicts that arise when one troop encounters another (Kitchen 2004), it would still seem in the howlers' best interests to conserve as much energy as possible (see Chapter III for a discussion).

The howlers vocalized more when I first arrived in Nahá at the beginning of June 2006, though their vocalizations were also not predictable during that time period. I discovered during my interviews with the Lacandon (see Chapter IV) that the howlers are heard most often in the dry season months of March, April, and May as that is when one of their preferred food sources, *Brosimum alicastrum* (Coelho *et al.* 1976, Milton 1980 and see Chapter III), produces fruit. Howler troops would be more apt to encounter each other during this time period since they would all seek out the same favored fruiting trees; thus, they would also be more apt to vocalize during this time period as well. It appears that my arrival in Nahá coincided with the end of the fruiting season for *Brosimum alicastrum*. At the end of this fruiting season, it is possible that the howlers then returned to territories that do not overlap with other troops, resulting in a decreased frequency of vocalizations.

There is another possible explanation for the decreased howler calls. After I had started conducting census walks, I began to notice that there was an increase in the amount of human activity in the forest. I regularly heard the sound of chainsaws throughout the day. Many of the secondary trails that I walked led to small logging areas within the forest, and several more secondary trails appeared after I had established my trail system. It appeared that the villagers (or hired help from outside of Nahá) were cutting short trails for selective logging purposes (see Chapter IV), and that the logging was occurring in the areas from which I had originally heard the howler vocalizations. I noted seven new construction sites across the length of the village, which meant that trees were being cut in several different areas within the forest around Nahá. In addition to the increased activity and noise from the chainsaws within the forest, there was also a heightened level of activity and noise associated with the construction of new buildings within the village itself. There is the possibility that the howlers moved further away from the village when human activity within the forest and within the village increased.

I had originally thought it likely that the howlers had moved further away from the village due to the increase in human activity. However, after interviewing the Lacandon villagers and subsequently discovering that the annual pattern of howler vocalizations has been the same since their return to the Nahá forest, I now feel that the decrease in howler calls after my arrival was more likely due to seasonal foraging patterns than to increased human activity in the forest. Nevertheless, more research needs to be conducted in this region to determine if this pattern truly recurs on an annual basis, especially given the fact that the howlers have only been back in the area for approximately two years.

While I did not encounter howlers during the course of my census walks, I and a student assistant sighted at least two howlers while conducting an early morning survey of the forest during the set-up period of my study. Additionally, several students heard quiet grunt vocalizations during this same time. On this particular day, a group of three students and I left at daybreak and walked to one of the *milpas* from which the owner had stated that he had frequently seen howlers. We did not hear a dawn chorus that day and spent approximately 45 minutes observing the perimeter of the *milpa* before there was any indication of howler presence. We noted a flock of birds flushed out of a tree and, shortly following that incident, I observed one howler crossing from the canopy edge towards the trunk of the tree. We moved closer to the perimeter of the *milpa* on the side from which I sighted the howler, which was also the same area from which the flock of birds had flown. It was there that a student sighted two individuals moving from one tree to the next. It was not clear whether one of the two individuals was the same individual that I sighted or if there were, in fact, a total of three individuals. We heard the quiet grunts of more than one individual spread out within the forest adjacent to the *milpa*, though we did not have any further sightings. This was a casual observation and not part of my formal surveys; however, it further supports the idea that howlers have returned to the Nahá rain forest.

Conclusion

It is likely that the number of distinct howler troops in the forest area surrounding Nahá is currently small and, therefore, the howlers do not vocalize on a consistent basis, making it considerably more difficult to locate them. It is important to note that *Alouatta*

pigra has only been back in this region for approximately two years, which is not a significant amount of time; therefore, it is entirely possible that not enough time has passed to allow for multiple outside troops to immigrate or for multiple new troops to develop from migrating offspring and the splintering of larger groups. As long as sufficient food sources exist and Lacandon attitudes towards and perceptions of howlers have changed in a positive direction, it is plausible for fledgling populations within the Nahá forest to thrive, grow and multiply.

While the Nahá Lacandon forest is not large, it appears that corridors still exist that would link this forest to others (see Figure 2.1). Currently, there has been, to my knowledge, no other research conducted on *Alouatta pigra* in the region surrounding

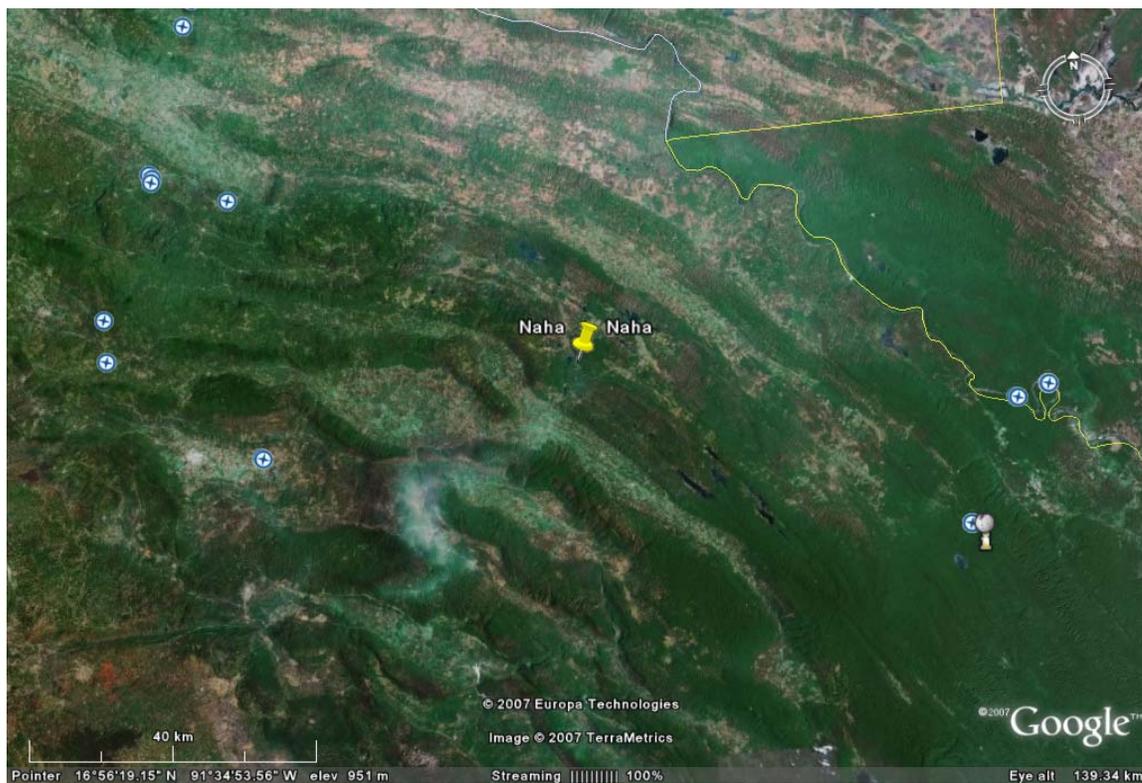


Figure 2.1: Regional Image: Satellite View of Forest Coverage and Corridors from Nahá.

Nahá, including those areas that are not owned by the Lacandon. Little is known about the distribution of howlers in the forests of Chiapas that lie south of Palenque. More research is needed in this region in general, as well as specifically in the Nahá forest. I was able to establish neither population estimates nor general home range territories of existing troops, though it was apparent these troops were present. Future longitudinal studies would aid in establishing population densities and, furthermore, in tracking changes in the existing populations of *Alouatta pigra* in the forest surrounding Nahá.

Given the ongoing deforestation issues in Chiapas (Estrada and Coates-Estrada 1984, Medellín 1994, O'Brien 1998a and Estrada *et al.* 2004), the future conservation of *Alouatta pigra* is dependent on maintaining areas of the forest large enough to support multiple populations of this species while allowing adequate gene flow to maintain healthy and viable populations. In the early 1980s, Estrada and Coates-Estrada (1984) noted concerns regarding the conservation of *Alouatta pigra* due to habitat destruction. Aside from extensive hunting of this species, deforestation is the greatest threat to the black howlers continued existence (Estrada and Coates-Estrada 1984). At this time, *A. pigra* seem to be filtering back into the Nahá rainforest, and though the reasons for this move are currently not known, forest conditions will play a critical role in maintaining current and future populations within the region.

CHAPTER III

BOTANICAL ANALYSIS

Introduction

In order for any species of primate to be successful in its environment, it must obtain adequate foods that will provide not only enough energy, but also enough nutrients to meet daily dietary requirements, while concurrently ingesting fewer toxins than the maximum an individual can manage (Glander 1982 and Altmann 1998). In general, fruits provide more nutrients with fewer hard to digest fibers and tannins than do leaves; however, the patchy distribution of fruit makes it more difficult to obtain (Cowlshaw and Dunbar 2000). Glander (1982) suggests that howlers will select trees with fewer tannins and greater nutritional value, including those mature leaves that resemble young leaves in chemical compound structure and nutritional value. Food selection is based on a combination of secondary compounds and nutritional factors, and different primates exhibit varying mechanisms with which to manage secondary compounds, either through biological or behavioral adaptations (Glander 1982).

Alouatta pigra exhibit a larger degree of dietary flexibility than more frugivorous primates (Milton 1980 and Silver *et al.* 1998), possibly due in part to a slightly larger caecum (Milton 1980 and Cowlshaw and Dunbar 2000). This allows them to subsist on a wider variety of foods, including both fruit and leaves, given an increased ability to digest tannins due to gut adaptations. However, as Milton (1980) notes, the

differences in gut adaptations are not large, and howlers do not exhibit the degree of adaptations seen in folivorous Old World monkeys such as the Colobinae (Cowlshaw and Dunbar 2000), a species that exhibits an enlarged sacculated stomach designed for digesting secondary compounds (Milton 1979). Kinzey (1986) also suggests that howlers have a dietary advantage in that they are able to more readily discern green fruits that are perhaps not as readily detected by other primates, in addition to ripe fruits, by hanging from their prehensile tails to search for food. If true, this would serve to further increase the dietary range and flexibility for *Alouatta pigra*. The authors of at least one study, Pavelka and Knopff (2004), suggest that the diet of *A. pigra* is actually more frugivorous than that of other species of howlers.

Alouatta pigra's dietary flexibility allows for the species to exist in a wide range of habitats, from riverine forests to fragmented and disturbed forests (Crockett 1998). Horwich and Johnson (1986) found elevation to be one constraint to the variation in howler environment in that howlers seem to live primarily at elevations < 1,300 meters. The region surrounding Nahá falls within these parameters. According to recent information from the GES, peak elevations around Nahá generally do not reach any higher than just over 1,200 meters. The Nahá forest is also a fragmented landscape due to current and, primarily, past Lacandon subsistence practices. Presently, however, the Nahá region still contains forest cover, while many of the surrounding areas have been stripped (see Figure 3.1). Crockett (1998) suggests that though howlers can live in fragmented forest conditions, the long-term prognosis for survival is not necessarily good. Estrada (2002) shares this view, citing issues inherent in isolated forest islands that do not connect with other forest regions and therefore do not allow for the dispersal of



Figure 3.1: Nahá and Surrounding Regions: Current Deforestation Conditions.

individual howlers and subsequent gene flow with other populations. Furthermore, even if a primate species initially survives within a fragmented forest, if the size of the forest fragment is not large enough for the species in residence, local extinction will inevitably follow (Marsh 2003).

Currently, tracts of forest exist that extend from the Nahá region outwards to surrounding areas (see Figure 3.1). However, reports from the Lacandon indicate that the howlers are primarily in the area to the north–northeast of the road that runs through the middle of the village. Examination of figure 3.1 reveals that the regions further to the

north–northeast are highly fragmented with large tracts of cleared land. Forest conditions are somewhat improved to the northwest and much improved to the southeast; however, in order to access those regions, howlers would be required to cross roads, an inherently risky endeavor. Additionally, those remaining tracts of relatively intact forests would need to be maintained for the howlers' long-term survival to be possible. O'Brien (1998a) estimates that approximately 40 percent of the Selva Lacandona has been either cleared or, at the least, disturbed prior to 1996. These estimates do not bode well for the conservation of *Alouatta pigra* unless immediate efforts are made to preserve the remaining tracts of forest and forest corridors.

The fragmented conditions of the forest further constrain the ability of howlers to procure adequate food resources to meet daily requirements. Forest productivity and available resources determine the extent to which howlers can meet their dietary and nutritional requirements (Coehlo *et al.* 1976). Though *Alouatta pigra* seem to be able to eat a wide variety of foods, the question still remains as to whether or not the Nahá forest contains enough food source trees to support the health and growth of howler populations during the natural reintroduction of the species to this region. Human forest use in the region can change forest composition and, ultimately, can have an effect on the tree species available to howlers.

Chapman and Balcomb (1998) found no correlation between forest productivity and howler density *per se*, though they did suggest that changes in howler habitat do negatively affect density. The Lacandon Maya practice slash and burn, or swidden, farming, a technique that involves rotating land plots that are cultivated with those that are allowed to fallow for several years (Cowgill 1962 and Diemont *et al.* 2006). Fallow

milpas necessarily contain secondary growth, with an abundance of pioneering species and immature plants and trees that could potentially be neither large enough nor productive enough to support howlers, thus limiting the availability of resources for howlers and thereby constricting species density in the region. However, if *milpas* are allowed to lie fallow for long enough periods of time, and if there are large enough regions of connecting forest that contain mature food resource trees at any given time, then higher densities of howler could be supported without long-term detrimental effects.

Studies on the feeding ecology of *Alouatta pigra*, especially those that identify specific food resources, are limited (Silver *et al.* 1998). However, the need to improve our understanding of the subject is increasing due to the conservation concerns implicit in dramatic population reductions and continued habitat loss. Early studies, from the late 1970s, on the feeding ecology of *Alouatta pigra* came out of Tikal, Guatemala, where populations were reliant on one primary tree species, *Brosimum alicastrum* (Silver *et al.* 1998). Coehlo *et al.* (1976) provide a partial list of 29 additional tree species in Tikal from which they observed howlers eating, though they suggest that the *B. alicastrum*, a preferred food source for *A. pigra*, are so numerous in Tikal that this single species alone could support more than 42,500 combined howler and spider monkeys over the duration of each of its three fruiting cycles. It is for this reason *Alouatta pigra* were originally deemed as dietary specialists (Silver *et al.* 1998).

More recent studies identifying specific food source species outside of Guatemala, beginning with Silver *et al.* (1998), have determined that black howlers are indeed much more flexible in their diets than originally presumed. To date, feeding ecology studies are limited to the Community Baboon Sanctuary and the Cockscomb

Basin Wildlife Preserve within Belize (Silver *et al.* 1998) and a cocoa plantation in Comalcalco, Mexico (Muñoz *et al.* 2006). Milton's (1980) very thorough study on the feeding ecology of *Alouatta palliata* is also relevant, given *Alouatta pigra* and *Alouatta palliata* are sympatric in at least one locale in Mexico (Estrada and Coates-Estrada 1984 and Horwich and Johnson 1986). All three of the above studies identify observed food resources for *Alouatta pigra* and *Alouatta palliata*. There is very little overlap between the three studies in the tree species identified, with notable exceptions from the genera *Ficus* and *Brosimum*.

The research conducted by Silver *et al.* (1998) and Muñoz *et al.* (2006) are just the beginning of the work that is necessary to more fully understand the dietary flexibility exhibited in black howlers. One component of my work in Nahá is an attempt to begin to identify potential food sources for black howlers in an environment that is different from those locations in which previous studies of howler food sources have been conducted. To date, there has been no botanical research conducted in forest of the Nahá region. Additionally, studies on howlers in the area are also lacking, with no studies conducted, to my knowledge, during the period before the howlers' local extinction in the early 1980s and no studies conducted after their recent return. This study is an initial effort to begin to understand the howler habitat around Nahá, including the availability and accessibility of food resources.

Methodology

Botanical Plot

The rain forest around Nahá is a fragmented secondary growth montane rain forest (Kashanipour and McGee 2004). Ground cover is often thick with new growth, and there is evidence of *milpas* that have been left to lie fallow. Young trees are abundant, with large tracts of forest where the canopy is relatively open. However, it is also apparent that there are sections of the forest that do contain older and larger trees creating a denser canopy. Gómez-Marin *et al.* (2001) suggest that *Alouatta pigra* can adapt to the conditions of a fragmented forest with long-term success. However, it is still necessary to determine whether adequate food resources exist that would support a population of howlers and whether a sufficient number of trees are present that are large enough to support the weight of howlers.

For the primary botanical plot (BP1), from which I would assess potential food sources, I selected an area of the forest that was moderately fragmented. BP1 was situated on a secondary trail located off the primary trail leading to the next village. The botanical plot was on relatively flat ground in a section of the forest that appeared to have been previously cultivated and contained a great deal of secondary undergrowth and many smaller, younger trees. This particular area of the forest was near a *milpa* in which howlers had frequently been sighted. In addition, one of the villagers indicated trees within this particular area in which the howlers had been observed sleeping, as well as other trees from which they had been seen eating.

The botanical plot measured 25 meters by 50 meters. Volunteers and I used survey tape to tag trees with circumferences greater than or equal to 10 centimeters

measured at breast height (breast height is equal to 1.3 meters), or CBH, and recorded the measurements for each tagged tree. I then converted the measurements to diameter at breast height, or DBH (diameter = circumference/3.1416). While the size of these trees is small and indicative of younger trees, I had discovered through personal communication with some of the Lacandon men that the Maya in Nahá are attempting to regenerate their forest. As such, I wanted to assess the breadth of the varieties of trees growing in a fallow *milpa* to determine future, as well as currently available, potential food sources.

After all of the trees in BP1 were measured and tagged, I hired two Lacandon, who each assisted in identifying and providing the Mayan name for the tagged trees (see Appendix A). With the Mayan names, I was able to determine the variety of tree species present and the relative density of each species. I attempted to find the scientific names for each tree species, using translations from the Mayan names, in order to identify possible food sources for *A. pigra*.

A previous study by Chapman *et al.* (1992) found basal area to be an indicator of fruit biomass. In addition, the total basal area of a tree species can indicate its relative importance within the botanical plot. I used basal area calculations ($BA = \Pi r^2$, where the radius is equal to $DBH/2$) to determine the relative coverage area ($RCA = \Sigma BA_x / \Sigma BA_T$, where BA_x is the basal area for a particular species and BA_T is the basal area for all species) for known food source trees.

I selected an area of forest off of a less traveled path and near the top of steep terrain for botanical plot number two (BP2). It was visually apparent that this area of forest contained less undergrowth and had a denser canopy than BP1. The trees in BP2 also appeared generally larger than those in BP1; it was evident that this area of the forest

had not been cultivated in recent years. I set the measurement of $DBH \geq 10$ centimeters, the standard measurement for botanical plot trees, as the comparison value between BP1 and BP2. Therefore, with the help of two assistants, I measured and recorded all trees with a $DBH \geq 10$ centimeters. I used these measurements to compare mean tree sizes based on DBH values for BP1 and BP2 and to determine and compare the total basal areas for both botanical plots.

Previous studies (e.g. Milton 1980) have suggested that *Alouatta pigra* require trees with a $DBH \geq 20$ centimeters to adequately support their weight as they feed and travel through the middle and upper levels of the canopy. While howlers will come down to the ground if necessary, they seem to prefer to stay in the trees (Milton 1980). In a final analysis of BP1 and BP2, I determined how many trees were in each botanical plot with a $DBH \geq 20$ centimeters and, further, which botanical plot had a greater density of trees this size. The greater the number of trees of this size, the less likely it is that the howlers would need to travel on the ground.

Random Fruit and Pod Sampling

Alouatta pigra are primarily folivorous primates; however, they supplement their diets to a large extent with fruits (Milton 1980 and Silver *et al.* 1998). Therefore, in addition to the botanical plot, I conducted a random sampling of fruits and pods within the forest. The purpose of this sampling was not to determine densities or abundance, but rather to provide a partial assessment of the variety of supplemental foods available to the howlers within the Nahá forest. As the tree canopy was inaccessible, I collected samples from the ground in various areas of the forest. I consulted one of the men from the

village to obtain identifications and Mayan names for the samples and to ascertain whether or not the howlers had been known to eat that particular food item.

Rain and Temperature Data

I collected data on daily rainfall accumulations and temperature ranges. Rainfall data were collected from June 18, 2006 through July 22, 2006. I added daily rainfall amounts over the course of a week to obtain weekly rainfall amounts. I obtained daily high and low temperatures, also from the period of June 18, 2006 through July 22, 2006. I recorded daily lows upon waking in the mornings and daily highs at dusk. I determined averages for both high and low temperatures over the course of each week.

Results

Botanical Plot

Botanical Plot 1 (BP1), a fallow *milpa*, contained 274 trees with a circumference at breast height (CBH) greater than or equal to 10 centimeters (diameter at breast height, or DBH, is greater than or equal to 3.18 centimeters). Two Mayan villagers assisted in naming 37 different species, of which I was able to determine genus names for 23 types and species names for 19 of the 23 genera (see Table 3.1). Relative densities were calculated for all species (see Table 3.1). The tree species with the highest density in BP1 was the *Trema* spp., or, in Mayan, the *tao* and the *hach tao* (both trees would be from *Trema* spp., as it seems that the Maya refer to a more mature *tao* as *hach tao*, or “real” *tao*).

Table 3.1: BP1 Species Names and Relative Densities.

Tree Name, Mayan	Tree Name, Scientific	Quantity	Relative Density
chech anish	Unknown	1	0.0037
t'oop che	“Flowering tree”	19	0.0696
k'uxu che	<i>Bixa orellana</i>	3	0.011
hach tao	<i>Trema</i> spp.	49	0.1795
pukte	<i>Bucida buseras</i>	3	0.011
bämäx	<i>Brosimum alicastrum</i>	9	0.033
chäk ya	<i>Dipholis salicifolia</i> or <i>Manilkara achras</i>	1	0.0037
tasi pom	<i>Bursera simaruba</i>	3	0.011
k'ik' che	<i>Castilla elastica</i>	1	0.0037
nä xa-ik che	Unknown	4	0.0147
babah	<i>Sapindus saponaria</i>	3	0.011
äh bahun (balamte or balum te?)	Unknown	3	0.011
säk balche	<i>Lonchocarpus</i> spp.	2	0.0073
yooch bach	Unknown	1	0.0037
tao	<i>Trema</i> spp.	121	0.4432
k'an chuluche	Unknown	1	0.0037
haban su	Unknown	1	0.0037
k'arok che	Unknown	1	0.0037
kuti	<i>Talauma mexicana</i>	3	0.011
chili trux	Unknown	1	0.0037
äh xidi	Unknown	1	0.0037
ixi (ix?) che	<i>Diospyros texana</i>	2	0.0073
ek balche	<i>Guatteria anomala</i>	3	0.011
muxän che	<i>Calathea</i> sp.	10	0.0366
chak tao	<i>Trema micrantha</i>	2	0.0073
che chäkän	<i>Croton draco</i>	3	0.011
käbä te	<i>Pachira acuatica</i>	5	0.0183
yache kab	<i>Ceiba</i> spp. or <i>Ceiba pentadra</i>	1	0.0037
uk' che	<i>Porophyllum punctatum</i>	1	0.0037
chöyok	<i>Cnidoscolus aconitifolius</i>	1	0.0037
wiich	“fruit”	5	0.0183
ch'alol	<i>Quercus</i> sp.	4	0.0147
muste'	<i>Clerodendrum ligustrinum</i>	1	0.0037
kukuchet achtu	Unknown	1	0.0037
chäkal	<i>Euphorbia lasiocarpa</i>	1	0.0037
k'ak' alche'	<i>Bourreria pulchra</i>	1	0.0037
le k'ado	Unknown	1	0.0037
Total		273	1.0007

The majority of the literature on the feeding ecology of and food sources for *Alouatta pigra* come from studies outside of the region of Chiapas, Mexico. An example of one of these studies is one that was conducted in Belize at the Baboon Sanctuary (Silver *et al.* 1998). Muñoz *et al.* (2006) examined the feeding ecology of *A. pigra* in a study they conducted on a cocoa plantation in Tobasco, Mexico. In addition, Milton (1980) conducted an extensive research project in the Panama Canal on Barro Colorado Island on the feeding ecology of *Alouatta palliata*, a species that can live in similar environments to *Alouatta pigra*. Gómez-Marin *et al.* (2001) conducted another study on *A. palliata* in Los Tuxtlós, Mexico. This study, though on *A. palliata* rather than *A. pigra*, is relevant to the current study in that Los Tuxtlós is closer in proximity to Nahá than are any of the other studies. However, the forest environment for all areas is divergent from that which is found around Nahá.

I found only five types of trees, from those for which I had been able to determine scientific names within my botanical plot, that were named as food sources within the four regions mentioned above: *Castilla elastica* (Gómez-Marin *et al.* 2001), *Lonchocarpus* spp. (Silver *et al.* 1998), *Brosimum alicastrum* (Milton 1980 and Gómez-Marin 2001, also mentioned in an earlier study conducted in Tikal, Guatemala by Coehlo 1976), *Bursera simaruba* (Gómez-Marin 2001 and Muñoz *et al.* 2006), and *Ceiba pentandra* (Milton 1980). Three of these studies determined relative densities, thus, I could compare relative density for three of the five species. Milton (1980) determined that *Ceiba pentandra* was a food source for howlers; however, she did not note the relative density for this species. The relative density for *Brosimum alicastrum* in BP1 was .033, or 3.3 percent; while for Milton's (1980) study, the relative density was .27

percent and for Gómez-Marin (2001), the density was 2 out of a total of 168 trees, or 1.2 percent. I determined the relative density for *Castilla elastica* as .37 percent, and in Gómez-Marin (2001) the relative density for this tree was .59 percent. Finally, the relative density for *Bursera simaruba* in BP1 was 1.1 percent. In Gómez-Marin (2001), it was 26.8 percent, and the most abundant tree within this particular study area. Muñoz *et al.* (2006) determined the relative density for *Bursera simaruba* in their study area to be .50 percent.

Through discussions with one of the Lacandon men, I established six other food sources for howlers within BP1. I determined scientific names for five of the six trees: *Quercus* sp., *Bucida buceras*, *Talauma mexicana*, *Cnidoscolus aconitifolius*, *Diospyros texana*, and k'arok che. I could not determine whether or not the remaining 26 trees within BP1 were food sources for howlers; however, it is possible that more of the species are definite or potential food sources. Of the eleven tree species identified, the most abundant food source was the *Brosimum alicastrum*, with nine trees in BP1 and a

Table 3.2: Relative Densities and Relative Coverages of Known Food Tree Species.

Food Tree Species	Quantity in BP1	Relative Density	Relative Coverage
<i>Brosimum alicastrum</i>	9	0.033	0.036770211
<i>Bursera simaruba</i>	3	0.011	0.004392706
<i>Ceiba pentandra</i>	1	0.0037	0.001279249
<i>Lonchocarpus</i> spp.	2	0.0073	0.001100769
<i>Quercus</i> sp.	4	0.0147	0.558185892
<i>Bucida buceras</i>	3	0.011	0.214907629
<i>Talauma mexicana</i>	3	0.011	0.007648604
<i>Cnidoscolus aconitifolius</i>	1	0.0037	0.001168937
<i>Castilla elastica</i>	1	0.0037	0.000588907
<i>Diospyros texana</i>	2	0.0073	0.003722284
k'arok che	1	0.0037	0.000179121
Totals	30	0.1101	0.829944309

relative density of 0.033, or 3.3 percent (see Table 3.2). The relative density of *Brosimum alicastrum* was over twice as high as the next most abundant tree, *Quercus sp.*, with four trees present and a relative density of 0.015, or 1.5 percent (see Table 3.2).

While *Brosimum alicastrum* had the greatest relative density for food source trees as determined by proportion of trees represented within BP1, it did not have the highest relative coverage as determined by the basal area of trees represented within BP1. *Quercus sp.* had just under half as many trees in quantity within BP1; however, these trees had a relative coverage of 0.558 due to large DBH values. Therefore, in terms of importance based on basal area alone, I determined that *Quercus sp.* was the most important food source tree in BP1. *Bucida buceras*, with three trees in BP1, had the second largest relative coverage at 0.215, followed by *Brosimum alicastrum* with a relative coverage of 0.037 (Table 3.2 and Figures 3.2 and 3.3). Chapman *et al.* (1992) have indicated that basal area is a predictor of fruit biomass, and, as such, it would seem

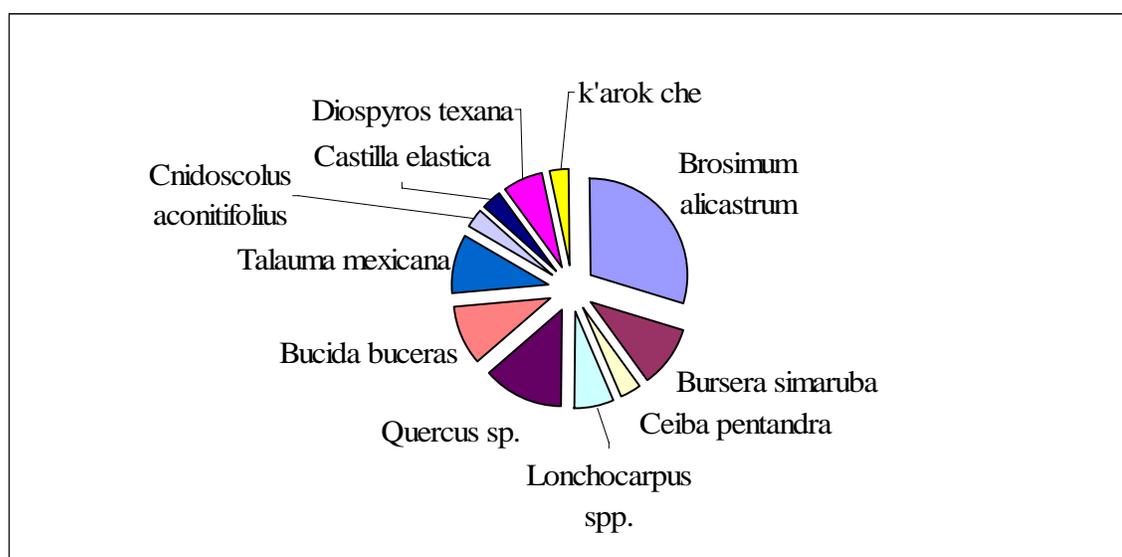


Figure 3.2: Density Comparison of Food Tree Species.

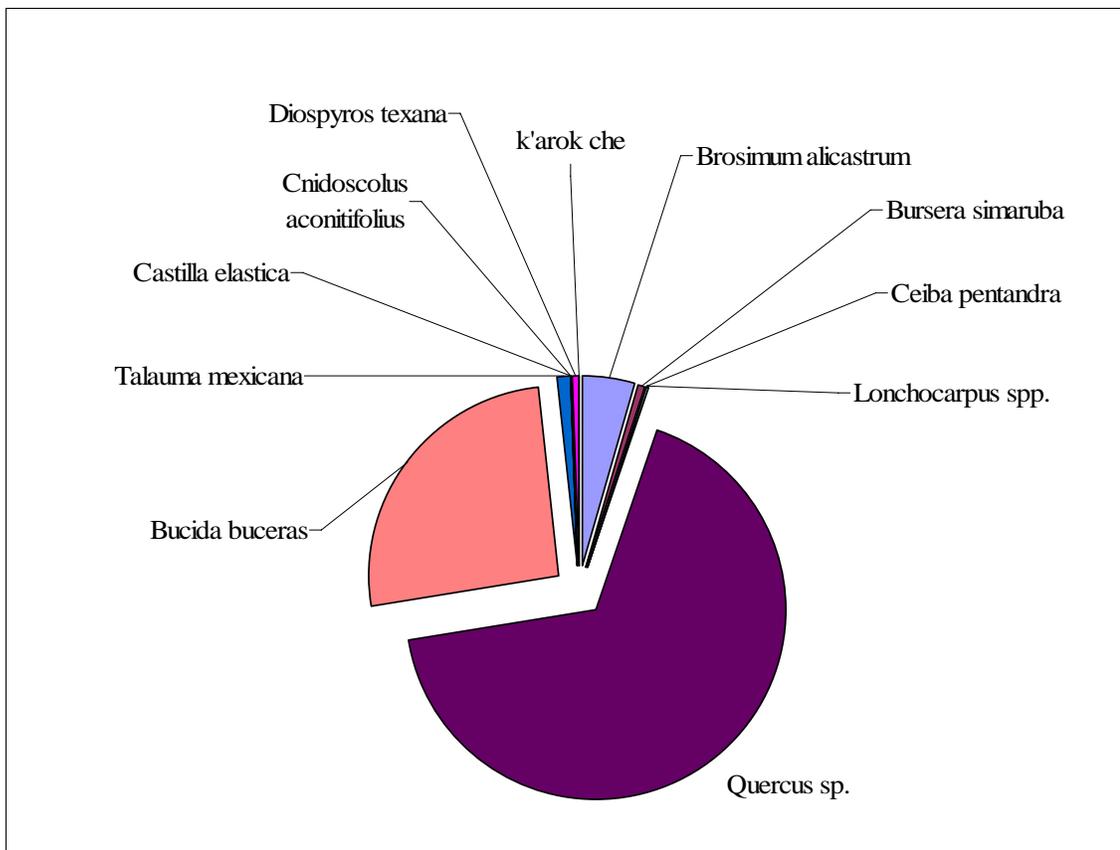


Figure 3.3: Relative Coverage Comparison of Food Tree Species.

that dominance based on basal area is a more important measurement in terms of food source than is dominance based on relative density. However, it is not clear *how* basal area predicts fruit biomass, nor is it entirely clear that this prediction holds for the entire fruiting season or only for the period of time that a species is actually producing fruit. Since fruit production is not consistent across genera, the above delineations are important and need to be clarified. Additionally, future research on the amount of time howlers spend feeding on each of these two species would be beneficial for comparing food source dominance to howler food preference within the Nahá region.

Aside from the information on potential current and future food sources, I compared BP1 to a second botanical plot, BP2. When I eliminated trees within BP1 that

were < 10 centimeters DBH, I found that BP1 contained 67 trees with a DBH ≥ 10 centimeters. Eighty-four trees within BP2 had DBH measurements ≥ 10 centimeters. The mean tree size for the 67 trees in BP1 was 21.486 centimeters, while the mean tree size for the 84 trees in BP2 was 24.602 centimeters. It is evident that not only are there more trees in BP2 with DBH ≥ 10 centimeters, but the mean size of these trees is also greater. I tested for significance in the difference between means using a two-tailed t-test. The results of the test demonstrated that the means were significantly different, with $t = 18.953$, $df = 149$, and $P = 0.05$.

I calculated the total basal area for trees with DBH ≥ 10 centimeters in each botanical plot to determine which botanical plot had greater tree coverage. The total basal area for BP1 was 53101.06 centimeters squared and the total basal area for BP2 was 64128.79516 centimeters squared. Thus, the total basal area for BP2 was 17.2 percent greater than the total basal area for BP1. Therefore, the botanical plot located in the fallow *milpa*, BP1, had not yet developed to the level of maturity seen in BP2 based on number of trees with DBH values ≥ 10 centimeters and the mean DBH and total basal area for those trees.

In previous studies (e.g. Milton 1980) on the feeding ecology of *Alouatta*, the minimal DBH value used in botanical plots has been 20 centimeters, as this size is sufficient to support the weight of one or more howlers between 5 and 9 kilograms. In a final analysis and comparison between BP1 and BP2, I determined the number of trees in each botanical plot with a DBH ≥ 20 centimeters. BP1, the fallow *milpa*, contained only 15 trees with a DBH ≥ 20 centimeters. The second botanical plot, BP2, contained 34

trees with a DBH \geq 20 centimeters, more than twice the number found in BP1. BP2 had more trees that were of a sufficient size to support the weight of howlers.

Random Fruit and Pod Sampling

I collected a total of 15 types of fruits or pods from various areas within the forest surrounding Nahá. I asked one of the Lacandon men in the village to name the fruits and to identify which ones were eaten by howlers. I was able to determine the scientific names for 7 of the 15 species. Of the 15 fruits and pods identified, the villager named 12 species as a food source for howlers. Seven of these food source fruits were from tree species that were also found in BP1 (see Table 3.2).

Table 3.3: Random Fruit and Pod Sample.

Mayan Name	Scientific Name	Food Source
k'ute che	<i>Cedrela odorata</i>	Yes
k'ik' che	<i>Castilla elastica</i>	Yes
ton kuk	Unknown	Yes
chudan	Unknown	Yes
k'arok che	Unknown	Yes
k'an che	Unknown	Yes
chulan	Unknown	Yes
tuch	<i>Ficus sp.</i>	Yes
ix che	<i>Diospyros texana</i>	Yes
chäyok	<i>Cnidocolus aconitifolius</i>	Yes
päpox	<i>Psidium guajava</i>	Yes
säk balche	<i>Lonchocarpus spp.</i>	Yes
k'ume che	Unknown	No
k'ado che	Unknown	No
nuxman	Unknown	No

Rain and Temperature Data

The total rainfall for June 18, 2006 through July 22, 2006 was 560.5 millimeters, and was, according to the local Lacandon, high for that particular time of year (see Figure 3.4 for weekly totals). In addition, the pattern of rainfall was unusual for that time of year. During the study period, rain fell during daylight hours rather than overnight, as is the case in most years (personal communication from Jon McGee and the local villagers). The average weekly temperature high for June 18, 2006 to July 22, 2006 was 33.88° Celsius, and the average weekly temperature low for the same time period was 18.57° Celsius. The overall average temperature over the course of the study period was 26.43° Celsius (see Figure 3.5 for weekly averages), just above the average indicated for the Montes Azules Biosphere Reserve.

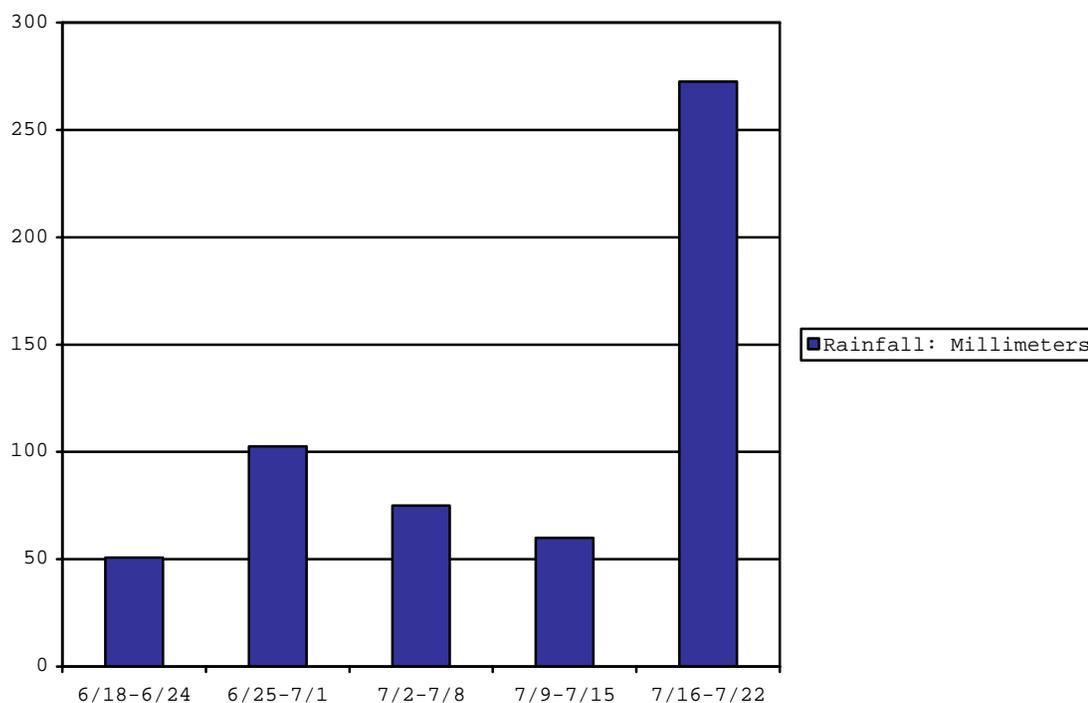


Figure 3.4: Weekly Rainfall Totals.

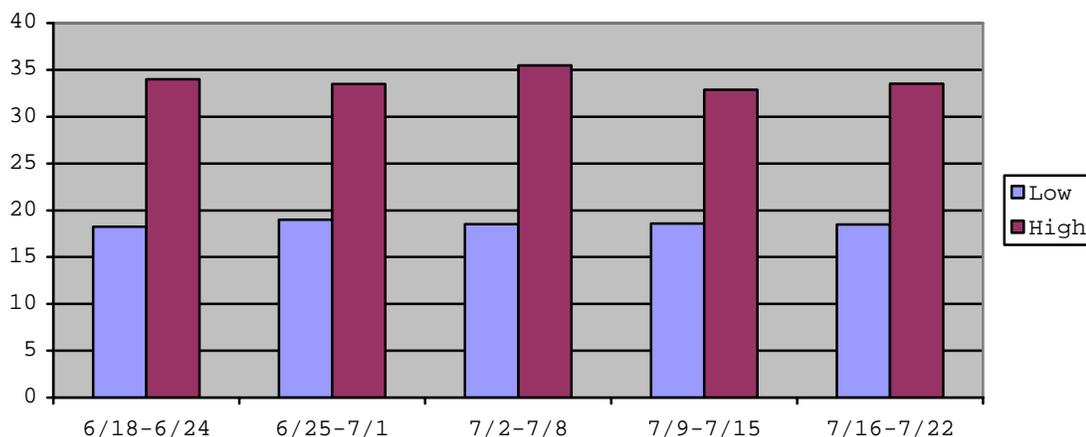


Figure 3.5: Weekly Average Temperatures in Degrees Celsius.

Discussion

There are two inherent challenges in determining potential howler food sources in the Nahá rain forest at this time: the first of these is the lack of botanical censuses and analyses in this region, and the second challenge is the language barrier. Given differences in the types of species found in the studies conducted in varying regions (Milton 1980, Silver *et al.* 1998 and Muñoz *et al.* 2006), there are potentially extensive regional differences in the types of tree species that rain forests contain. As such, it is difficult to fully and reliably determine the howler diet for populations from Nahá based on studies of howler diets in other environments, especially given the howlers' flexibility in diet composition (Milton 1980 and Silver *et al.* 1998). In addition, translations from the Lacandon Mayan names for trees to the scientific, or even the common, name for tree species are extremely limited. As there have been no botanical censuses and analyses in the Nahá forest, it follows that there have also been no concerted efforts between botanists and the few anthropologists who speak Lacandon Mayan to provide an

extensive list of translated species names for existing species in the region. There are, however, two types of trees from howler environments within various regions that appear repeatedly in the literature: trees from the genus *Ficus* (fig trees) and *Brosimum alicastrum* (breadnut trees).

Both *Ficus* and *Brosimum alicastrum* seem to be staples in the howler diet. There are regions in which one type of tree is more prominent than the other, for instance, *Brosimum alicastrum* in Guatemala (Coehlo *et al.* 1976) and *Ficus* trees in Belize (Silver *et al.* 1998). Nevertheless, one or both species are always present in areas in which *A. pigra* troops are established. While howlers have flexibility in the overall composition of their diets, it does appear that there is a heavy reliance on these two species as a primary dietary component. Their prevalence in the howler diet may be in part due to the physical makeup of the trees. *Ficus* trees tend to be asynchronous in their fruiting cycles (Milton 1980), allowing for access to fruit at varying times throughout the year. Additionally, Milton (1980) reported that *Alouatta palliata* on Barro Colorado Island eat all parts of the *Brosimum alicastrum*, meaning the leaves, fruit and flowers. Because Silver *et al.* (2001) suggest that *Alouatta pigra* and *Alouatta palliata* do not vary significantly in their diet composition; it is very likely that *A. pigra* also consume all parts of the *Brosimum alicastrum*, including mature and immature leaves, flowers and fruits.

The botanical plot, BP1 did not contain any species of *Ficus*, inasmuch as I can ascertain from available translations, but it did contain quite a few *Brosimum alicastrum*. Within a 25 meter by 50 meter botanical plot, *B. alicastrum* had the highest density of the known food source trees. This might explain the reason why villagers reported seeing howlers in this particular area of the forest, despite a higher level of fragmentation than

was seen in BP2. While seven of the nine *B. alicastrum* in BP1 were not large enough to support the weight of howlers, if neighboring trees were large enough, it is possible that howlers could reach the fruit and leaves on the *B. alicastrum* without relying on that tree to support its weight. In addition, it is important to note that the remaining seven trees will eventually be of sufficient size to support the weight of howlers, potentially making them significant future resources.

While BP1 provides evidence of a high density of *B. alicastrum* in the region, it is important to note that I situated BP1 within the area of a fallow *milpa* and, thus, BP1 is not necessarily reflective of species represented in all regions of the forest. However, it is probable that *B. alicastrum* is present in many other areas as well, given the Maya practice of swidden agriculture in which fallow and cultivated *milpa* plots are rotated (Cowgill 1962 and Diemont *et al.* 2006). While the Lacandon in Nahá have begun to rely less on an agricultural economy and more on a cash based economy (McGee 2002), all of the villagers with whom I spoke still generally worked one *milpa* (see Chapter IV). As such, it is reasonable to assume that many of the *milpas* cultivated in previous generations have been left to lie fallow for a number of years. If these areas remain uncultivated, growing populations of tree species will eventually mature to sizes seen in BP2. If *B. alicastrum* can frequently colonize open areas and can grow in clumped and self-regenerating groups as has been suggested (Peters 1983), then other areas of the Nahá forest are also likely to contain higher densities of *B. alicastrum*. However, more botanical research needs to be conducted to verify this assumption.

In addition to *B. alicastrum*, I was able to determine seven other food sources from the combined botanical plot and fruit and pod sampling data. Given that I relied on

information from studies conducted outside of the region and from information given to me by the local Lacandon, the list of available food sources *Alouatta pigra* in the Nahá rainforest is more than likely far from complete. Silver *et al.* (1998) identified a total of 74 plant species that the howlers ate, 53 of which were tree species and 21 of which were epiphytes or lianas. Milton (1980) found 109 food source species for *Alouatta palliata* on Barro Colorado Island. Therefore, it is clear that howlers eat a wide variety of foods. Both studies also noted that howlers ate leaves (both mature and young), fruit and flowers (Milton 1980 and Silver *et al.* 1998). On the other hand, Muñoz *et al.* (2006) identified only sixteen plant species eaten by howlers on a cocoa plantation in Comalcalco, Mexico, though they also stated that howlers ate multiple parts of different food source species. The Muñoz *et al.* (2006) study found far fewer food source species than did the other two; however, the number found even in this study is more than twice the number I was able to identify in the Nahá forest. The above studies suggest that there are likely many more species available to and utilized by howlers as food sources within the Nahá forest.

In order for howlers to succeed in the Nahá rain forest, it is necessary for them to have access to adequate food sources to support their energy requirements (Coehlo *et al.* 1976). Thus, if the current howler populations are expected to grow and thrive, they must be able to obtain enough food in their diets to successfully reproduce. According to Coehlo *et al.* (1977) for a howler group that contained one adult male and seven lactating females, the total amount of food need to meet the daily diet requirements of the male is 537 grams, while the daily requirement for all the females is 5,072 grams. Additionally, Milton (1979) suggests that howlers need to balance their diet between the protein that is available in leaves and the nonstructural carbohydrates that are found fleshy fruits. In

other words, if reproduction is to be successful for howlers, individuals must be able to consume enough food in their daily diets to fulfill quantitative and nutritional requirements. Both availability and access are key components in the ability for howlers to be successful; if one or the other is lacking, the fledgling howler populations in Nahá will decline rather than grow.

Conclusion

The Nahá rain forest exhibits a range of forest conditions, from cultivated *milpas* to tracts that more closely resemble primary forest growth. Levels of fragmentation vary throughout the region; though the level of deforestation in areas adjacent to Nahá is high (see Figure 3.1). The present study provides a preliminary indication of food resources available for populations of *Alouatta pigra* in the rain forest surrounding Nahá. One of the staple food source trees for howlers is the *B. alicastrum*. This tree species was present within a botanical plot inside of a fallow *milpa*. While the majority of the *B. alicastrum* trees found within BP1 do not meet the size requirements needed to support the body weight of individual howlers, those trees are potential food sources for future populations of howlers. I determined a total of seven food source trees for *Alouatta pigra*; however, in-depth botanical analysis in the region is much needed in order to obtain a more complete inventory of plant species and to more adequately determine the likelihood for the success of the howler populations in the area.

CHAPTER IV

THE LACANDON PERSPECTIVE

Introduction

The potential for the success of any primate species relies not only on adequate available resources, but also on the attitudes and practices of the humans with which primates must coexist. Primate conservation policies must take into account the human component in the environment of wild primates, especially given the ever-increasing human population and the resultant wide-spread deforestation (Lizarralde 2002 and Strier 2002). Human and non-human primates are often sympatric, and humans indirectly and directly affect non-human primates through the use of the physical environment and through the consumption, trade and social use of primates (Fuentes and Wolfe 2002 and Fuentes 2006). To disregard this coexistence is obviously detrimental to primate survival. Therefore, the human perspective needs to be considered in primate conservation so that efforts benefit both human and non-human primates (Cormier 2002).

The challenge in conservation of non-human primates stems from the technologies and economies of the people with whom primate species come into contact. Primates frequently share space and resources with humans populations living in impoverished regions, where ready access to guns and ammunition combined with hunger lead to dramatic declines, and even extinction, for primate populations (Fuentes and Wolfe 2002). Humans and primates in these regions are similarly faced with the

reduction of habitat and food resources (Fuentes 2002), placing additional pressures on the environment and on the human and non-human primates that rely on the environment for survival. Human politics, global and local economies and land use practices have far-reaching effects on primate populations (Fuentes and Wolfe 2002 and Louden *et al.* 2006).

Habitat loss is perhaps the biggest threat to primate species survival (Alvard *et al.* 1997 and Cormier 2002). Habitat loss can occur from natural disasters (e.g. Pavelka and Behie 2005), though the primary issue of concern across the globe is tropical deforestation at the hands of humans (O'Brien 1998a). Logging has been deemed a primary cause in the deforestation of the Selva Lacandon as a whole, with exploitation beginning in the late 1800s, prior to the onset of modern logging practices in the 1960s (O'Brien 1998a). Timber companies exploited the Lacandon jungle specifically for approximately 20 years, until highly valued trees, and even many less valued trees, were nearly stripped from the forest (Kashanipour and McGee 2004), thereby contributing significantly to the fragmentation of the Lacandon forest.

In addition to habitat loss, human predation of primates is another leading threat to species survival. Subsistence hunting of primates by indigenous peoples is not necessarily detrimental in and of itself; it is when hunting extends beyond subsistence to profit sales (Cormier 2002), or when hunting is combined with population growth and habitat loss, that primate survival is threatened (Peres 2001 and Liazarralde 2002). *Alouatta pigra* are considered large bodied primates in the Neotropics, and, thus, are more prone to human predation (Peres 1990 and Cormier 2006). The over-hunting of a species, regardless of whether the hunting is for subsistence or otherwise, can lead to

population depletion or to local extinction for the hunted species (Peres 1990 and Bodmer *et al.* 1997).

Within the Nahá forests, *A. pigra* had been locally extinct since the early 1980s due to the hunting and deforestation practices of the Lacandon Maya (Jon McGee, personal communication) as well as habitat loss that can be attributed to the deforestation practices of loggers (Kashanipour and McGee 2004). Therefore, the possibilities for the success and for the conservation of a new population of howlers in this region would largely depend on a shift in the local perceptions and practices from what they had been twenty-five years ago. In order to more completely understand the current status of, as well as the potential for success for, returning populations of howlers to the Nahá forest, it is necessary to determine current Lacandon perceptions towards howlers as well as current forest use levels and hunting practices.

Methodology

I created a set list of interview questions and conducted interviews with some of the local Lacandon Maya. I asked of all interviewees each of the questions on the list (see Table 4.1). Interviewees were individuals with whom I had become familiar over the course of my study and with whom there had developed a level of mutual trust. With the assistance of an interpreter, I interviewed a total of eight individuals representing three generations. There were three females and one male over the age of sixty, one male and one female approximately in their forties, and one male and one female in their early twenties. Interviews were conducted with two individuals at one time, with all but one pairing being husband and wife. Two of the elder women interviewed were co-wives of

Table 4.1: Interview Questions.

<ol style="list-style-type: none"> 1. Why did the howlers disappear from Nahá? 2. When did the howlers return? 3. Have you seen the howlers? Where? How many? 4. When do the howlers call and from which direction? 5. Do they call more at certain times of the year? 6. What do the howlers eat? 7. Do you use trees from the forest? Which ones? 8. How many <i>milpas</i> do you have? 9. Does anyone in Nahá hunt howlers now? 10. Would you like people to come to Nahá to see the forest and the howlers?
--

the now deceased, spiritual leader of the village. As Lacandon men tend to go into the forest more frequently than Lacandon women, the men provided the most detailed information. The two elder women, however, perform all of the work for their household, including working their *milpas* and gathering firewood; therefore, they had ample occasion to be in the forest. Interviews were recorded with the permission of the interviewees.

Results

I asked the interviewees the same set of questions (see Table 4.1) and all of the respondents' answers were relatively consistent. All respondents indicated that the howlers disappeared from Nahá either due to hunting pressures or to deforestation. One

woman and one man over the age of sixty specified both hunting and deforestation as causes for the disappearance of howlers. The man and woman in their twenties implicated deforestation as the primary cause and stated specifically that there were fires in their forest that drove the howlers out. Due to the manner in which the Lacandon Maya have historically conceptualized time, I was unable to determine through my interviews a time frame for the disappearance of the howlers. However, R. Jon McGee (personal communication), an anthropologist who has conducted research in Nahá since 1980, indicated that populations of howlers were on the decline shortly after his first visit to the village and were absent by the early to middle 1980s.

All of the villagers that I interviewed stated that the howlers were now returning to their forest because people in surrounding areas were cutting down the forest, while the Lacandon in Nahá have made efforts to improve their forest conditions. Furthermore, the villagers no longer hunt or consume monkeys, a decision according to one respondent, made in part because tourists are interested in learning about the monkeys. The younger generations of Lacandon seemed to be more familiar with the Roman calendar, likely due to an increase in the number of individuals who have learned Spanish, were educated in the village primary school (both males and females), and who interacted with tourists (McGee 2002). As such, I was able ascertain an approximate time frame for the return of *A. pigra* to the Nahá forests during the course of my interview with two villagers who have three children who attend high school in the city of Palenque and who have built a business for themselves based largely on tourism. Both individuals indicated that the howlers had returned to the Lacandon forest approximately two years ago, which, from the time of my visit to Nahá, would have been in 2004.

When asked whether or not they had seen the howlers, all of the respondents verified that they had seen between six and eight at one time, either while in their *milpas* or while in the forest. One man and one woman stated during a previous conversation that they had also seen howlers in their fruit trees, which are located at the forest's edge near their home. Each respondent indicated that they had seen at least one infant. However, the respondents informed me that the howlers were generally seen and heard during the dry season months of March, April and May; during the remainder of the year, they dispersed further into the forest. One individual stated that the howlers were heard more during the spring because that is when the howlers preferred food tree in this region, the *bämäx* (*Brosimum alicastrum*), is fruiting. Others indicated that the howlers called less often during the rainy season, therefore, when the rains begin in June, the howlers become silent. Responses regarding the time of day in which howler vocalizations could be heard ranged from morning and afternoon to mid-day, when the sun was directly overhead, and eight or nine o'clock at night. One individual indicated that the howlers vocalized when they were traveling. Howlers seemed to call most frequently from the forest areas to the south-southeast and the north-northeast of the village, as indicated from gestural and verbal responses from interviewees. This is consistent with my own experiences, as all of the vocalizations that I heard were also from these two areas of forest.

In an attempt to discover more with regards to what the Lacandon know about howler ecology, I asked interviewees for information on howler food sources. All respondents named two sources, one specific and one general. They specifically named the *bämäx* (*Brosimum alicastrum*) tree as well as fruit in the general sense. In addition,

two men and one woman mentioned *kolpol* (scientific name unknown), two men and one woman said that the howlers ate from *balche* (*Lonchocarpus* spp. or *Guatteria anomala*) trees, and two men named the *chicle sapote* tree (*Manilkara zapota*) as a howler food source. The following food sources were mentioned by one respondent each: *nal* (corn: *Zea mays*), *boox* (bananas: *Musa* sp.), *oop* (custard apple: *Annona squamosa*), *chimon äh* (fig tree: *Ficus* spp.), *fruitas de aqua*, *hach buul* (bean plant: *Phaseolus* spp.), *uva* (wild grapes: *Vitis* sp.), *k'oho*, *chäk ya* (*Dipholis salicifolia* or *Manilkara achras*), *chechen* (*Metopium brownie*), and *ch'alol* (acorn tree: *Quercus* sp.). One individual stated that the howlers ate everything. Another indicated that there were an abundance of trees with fruits from which the howlers ate and that they would travel through the trees tasting different foods. If the howlers liked the taste, they continued eating, while if they did not like it, they would move on to the next tree. One respondent stated that one of the trees in which howlers sleep is *kud che* (scientific name unknown).

I asked the Lacandon whom I interviewed what trees they used within the forest in order to assess which resources the howlers share with humans in the vicinity of Nahá. One couple stated that they used *pukte* (*Bucida buseras*), *chicle sapote* (*Manilkara zapota*) for arrows, *chicle* for gum inside the house, and *puna* (mahogany: *Swietenia macrophylla*) for building furniture. They claimed not to use the same trees for food that the howlers use for food. Another couple stated that they used all of the trees in the forest including *puna* (mahogany: *Swietenia macrophylla*) and *ch'alol* (acorn trees: *Quercus* sp.). The youngest couple stated that they did not use the trees in which howlers eat or sleep and only used *puna* (mahogany: *Swietenia macrophylla*) for building construction. The two elder women did not seem to understand the question, and instead

continued to discuss the trees that the howlers used. In addition to using trees from the forest, all three husband-and-wife couples had one large *milpa* each, while the two elder women worked three *milpas*.

At the beginning of each interview session, the respondents established that hunting pressures were, at least in part, responsible for the local extinction of *Alouatta pigra* in the forests surrounding Nahá. I asked the interviewees whether or not anyone still hunted howlers and all of the respondents replied that the Lacandon in Nahá no longer hunt monkeys of any species. All of them re-stated that hunting had occurred in the past, but did not occur presently. One couple stated that they now guarded the howlers and that they wanted more of them to come to their forest. The elder women admitted that at one time they had liked consuming howlers, but that now, however, they felt bad for the howlers and no longer ate them. Another couple seemed to place the blame for hunting on other Maya groups, and furthermore stated that, while other Maya were destroying their forests, the Lacandon were now taking care of theirs.

For my final question, I asked interviewees if they approved of tourists coming to visit their forest and to see the howlers. All respondents enthusiastically stated that they would like to have tourists come to Nahá. One man indicated that he was pleased that tourists were interested in knowing more about the howlers.

As an interesting note, all but two respondents indicated that they had also seen spider monkeys (*Ateles geoffroyi yucantensis*) in their forest. One male said that he had seen a total of three spider monkeys, but that he had not seen them for two months. Another male said that while they used to hunt spider monkeys as well as howlers, this is a practice in which they also no longer engage.

Discussion

Taken at face value, the results of these interviews would seem to signify a promising future for the survival of *Alouatta pigra* in the Nahá forest. The Lacandon claim to no longer hunt howlers, or spider monkeys for that matter, and even indicated that they desired more monkeys in their forest. Interviewees generally asserted that they did not tend to utilize forest resources also used by howlers, though their responses somewhat contradicted this assertion when asked to specify the forest trees that they used. However, the number of trees identified was small compared to the number of trees named as resources for howlers. Furthermore, as I indicated in Chapter III, there are likely more potential howler resources than those that I discovered over the course of my project. Additionally, *bämäx* (*Brosimum alicastrum*), a primary food source for howlers, was not named as a personal resource by any of the interviewees. While in areas within the Yucatan, *B. alicastrum* is a tree species grown in home gardens specifically for the purpose of livestock feed (Gillespie *et al.* 2004), Kashanipour and McGee (2004) do not list *B. alicastrum* as a home garden tree for the Lacandon, nor do they list it as a medicinal plant. Given that *B. alicastrum* was relatively abundant in BP1, that it tends to grow well in cleared areas (Peters 1983), and that the Lacandon do not seem to use it as a resource, it is likely that *bämäx* is currently, and will remain, available largely for howler consumption.

In naming the plants and trees that they used, the interviewees seemed to name only those trees that perhaps they had occasion to use more frequently, or those whose use required the felling of the tree. The interviewees did not name medicinal plants or trees, perhaps because they use them infrequently or perhaps because they use only a

particular part of the tree and do not need to cut down the tree. Kashanipour and McGee (2004) identify three trees that are used by the Lacandon for medicinal purposes: *k'uh* (*k'ute*) *che* (*Cedrela odorata* L.), of which they use the leaves; *uva* (*Vitis* spp.), of which they use the roots; and *ton k'uk* (scientific name unknown), of which they use the leaves and the fruit. Only the use of the *Vitis* spp. would be destructive to the whole plant since to access the roots the Lacandon would need to uproot the plant. The Lacandon use of these plants for medicinal purposes inherently limits the frequency with which each plant is utilized. Though still used to some extent, medicinal plant treatment is further reduced due to the availability of a range of medical resources through the clinic in Nahá and through health care clinics and hospitals in Palenque and San Cristobal de las Casas (Kashanipour and McGee 2004).

Historically, logging has been an issue in the Lacandon forest (O'Brien 1998a and Kashanipour and McGee 2004), though it appears less of an issue today. One interviewee specifically stated that the Lacandon would like to regenerate their forest. Forest trees are currently used for building; however, the patches of forest that the Lacandon use are small and trees are selectively cut. During the course of my stay in Nahá, I came upon a number of these small logging sites in the forest, and new ones appeared regularly. It seems that the level of new construction led to the increase in the number of logging areas in the forest; though I do not know whether or not the level of construction that I witnessed is a seasonal activity or an unusual occurrence. In addition to new logging sites, I regularly came upon previously logged sites that appeared to have fallen into disuse. Within these sites, I frequently witnessed entire trees remaining where they were felled, perhaps because they were deemed unusable for some reason or perhaps

because they were felled in order to get to a more desired tree or were intended for later use. Jon McGee (personal communication) indicates that the Lacandon at times use trees on repeated occasions. Despite the presence of multiple logging sites, they all appeared to be for Lacandon use and not for commercial use; furthermore, each individual site was small in scale. I am not certain as to how often the Lacandon in Nahá construct new homes or buildings or how often they remodel those they have. Future visits to the village would aid in determining whether the level of building that occurred in the summer of 2006 is a novel situation, or whether this level of construction is prevalent in present day Nahá on a regular and predictable basis.

Presently, the biggest threat to the Lacandon forest appears to be the encroachment into the forest by neighboring groups clearing the forests for large-scale commercial agriculture and cattle pasture (O'Brien 1998a, McGee 2002 and see Figures 2.1 and 3.1). At least one respondent discussed the fact that the Lacandon were attempting to regenerate their forest. This individual informed me that, at one time, they had allowed others to come in and cut their trees down, but that eventually the villagers realized that their forest was being destroyed and that they wanted to restore it, along with the wildlife that used to exist in the forest. This same interviewee mentioned, on a separate occasion, that other groups of non-Lacandon Maya continually attempted to take away the Lacandon forest by cutting down their trees and using the land for themselves. Given ongoing encroachment issues, this individual's concern seems warranted. Surrounding areas have been cleared for use in a manner that does not allow for soil regeneration; therefore, the soil eventually becomes depleted and can no longer support growth, including the grasses needed for cattle grazing (O'Brien 1998a). As this process

continues to happen, it will become increasingly difficult for the Lacandon in Nahá to hold onto their land.

Hunting, at least for the moment, does not appear to be an issue in the potential success of *Alouatta pigra* populations within the Lacandon forest, though this threat in all likelihood continues in surrounding areas. Within Nahá, however, wealth has generally increased in Nahá as the younger generations participate in the tourist industry and purchase their food rather than grow or hunt it (McGee 2002). As long as the tourist industry on which many in this community rely continues to provide a means for existence, then it is likely that the Lacandon will not have the *need* to hunt. An additional motivation to preserve the howlers and to continue to abstain from hunting them lies in the Lacandon's interest in the tourist industry, and the subsequent realization that tourists would want to see howler monkeys, as well as other fauna, in their visits to Nahá.

While tourism can have varying effects on wildlife populations, with the potential for great disruption in howler ecology and harm to individuals and populations (e.g. Grossberg *et al.* 2003 and Treves and Brandon n.d.), ecotourism, *if* managed responsibly, can potentially be an appropriate conservation method (Yu *et al.* 1997 and Grossberg *et al.* 2003), especially in an area that is already beginning to promote active tourism. The challenge in Nahá is to instigate proper management that incorporates sustainability for the howlers and the forest before tourism in the area gets out of control. At this time, there are no paved roads into Nahá, thus limiting the numbers of tourists coming to the area and reducing the effects of tourism on the rainforest and on the howlers. This situation will likely not remain the same in years to come, therefore, conservation strategies need be considered sooner rather than later. With the territories of *Alouatta*

pigra populations shrinking and the numbers of howlers also in decline, now is the time to consider all potential conservation approaches in the areas where howlers exist.

Conclusion

The Lacandon Maya in Nahá are taking strides to regenerate and preserve their forest and to protect the wildlife, especially, it seems, the howler and spider monkeys that are beginning to return. Though the forest is fragmented, if ongoing repair continues and howler populations continue to grow, Peres' (2001) study suggests that the approximate 10,000 ha of Lacandon forest (Kashanipour and McGee 2004) might be enough to maintain species diversity as long as human predation is minimal to nonexistent. Nevertheless, the Lacandon have an uphill battle, and one that likely cannot be won without concerted effort from conservation agencies and the Mexican government. Long-term preservation of the forest, and hence the howlers in the Lacandon forest, will likely depend on more intensive and extensive conservation policies within the region. However, these policies can only potentially be successful if the larger political, economic, cultural, and environmental conditions outside of the Lacandon forest are addressed, including, and perhaps most importantly, the conditions within the neighboring communities.

CHAPTER V

CONSERVATION IMPLICATIONS AND FUTURE DIRECTIONS

Conservation Implications

The future for *Alouatta pigra* is an uncertain one. The fact that the species has been listed in the IUCN Redlist of Threatened Species (2003) as endangered should raise a red flag for conservationists and primatologists. One of the major challenges in the conservation of this species is the general lack of in depth knowledge and understanding regarding *A. pigra* ecology (Gómez-Marin *et al.* 2001 and Estrada *et al.* 2004). While the amount of data is increasing, conservation efforts should be simultaneous with research efforts, as current threats to howlers will most likely continue to disintegrate rather than improve in the immediate future. There are two categories of threats to primates in general: threats to the primates themselves and threats to the environment in which primates live (Mittermeier *et al.* 1993). The most effective conservation efforts focus on both types of threats.

The biggest factor affecting primate populations globally is the loss of habitat that has been the result of the human population explosion (Terborgh 1986, Estrada and Coates-Estrada 1988, Arámbulo III and Ruíz 1993, Mittermeier *et al.* 1993, Paulo 1993 and Fuentes and Wolfe 2002). This is especially true in developing countries that are situated in the tropical forests where a majority of primate live (Mittermeier *et al.* 1993). The rain forests in Chiapas are rapidly disappearing (Estrada and Coates-Estrada 1984,

Estrada and Coates-Estrada 1988 and O'Brien 1998a), leading to a reduced habitat for primate species in that region, including *Alouatta pigra*. While howlers are found in fragmented forests and are, at least in the short term, successful in these environments (Crockett 1998 and Estrada *et al.* 2002b), the long term effects of fragmented forest conditions on howler populations needs to be more fully investigated.

Forest conservation efforts that have a focus on improving the size and quality of forests and creating or maintaining corridors that lead from one forest fragment to another will likely prove beneficial for black howler survival. Forest islands are created when forest fragments are entirely cut off from other forest areas, and the effects on howler populations are potentially detrimental. Estrada and Coates-Estrada (1984) notes that in the early 1980s forest islands resulted in declining howler populations, with groups consisting of two to four individuals rather than the higher numbers that can be seen in healthier environmental conditions. Crockett (1998) also suggests that the number of howlers found in any given forest fragment is positively correlated with the size of the fragment.

Howlers in Chiapas are found within the region known as the Selva Lacandona. While the Selva Lacandona prior to the mid 1900s consisted primarily of continuous forest, a large portion of the Selva Lacandona today consists of fragmented regions (O'Brien 1998a). Medellín (1994) indicates the importance in conserving the Selva Lacandona for its richness in biodiversity. Howlers in the Nahá forest would benefit from forest conservation efforts in the Selva Lacandona, especially if, in the process, large corridors can be maintained that link the Nahá forest to larger forested areas such as the Montes Azules Biosphere Reserve. According to the GES, broad corridors currently

exist, and would provide howlers in the Nahá forest more viable territory in which to establish troops and would allow for dispersal to occur.

Corridors can have some negative effects, such as an increase in disease transmission, an increase in the chance of fire spreading from one region to the next, and an increase in edge effects and the corresponding human extraction of accessible forest products (Cowlshaw and Dunbar 2000). According to R. O. Bierregaard Jr. and V. H. Dale (Marsh 2003), species types along the forest edges can differ from those within the forest interior. However, without corridors linking forest fragments to other forest regions, dispersal cannot occur and howler populations eventually suffer the genetic effects of inbreeding. Inbreeding reduces genetic diversity and results in a lack of heterozygosity (Cowlshaw and Dunbar 2000), thereby decreasing the fitness of the population. *Alouatta pigra* already exhibit higher levels of homozygosity, a consequence of apparent population bottlenecks and epidemics leading to dramatic population reduction (Crockett 1998 and Cowlshaw and Dunbar 2000). Inbreeding would only serve to further decrease heterozygosity in howlers.

Hunting is another principal threat to primate conservation (Terborgh 1986, Mittermeier *et al.* 1993, Horwich 1998, Peres 2001 and Marsh 2003). Hunting primates in forest fragments can decimate the local population (Crockett 1998 and Peres 2001). Larger animals, in general, are more at risk from hunting pressures (Terborgh 1986), and in the Neotropics, howlers are among the larger bodied primates. Roads allow easier access to the forest and increase the likelihood that hunting, whether legal or not, will occur. *Alouatta pigra* are hunted in various areas in Chiapas and regulations against the indiscriminant hunting of howlers are not enforced (Estrada and Coates-Estrada 1984).

Therefore, even when forest conditions are maintained at levels that allow for viable populations, the majority of forest areas are fragments, and thus increase the threat of extinction for howlers.

Any howler troops moving into the Nahá forest will experience benefits perhaps not seen in many other regions. The Lacandon have taken independent initiative towards the conservation of their forest and of howlers. Now is perhaps a crucial time for howler conservation strategies within this region. The Lacandon perception has altered and presently favors forest regeneration and howler preservation. Effective conservation strategies in areas where primates and humans are sympatric must involve the community with which primates share environmental resources (Cowlshaw and Dunbar 2000). Cowlshaw and Dunbar (2000) identify three forms of community-based conservation projects (CBC): those that provide a direct benefit to the community through a cash income, those that provide an indirect benefit through local development projects, and those that empower the community as managers of the resources.

Based on my interviews with some of the villagers in Nahá, it seems that both the direct benefits and management approaches to conservation would be appropriate approaches to the conservation of *A. pigra* in this region, as the Lacandon have already begun to implement strategies that are geared in these two directions. The Lacandon in Nahá are already participating largely in a cash-based economy and have begun to develop a tourist industry. Some members of the community are interested in bringing tourists into Nahá rather than conducting all of their tourist-based industry in nearby cities. As I previously discussed in Chapter IV, there are currently no paved roads into Nahá and this limits the number of tourists that come to the village. However, the current

situation would also allow for coordinated and careful planning in how to manage tourism within the Nahá rainforest. Proactive planning would potentially provide a long-term benefit for the howlers, the forest, and the Lacandon, provided an effective conservation system is already in place if and when the road to Nahá is paved.

Future Directions

Research on *Alouatta pigra* in the Nahá forest is in its infancy. There is still a great deal of information to be gleaned from this area that is perhaps unique in a number of important ways. First, the fact that howlers have returned to an area in which they had been locally extinct for approximately a quarter of a century provides a situation in which useful data regarding howler colonization can be obtained. The ability of howlers to colonize new areas of forest, even when those regions consist of fragmented forests, has important implications for conservation. In addition, the change in attitude and perceptions of the Lacandon toward their forest and toward howlers can provide useful insight into effective CBC strategies.

I was limited in my current project by the duration of the study. According to the local villagers with whom I spoke, the ecology of the new populations of howlers in the region varies dramatically over the course of the year. In addition, it appears that the seasonal conditions in Nahá during the summer of 2006 were unusual. I intend to follow up my initial research with more longitudinal studies to determine the extent to which howler ecology varies over the year and during changing seasonal patterns. It will also be important to obtain more data on the behavioral ecology of howlers in regions in which they are sympatric with humans. The relationship between the Lacandon and the

howlers is especially important to howler conservation given the larger economic and political conditions that exist outside of the Nahá forest.

More research is also needed in this area to monitor changes in the howler population. My census walks yielded no visual sightings of howlers, thereby suggesting low population densities, which perhaps should be expected since it seems that howlers returned to the area only two years prior to my study. I was only able to determine the presence of howlers through their vocalizations and one casual observation rather than through sightings on census walks. It would be useful to begin to get an idea of population density by visiting during the time of year that the locals indicate they see the howlers most often. In addition, estimation of home ranges for any troops contacted would be advantageous in order to more closely monitor those populations.

An additional limitation in this study was the lack of information available for the botany specific to this forest. Part of the issue was in the translation of species name from the Lacandon name to the scientific name for each species. Future collaborative work with botanists and with cultural anthropologists who can assist in translating Maya would be valuable in identifying plant species in the forest. Furthermore, future work should investigate more thoroughly the food resources available to howlers in the Nahá forest.

Any future work conducted in this region needs to consider conservation strategies. Effective conservation strategies are important to the survival of new populations of howlers coming into the Nahá forest, and exploration of possible CBC options is imperative. New populations of howlers will thrive in the Nahá forest only through the concerted efforts of the Lacandon, conservation organizations, scientists, and

the Mexican government. As with many other primate species, timing is a critical factor in successful conservation; we cannot wait until we have all of the answers to begin finding the solutions.

APPENDIX A

BOTANICAL PLOT LONG LIST

Botanical Plot One: Long List

Tree #	CBH: CM	DBH: CM	Radius	Basal Area	Maya Name	Scientific Name
1	20.32	6.47	3.23	32.86	chech anish	
2	14.73	4.69	2.34	17.27	t'oop che	
3	13.72	4.37	2.18	14.97	k'uchu che	<i>Bixa orllana</i>
4	24.89	7.92	3.96	49.31	hach tao	<i>Trema spp.</i>
5	13.97	4.45	2.22	15.53	hach tao	<i>Trema spp.</i>
6	13.72	4.37	2.18	14.97	hach tao	<i>Trema spp.</i>
7	189.74	60.40	30.20	2864.82	pukte	<i>Bucida buseras</i>
8	26.16	8.33	4.16	54.47	bämäx	<i>Brosimum alicastrum</i>
9	17.78	5.66	2.83	25.16	hach tao	<i>Trema spp.</i>
10	14.22	4.53	2.26	16.10	chäk ya	<i>Dipholis salicifolia</i> or <i>Manildara achras</i>
11	36.58	11.64	5.82	106.46	tasi pom	<i>Bursera simaruba</i>
12	67.56	21.51	10.75	363.26	k'uchu che	<i>Bixa orllana</i>
13	19.81	6.31	3.15	31.24	k'ik' che	<i>Castilla elastica</i>
14	325.12	103.49	51.74	8411.56	pukte	<i>Bucida buseras</i>
15	54.10	17.22	8.61	232.92	nä xa-ik che	
16	36.58	11.64	5.82	106.46	tasi pom	<i>Bursera simaruba</i>
17	13.97	4.45	2.22	15.53	t'oop che	
18	11.94	3.80	1.90	11.34	babah	<i>Sapindus saponaria</i>
19	11.68	3.72	1.86	10.86	t'oop che	
20	17.27	5.50	2.75	23.74	ixi (ix) che	<i>Diospyros texana</i>
21	24.38	7.76	3.88	47.32	nä xa-ik che	
22	26.67	8.49	4.24	56.60	babah	<i>Bursera simaruba</i>
23	18.80	5.98	2.99	28.11	äh bahun	
24	11.94	3.80	1.90	11.34	t'oop che	
25	12.45	3.96	1.98	12.33	t'oop che	
26	19.30	6.14	3.07	29.65	säk balche	<i>Lonchocarpus spp.</i>
27	12.45	3.96	1.98	12.33	t'oop che	
28	11.18	3.56	1.78	9.94	yooch bach	
29	53.85	17.14	8.57	230.74	nä xa-ik che	
30	28.70	9.14	4.57	65.56	babah	<i>Bursera simaruba</i>
31	14.22	4.53	2.26	16.10	tao	<i>Trema spp.</i>
32	13.21	4.20	2.10	13.88	k'an chuluhe	

Botanical Plot One: Long List Continued

Tree #	CBH: CM	DBH: CM	Radius	Basal Area	Maya Name	Scientific Name
33	30.23	9.62	4.81	72.70	haban su	
34	21.08	6.71	3.36	35.37	tao	<i>Trema</i> spp.
35	34.04	10.83	5.42	92.19	tao	<i>Trema</i> spp.
36	13.46	4.29	2.14	14.42	tao	<i>Trema</i> spp.
37	11.18	3.56	1.78	9.94	tao	<i>Trema</i> spp.
38	10.67	3.40	1.70	9.06	tao	<i>Trema</i> spp.
39	19.56	6.23	3.11	30.44	tao	<i>Trema</i> spp.
40	13.21	4.20	2.10	13.88	tao	<i>Trema</i> spp.
41	16.00	5.09	2.55	20.38	tao	<i>Trema</i> spp.
42	11.68	3.72	1.86	10.86	tao	<i>Trema</i> spp.
43	10.92	3.48	1.74	9.49	k'arok che	<i>Trema</i> spp.
44	22.35	7.11	3.56	39.76	tao	<i>Trema</i> spp.
45	20.32	6.47	3.23	32.86	tao	<i>Trema</i> spp.
46	28.19	8.97	4.49	63.26	tao	<i>Trema</i> spp.
47	35.31	11.24	5.62	99.19	tao	<i>Trema</i> spp.
48	18.80	5.98	2.99	28.11	tao	<i>Trema</i> spp.
49	34.80	11.08	5.54	96.36	tao	<i>Trema</i> spp.
50	16.26	5.17	2.59	21.03	tao	<i>Trema</i> spp.
51	16.76	5.34	2.67	22.36	tao	<i>Trema</i> spp.
52	34.80	11.08	5.54	96.36	tao	<i>Trema</i> spp.
53	10.92	3.48	1.74	9.49	tao	<i>Trema</i> spp.
54	19.81	6.31	3.15	31.24	tao	<i>Trema</i> spp.
55	14.48	4.61	2.30	16.68	tao	<i>Trema</i> spp.
56	61.98	19.73	9.86	305.66	tao	<i>Trema</i> spp.
57	11.18	3.56	1.78	9.94	tao	<i>Trema</i> spp.
58	12.95	4.12	2.06	13.35	tao	<i>Trema</i> spp.
59	45.21	14.39	7.20	162.67	kuti	<i>Talauma mexicana</i>
60	13.21	4.20	2.10	13.88	k'uChu che	<i>Bixa orllana</i>
61	13.72	4.37	2.18	14.97	hach tao	<i>Trema</i> spp..
62	14.48	4.61	2.30	16.68	chili trux	
63	41.66	13.26	6.63	138.08	hach tao	<i>Trema</i> spp.
64	19.56	6.23	3.11	30.44	tao	<i>Trema</i> spp.
65	24.38	7.76	3.88	47.32	tao	<i>Trema</i> spp.
66	27.43	8.73	4.37	59.88	hach tao	<i>Trema</i> spp.
67	13.72	4.37	2.18	14.97	tao	<i>Trema</i> spp.
68	18.80	5.98	2.99	28.11	hach tao	<i>Trema</i> spp.
69	26.92	8.57	4.29	57.69	hach tao	<i>Trema</i> spp.
70	11.94	3.80	1.90	11.34	tao	<i>Trema</i> spp.
71	29.72	9.46	4.73	70.28	tao	<i>Trema</i> spp.
72	14.73	4.69	2.34	17.27	tao	<i>Trema</i> spp.
73	33.78	10.75	5.38	90.82	hach tao	<i>Trema</i> spp.
74	19.05	6.06	3.03	28.88	hach tao	<i>Trema</i> spp.
75	13.46	4.29	2.14	14.42	äh xidi	
76	17.53	5.58	2.79	24.44	hach tao	<i>Trema</i> spp.
77	13.97	4.45	2.22	15.53	hach tao	<i>Trema</i> spp.

Botanical Plot One: Long List Continued

Tree #	CBH: CM	DBH: CM	Radius	Basal Area	Maya Name	Scientific Name
78	29.97	9.54	4.77	71.49	kuti	<i>Talauma mexicana</i>
79	15.75	5.01	2.51	19.74	tao	<i>Trema</i> spp.
80	26.67	8.49	4.24	56.60	äh bahn	
81	25.40	8.09	4.04	51.34	hach tao	<i>Trema</i> spp.
82	13.46	4.29	2.14	14.42	tao	<i>Trema</i> spp.
83	19.56	6.23	3.11	30.44	hach tao	<i>Trema</i> spp.
84	46.74	14.88	7.44	173.82	ixi (ix) che	<i>Diospyros texana</i>
85	15.24	4.85	2.43	18.48	tao	<i>Trema</i> spp.
86	32.51	10.35	5.17	84.12	hach tao	<i>Trema</i> spp.
87	12.70	4.04	2.02	12.84	tao	<i>Trema</i> spp.
88	109.73	34.93	17.46	958.13	ek balche	<i>Guatteria anomala</i>
89	29.21	9.30	4.65	67.90	tao	<i>Trema</i> spp.
90	20.32	6.47	3.23	32.86	tao	<i>Trema</i> spp.
91	22.86	7.28	3.64	41.59	äh bahn	
92	16.51	5.26	2.63	21.69	tao	<i>Trema</i> spp.
93	16.76	5.34	2.67	22.36	tao	<i>Trema</i> spp.
94	47.75	15.20	7.60	181.46	hach tao	<i>Trema</i> spp.
95	23.88	7.60	3.80	45.36	tao	<i>Trema</i> spp.
96	16.51	5.26	2.63	21.69	muxän che	<i>Calathea</i> sp.
97	22.10	7.03	3.52	38.86	hach tao	<i>Trema</i> spp.
98	16.00	5.09	2.55	20.38	tao	<i>Trema</i> spp.
99	12.45	3.96	1.98	12.33	hach tao	<i>Trema</i> spp.
100	44.20	14.07	7.03	155.44	hach tao	<i>Trema</i> spp.
101	51.05	16.25	8.13	207.42	chak tao	<i>Trema micrantha</i>
102	26.67	8.49	4.24	56.60	hach tao	<i>Trema</i> spp.
103	29.21	9.30	4.65	67.90	hach tao	<i>Trema</i> spp.
104	39.88	12.69	6.35	126.55	hach tao	<i>Trema</i> spp.
105	44.45	14.15	7.07	157.23	tao	<i>Trema</i> spp.
106	18.54	5.90	2.95	27.36	che chäkän	<i>Croton draco</i>
107	17.27	5.50	2.75	23.74	che chäkän	<i>Croton draco</i>
108	21.34	6.79	3.40	36.23	tao	<i>Trema</i> spp.
109	11.43	3.64	1.82	10.40	muxän che	<i>Calathea</i> sp.
110	24.89	7.92	3.96	49.31	hach tao	<i>Trema</i> spp.
111	16.76	5.34	2.67	22.36	tao	<i>Trema</i> spp.
112	28.45	9.06	4.53	64.40	hach tao	<i>Trema</i> spp.
113	11.43	3.64	1.82	10.40	hach tao	<i>Trema</i> spp.
114	32.51	10.35	5.17	84.12	hach tao	<i>Trema</i> spp.
115	45.47	14.47	7.24	164.50	hach tao	<i>Trema</i> spp.
116	16.76	5.34	2.67	22.36	muxän che	<i>Calathea</i> sp.
117	26.67	8.49	4.24	56.60	muxän che	<i>Calathea</i> sp.
118	11.68	3.72	1.86	10.86	tao	<i>Trema</i> spp.
119	11.18	3.56	1.78	9.94	tao	<i>Trema</i> spp.
120	30.99	9.86	4.93	76.41	muxän che	<i>Calathea</i> sp.
121	48.26	15.36	7.68	185.34	hach tao	<i>Trema</i> spp.
122	20.07	6.39	3.19	32.04	tao	<i>Trema</i> spp.

Botanical Plot One: Long List Continued

Tree #	CBH: CM	DBH: CM	Radius	Basal Area	Maya Name	Scientific Name
123	43.69	13.91	6.95	151.88	hach tao	<i>Trema</i> spp.
124	15.49	4.93	2.47	19.10	t'oop che	
125	18.54	5.90	2.95	27.36	muxän che	<i>Calathea</i> sp.
126	44.45	14.15	7.07	157.23	hach tao	<i>Trema</i> spp.
127	11.43	3.64	1.82	10.40	tao	<i>Trema</i> spp.
128	47.24	15.04	7.52	177.62	tao	<i>Trema</i> spp.
129	27.43	8.73	4.37	59.88	tao	<i>Trema</i> spp.
130	33.53	10.67	5.34	89.45	tao	<i>Trema</i> spp.
131	42.93	13.66	6.83	146.63	tao	<i>Trema</i> spp.
132	10.92	3.48	1.74	9.49	che chäkän	<i>Croton draco</i>
133	24.64	7.84	3.92	48.31	tao	<i>Trema</i> spp.
134	41.91	13.34	6.67	139.77	hach tao	<i>Trema</i> spp.
135	43.18	13.74	6.87	148.37	hach tao	<i>Trema</i> spp.
136	30.99	9.86	4.93	76.41	hach tao	<i>Trema</i> spp.
137	16.51	5.26	2.63	21.69	muxän che	<i>Calathea</i> sp.
138	37.34	11.89	5.94	110.94	tasi pom	<i>Bursera simaruba</i>
139	39.12	12.45	6.23	121.76	hach tao	<i>Trema</i> spp.
140	24.13	7.68	3.84	46.33	hach tao	<i>Trema</i> spp.
141	33.78	10.75	5.38	90.82	hach tao	<i>Trema</i> spp.
142	24.64	7.84	3.92	48.31	tao	<i>Trema</i> spp.
143	13.97	4.45	2.22	15.53	hach tao	<i>Trema</i> spp.
144	26.92	8.57	4.29	57.69	hach tao	<i>Trema</i> spp.
145	14.48	4.61	2.30	16.68	muxän che	<i>Calathea</i> sp.
146	22.10	7.03	3.52	38.86	hach tao	<i>Trema</i> spp.
147	21.59	6.87	3.44	37.09	hach tao	<i>Trema</i> spp.
148	11.94	3.80	1.90	11.34	muxän che	<i>Calathea</i> sp.
149	17.27	5.50	2.75	23.74	tao	<i>Trema</i> spp.
150	29.72	9.46	4.73	70.28	tao	<i>Trema</i> spp.
151	12.19	3.88	1.94	11.83	tao	<i>Trema</i> spp.
152	30.99	9.86	4.93	76.41	chak tao	<i>Trema micrantha</i>
153	36.83	11.72	5.86	107.94	tao	<i>Trema</i> spp.
154	20.07	6.39	3.19	32.04	tao	<i>Trema</i> spp.
155	44.45	14.15	7.07	157.23	hach tao	<i>Trema</i> spp.
156	12.70	4.04	2.02	12.84	hach tao	<i>Trema</i> spp.
157	40.39	12.86	6.43	129.79	hach tao	<i>Trema</i> spp.
158	38.61	12.29	6.14	118.62	tao	<i>Trema</i> spp.
159	44.45	14.15	7.07	157.23	tao	<i>Trema</i> spp.
160	58.42	18.60	9.30	271.59	ek balche	<i>Guatteria anomala</i>
161	19.05	6.06	3.03	28.88	säk balche	<i>Lonchocarpus</i> spp.
162	20.83	6.63	3.31	34.52	tao	<i>Trema</i> spp.
163	31.50	10.03	5.01	78.94	tao	<i>Trema</i> spp.
164	64.26	20.46	10.23	328.62	nä xa-ik che	
165	29.72	9.46	4.73	70.28	tao	<i>Trema</i> spp.
166	54.61	17.38	8.69	237.32	käbä te	<i>Pachira acuatica</i>

Botanical Plot One: Long List Continued

Tree #	CBH: CM	DBH: CM	Radius	Basal Area	Maya Name	Scientific Name
167	29.21	9.30	4.65	67.90	yache kab (yache)	<i>Ceiba</i> spp. or <i>Ceiba pentadra</i>
168	41.66	13.26	6.63	138.08	bämäx	<i>Brosimum alicastrum</i>
169	30.23	9.62	4.81	72.70	tao	<i>Trema</i> spp.
170	13.72	4.37	2.18	14.97	tao	<i>Trema</i> spp.
171	21.34	6.79	3.40	36.23	tao	<i>Trema</i> spp.
172	32.26	10.27	5.13	82.81	uk' che	<i>Porophyllum punctatum</i>
173	51.05	16.25	8.13	207.42	käbä te	<i>Pachira acuatica</i>
174	23.88	7.60	3.80	45.36	bämäx	<i>Brosimum alicastrum</i>
175	27.94	8.89	4.45	62.12	chöyok	<i>Cnidioscolus aconitifolius</i>
176	27.18	8.65	4.33	58.78	käbä te	<i>Pachira acuatica</i>
177	27.94	8.89	4.45	62.12	tao	<i>Trema</i> spp.
178	20.32	6.47	3.23	32.86	tao	<i>Trema</i> spp.
179	24.13	7.68	3.84	46.33	tao	<i>Trema</i> spp.
180	29.21	9.30	4.65	67.90	bämäx	<i>Brosimum alicastrum</i>
181	29.72	9.46	4.73	70.28	tao	<i>Trema</i> spp.
182	12.19	3.88	1.94	11.83	tao	<i>Trema</i> spp.
183	13.21	4.20	2.10	13.88	wiich	
184	10.92	3.48	1.74	9.49	t'oop che	
185	17.02	5.42	2.71	23.05	wiich	
186	31.75	10.11	5.05	80.22	tao	<i>Trema</i> spp.
187	28.96	9.22	4.61	66.72	tao	<i>Trema</i> spp.
188	24.64	7.84	3.92	48.31	tao	<i>Trema</i> spp.
189	80.01	25.47	12.73	509.42	bämäx	<i>Brosimum alicastrum</i>
190	21.59	6.87	3.44	37.09	tao	<i>Trema</i> spp.
191	45.21	14.39	7.20	162.67	käbä te	<i>Pachira acuatica</i>
192	28.19	8.97	4.49	63.26	käbä te	<i>Pachira acuatica</i>
193	12.95	4.12	2.06	13.35	wiich	
194	11.43	3.64	1.82	10.40	wiich	
195	19.81	6.31	3.15	31.24	tao	<i>Trema</i> spp.
196	41.15	13.10	6.55	134.74	pukte	<i>Bucida buceras</i>
197	200.15	63.71	31.86	3187.93	ch'alol	<i>Quercus</i> sp.
198	26.42	8.41	4.20	55.53	tao	<i>Trema</i> spp.
199	15.24	4.85	2.43	18.48	t'oop che	
200	15.75	5.01	2.51	19.74	t'oop che	
201	14.73	4.69	2.34	17.27	t'oop che	
202	16.76	5.34	2.67	22.36	t'oop che	
203	12.19	3.88	1.94	11.83	t'oop che	
204	12.70	4.04	2.02	12.84	tao	<i>Trema</i> spp.
205	37.34	11.89	5.94	110.94	muste'	<i>Clerodendrum ligustrinum</i>
206	46.48	14.80	7.40	171.93	kuti	<i>Talauma mexicana</i>
207	77.47	24.66	12.33	477.59	ek balche	<i>Guatteria anomala</i>
208	96.52	30.72	15.36	741.35	kukuchet achtu	
209	16.00	5.09	2.55	20.38	tao	<i>Trema</i> spp.
210	19.05	6.06	3.03	28.88	tao	<i>Trema</i> spp.

Botanical Plot One: Long List Continued

Tree #	CBH: CM	DBH: CM	Radius	Basal Area	Maya Name	Scientific Name
211	16.26	5.17	2.59	21.03	tao	<i>Trema</i> spp.
212	24.13	7.68	3.84	46.33	chäkäl	<i>Euphorbia lasiocarpa</i>
213	314.96	100.25	50.13	7894.05	ch'alol	<i>Quercus</i> sp.
214	11.68	3.72	1.86	10.86	tao	<i>Trema</i> spp.
215	12.95	4.12	2.06	13.35	tao	<i>Trema</i> spp.
216	24.13	7.68	3.84	46.33	tao	<i>Trema</i> spp.
217	10.92	3.48	1.74	9.49	t'oop che	
218	13.46	4.29	2.14	14.42	muxän che	<i>Calathea</i> sp.
219	147.83	47.06	23.53	1739.01	ch'alol	<i>Quercus</i> sp.
220	17.27	5.50	2.75	23.74	tao	<i>Trema</i> spp.
221	24.89	7.92	3.96	49.31	tao	<i>Trema</i> spp.
222	40.13	12.77	6.39	128.17	tao	<i>Trema</i> spp.
223	30.23	9.62	4.81	72.70	tao	<i>Trema</i> spp.
224	17.78	5.66	2.83	25.16	tao	<i>Trema</i> spp.
225	17.27	5.50	2.75	23.74	tao	<i>Trema</i> spp.
226	15.24	4.85	2.43	18.48	tao	<i>Trema</i> spp.
227	22.86	7.28	3.64	41.59	tao	<i>Trema</i> spp.
228	19.30	6.14	3.07	29.65	tao	<i>Trema</i> spp.
229	40.13	12.77	6.39	128.17	tao	<i>Trema</i> spp.
230	19.05	6.06	3.03	28.88	tao	<i>Trema</i> spp.
231	22.86	7.28	3.64	41.59	tao	<i>Trema</i> spp.
232	24.13	7.68	3.84	46.33	tao	<i>Trema</i> spp.
233	22.61	7.20	3.60	40.67	tao	<i>Trema</i> spp.
234	22.86	7.28	3.64	41.59	tao	<i>Trema</i> spp.
235	15.24	4.85	2.43	18.48	tao	<i>Trema</i> spp.
236	30.48	9.70	4.85	73.93	tao	<i>Trema</i> spp.
237	18.54	5.90	2.95	27.36	tao	<i>Trema</i> spp.
238	31.24	9.94	4.97	77.67	tao	<i>Trema</i> spp.
239	21.59	6.87	3.44	37.09	tao	<i>Trema</i> spp.
240	20.07	6.39	3.19	32.04	tao	<i>Trema</i> spp.
241	14.73	4.69	2.34	17.27	tao	<i>Trema</i> spp.
242	45.21	14.39	7.20	162.67	tao	<i>Trema</i> spp.
243	14.48	4.61	2.30	16.68	tao	<i>Trema</i> spp.
244	17.27	5.50	2.75	23.74	tao	<i>Trema</i> spp.
245	12.70	4.04	2.02	12.84	tao	<i>Trema</i> spp.
246	12.19	3.88	1.94	11.83	tao	<i>Trema</i> spp.
247	10.92	3.48	1.74	9.49	t'oop che	
248	11.43	3.64	1.82	10.40	t'oop che	
249	23.11	7.36	3.68	42.51	tao	<i>Trema</i> spp.
250	10.92	3.48	1.74	9.49	t'oop che	
251	32.51	10.35	5.17	84.12	bämäx	<i>Brosimum alicastrum</i>
252	14.22	4.53	2.26	16.10	t'oop che	
253	71.88	22.88	11.44	411.18	k'ak' alche'	<i>Bourreria pulchra</i>
254	30.48	9.70	4.85	73.93	bämäx	<i>Brosimum alicastrum</i>
255	16.51	5.26	2.63	21.69	tao	<i>Trema</i> spp.

Botanical Plot One: Long List Continued

Tree #	CBH: CM	DBH: CM	Radius	Basal Area	Maya Name	Scientific Name
256	16.26	5.17	2.59	21.03	tao	<i>Trema</i> spp.
257	12.95	4.12	2.06	13.35	wiich	
258	38.86	12.37	6.19	120.18	bămăx	<i>Brosimum alicastrum</i>
259	10.16	3.23	1.62	8.21	t'oop che	
260	13.46	4.29	2.14	14.42	tao	<i>Trema</i> spp.
261	14.73	4.69	2.34	17.27	tao	<i>Trema</i> spp.
262	16.51	5.26	2.63	21.69	tao	<i>Trema</i> spp.
263	12.45	3.96	1.98	12.33	hach tao	<i>Trema</i> spp.
264	12.19	3.88	1.94	11.83	hach tao	<i>Trema</i> spp.
265	22.35	7.11	3.56	39.76	hach tao	<i>Trema</i> spp.
266	459.74	146.34	73.17	16819.52	ch'alol	<i>Quercus</i> sp.
267	16.51	5.26	2.63	21.69	hach tao	<i>Trema</i> spp.
268	22.86	7.28	3.64	41.59	tao	<i>Trema</i> spp.
269	17.78	5.66	2.83	25.16	tao	<i>Trema</i> spp.
270	12.45	3.96	1.98	12.33	hach tao	<i>Trema</i> spp.
271	23.88	7.60	3.80	45.36	tao	<i>Trema</i> spp.
272	103.89	33.07	16.53	858.82	bămăx	<i>Brosimum alicastrum</i>
273	14.99	4.77	2.39	17.87	le k'ado	

APPENDIX B

PHOTOGRAPHS

Nahá Forest





Canopy Cover





Nahá



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