

WASHINGTON UNIVERSITY IN ST. LOUIS

Department of Anthropology

Dissertation Examination Committee:

Robert W. Sussman, Chair

Ellen Dierenfeld

Alejandro Estrada

Kenneth Olsen

Shanti Parikh

D. Tab Rasmussen

P. Mick Richardson

Crickette Sanz

The Feeding Ecology of Yucatán Black Howler Monkeys (*Alouatta pigra*)  
in Mangrove Forest, Tabasco, Mexico

by

LeAndra Luecke Bridgeman

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## CHAPTER ONE

### INTRODUCTION

In this study, I investigate the diet and behavior of a population of Yucatán black howler monkeys (*Alouatta pigra*) isolated in mangrove forest on the Pantanos de Centla Biosphere Reserve in Tabasco, Mexico. Mangroves are composed of relatively few species of plants specially adapted to tidal inundation and saline conditions. Mangrove communities are not considered ideal environments for most mammals, especially large-bodied arboreal herbivores, because of the low-diversity, and supposedly, low-quality vegetation. In addition to gathering data on dietary selection of the monkeys, I also profile the nutrient concentrations of plants in the mangrove to evaluate general quality of food and non-food items. The mangrove forest is noted to be used by various primates as a refuge to escape the destruction of their usual habitats, but only a few limited studies of its effects on the behavioral ecology of primates exist. This is the first study of New World primates who are confined to mangroves, with no access to other habitats and food resources.

In altered forest landscapes, the likelihood of animal species becoming locally extinct increases with decreasing fragment size and as food abundance and tree diversity decrease (Arroyo-Rodríguez and Dias, 2010). Researchers interested in habitat fragmentation ecology investigate fragment size, isolation, and species diversity and abundance and their possible effects on primate populations in order to understand primate responses to the growing incidence of habitat loss and degradation due to human activity. Fragmentation research models have also proven useful in studies regarding the effects of low-diversity habitats, such as agro-forestry (Brugiere et al., 2002; Williams-Guillén, 2003; Estrada et al., 2006b; Muñoz, et al., 2006) and

island communities (Serio-Silva et al., 2002; Ludwig et al., 2008) on primate populations, particularly those primates that feed mainly on leaves. Additionally, researchers have found that the intrinsic properties of foods eaten by primates can affect population characteristics, such as biomass (Waterman et al., 1988; Fashing et al., 2007) and behavior (e.g. Nowak, 2008). In this study, I apply these models to analyze habitat characteristics and phytochemical properties of foods in order to examine their possible influences on behavior and population characteristics of Yucatán black howlers (*Alouatta pigra*) inhabiting an island of mangrove forest in Tabasco, Mexico.

Within this chapter, I introduce what is known about the influence of the environment on primate populations and the relationships among habitat, food abundance, diet, and behavior. I describe forest diversity and tree species abundance as limiting factors on primate biomass, densities, group sizes, and demography. I present a literature review on the effects of habitat and food abundance on the activity patterns and foraging behavior of primates in general, and of primates that are considered primarily folivorous. In order to give general context for the study, I provide a brief overview of current foraging theory, of mangrove ecology, and of primates in mangroves, as well as background on what is known about the behavioral ecology of the genus *Alouatta*, especially *A. pigra*. I then outline the content of the dissertation chapters along with my associated hypotheses and predictions.

### **Forest Diversity and Abundance as Limiting Factors on Population**

The diversity and abundance of vegetation in a particular habitat contribute to the ability of animal populations to reproduce normally (Marsh, 2003) by limiting available food resources. Although it may seem that herbivores have an endless supply of food in a forest, this is not

always the case. Species used as food resources may not be the most common species in a particular habitat or they may be widely scattered. The diversity of plant species ranges along a continuum, with some habitats offering an enormous selection of food resources while others offer comparatively little. Diversity is made up of two measures; species richness is simply a count of the number of species in an area while species evenness compares the relative abundance of each species in an area. In studies of Old and New World primates, researchers have concluded that areas of high diversity, such as mosaic habitats or disturbed areas with secondary vegetation, could support larger primate populations than comparable areas with low diversity (Brugiere et al., 2002; Cristóbal-Azkarate et al., 2005).

The diversity and abundance of food resources have been shown to alter primate populations in terms of primate biomass and density (Struhsaker, 1973; Coelho et al., 1976; Altmann et al., 1985; Peres, 1997; Janson and Chapman, 1999; Mbora and Meikle, 2004; Van Belle and Estrada, 2006; Fashing et al., 2007; Pinto et al., 2009), group sizes (Clutton-Brock and Harvey, 1977; Estrada et al., 1999; Mbora and Meikle, 2004; Van Belle and Estrada, 2006), and population demographics (Dunbar, 1987; Cristóbal-Azkarate et al., 2005). The diversity and abundance of habitats are typically measured using vegetation plots and transects. Vegetation sampling methods allow for species identification, various measurements of forest structure, and calculations of density, abundance, and productivity. Productivity is estimated using methods such as above-ground biomass and basal area of tree species, which are related to primate population characteristics.

Basal area is a measure of the productivity volume of trees based on an area calculation from the diameter at breast height (DBH, 130 cm above ground) of sample trees. Evidence from empirical studies demonstrates that folivorous primate densities are positively correlated with the

*total* basal area of food trees and negatively correlated with the density of food trees and basal area per food tree (Umpathy and Kumar, 2003; Mbora and Meikle, 2004). For example, in the Tana River region of Kenya, high densities of food trees in one hectare cannot support a large population of red colobus monkeys (*Procolobus rufomitratu*s). This is because the trees have low basal areas, resulting in lower productivity of food resources, meaning they were not large enough to produce a sufficient amount of food to sustain high densities of colobus (ibid.). However, in a study of howler monkeys (*Alouatta palliata*) in fragments, tree density did not predict howler presence or density, which was instead related to the number (abundance) of food trees present (Cristóbal-Azkarate et al., 2005).

In addition to affecting primate population densities, low diversity and abundance of food resources can affect primate group sizes, demographics, and social structure (Sussman, 2000; Gillespie and Chapman, 2001). Red colobus group size correlates positively with the basal area of food trees, as is demonstrated in the study mentioned previously (Mbora and Meikle, 2004). Spider monkey (*Ateles* spp.) typically have large group sizes, in which small, variable subgroups of few individuals will form and break off from the main group during the day to forage more efficiently. This type of social organization is known as fission-fusion and is seen in *Ateles* and in a few other primate species, such as common and bonobo chimpanzees (*Pan troglodytes* and *P. paniscus*) (Fuentes, 2011). *Ateles* subgroup sizes expand and shrink according to the abundance and distribution of preferred resources (Chapman et al., 1995). However, the results for predicting group sizes from habitat characteristics within the genus *Alouatta* have proved to be puzzling. Knopff and Pavelka (2006) applied the ecological constraints model to determine group size for black howlers and found no correlation between number of individuals in a group and the availability of food. In contrast, Horwich et al. (2001) found a positive correlation

between black howler group sizes and population density, indicating that the study habitat was rich in resources.

In terms of demographics, Cristóbal-Azkarate and colleagues (2005) found high mortality rates of juveniles in howler monkey populations living in forest fragments with low food availability and high population densities. The authors concluded that in this population of howlers, juveniles were unable to obtain the nutrition they needed to survive. Inadequate foraging due to environmental constraints has been linked to juvenile mortality in other studies of bird and mammal populations (Clutton-Brock et al., 2001; Daunt et al., 2007). High mortality rates can then lead to local extinction if access to more abundant food resources is limited or non-existent and the population is unable to adopt new behavioral strategies for finding food.

### **Effects of Habitat, Food Abundance, and Distribution on Behavior**

In addition to abundance and diversity of food resources acting as limiting factors on primate population parameters, food abundance and distribution also influence behavior. Forests vary in terms of their degree of seasonality and food abundance, which dictates food resources available throughout the year, specifically for primates. Seasonality of flower and fruit production is a function of rainfall over certain periods, known as wet and dry seasons, and of climate (Smythe, 1970). While the production of new leaves may occur more than once a year, flowering and fruiting typically occur only once, making these resources ephemeral. During seasons when no flowers or fruits are available, herbivores must rely on perennial plant resources, such as leaves, stems, roots and bark. Generally speaking, leaves are the most common year-round resource for folivorous primates and are always available in tropical evergreen forest in varying states of senescence (Lambert, 2007). However, phytochemical

defenses and nutrients are present in variable combinations and concentrations to deter herbivory (Milton, 1980), thus affecting food choice and, in turn, affecting behavior patterns, such as traveling, calling, socializing, and copulation (Chivers, 1991). I discuss habitat seasonality and diet choice in this section, and botanical nutrition in the next section.

Diet, in conjunction with morphological parameters, dictates how and when animals forage, rest, travel, and engage in social behaviors. If food resources are dispersed in either time (seasonally) and space (density/abundance) or both, the animals that rely on them must make concessions to procure and process food. Seasonally, available foods may require primates to adjust energy expenditure for travel time and increase day ranges, depending on the density and abundance of food (Limeira, 1997; Strier, 2011), by engaging in energetically expensive behaviors not seen in times of scarce food availability (e.g. hunting by chimpanzees: Watts and Mitani, 2002), or by altering group competition, ranging patterns, and use of space in a population (Palacios and Rodriguez, 2001; Knopff and Pavelka, 2006; Lambert, 2007). Typically, primates adjust their daily routines according to their requirements and the availability of foods (Sussman, 2000). For some populations of black howlers, however, researchers found no compensation in activity budgets during times of fruit abundance and consumption (Horwich et al., 1993; Knopff and Pavelka, 2006), while in others, they found that locomotion/travel behavior significantly increased and social behavior significantly decreased during the season when the howlers ate more fruit (Pavelka and Knopff, 2004).

The selection of specific plants to feed upon is also dependent upon the number of food tree species and their density and abundance in an area. Species diversity, density, and abundance affect food selection by herbivores by limiting the variety or number of species or by providing abundant and varied resources, each end of the spectrum having different effects. In

terms of diversity, the number of different resources available directly influences what an animal eats. Areas with high diversity do not impress food selection limitations on animal populations because there are many different species to choose from and these areas have been shown to be beneficial to primate populations (Mbora and Meikle, 2004; Arroyo-Rodríguez and Dias, 2010). Conversely, areas with low diversity offer fewer species from which to choose, which is important to animals that eat a lot of leaves, especially, because too much of one type can lead to toxic overload or poor nutrient absorption due to chemical and mechanical defenses found in plant foliage in general. Very high food tree density can lead to lower production (biomass) of food available for herbivores because they do not have enough room or nutrients to grow properly (Mbora and Meikle, 2004). Very low density of food trees can pose problems for animals that depend on them such as increased energy expenditure (travel time) with little payoff in terms of amount of food available. There is also the inability to defend widespread resources, making travel time and the possibility of competition not energetically efficient. A middle-ground level of density is optimal for a “good” herbivore habitat. If the abundance of a food resource is high in an area, then it offers better chances for animals to partake, as scramble competition allows equal opportunities for all. If the resource is in low abundance and is not as available in space and time, contest competition and defensibility of these resources is likely to occur. However, evidence from field studies of aggressive social interactions indicate that this feeding competition may not be as prevalent or important as the aggression-competition paradigm suggests (Sussman and Garber, 2011). However, in poor habitats characterized by low diversity and low food abundance, where quality resources are limited, it may be that competition for access to these resources, either between individuals with a group or between groups, is greater than expected. Whether or not the low abundance food is selected depends on

if this is a good option for potential consumers in terms of reward versus cost and an evaluation of the prevalence and quality of food resources in needed.

As an example, these three factors influence the diet of primates in relation to various fig (*Ficus*) species, considered a staple food for many Old and New World primates (Milton, 1980; Nunes, 1998; Matsumoto-Oda and Hayashi, 1999; Serio-Silva et al., 2002; Rivera and Calme, 2006; Felton et al., 2009). Serio-Silva and colleagues (2002) demonstrated that when fig trees bloom asynchronously and are abundant in the home range of mantled howlers, the howlers select a diet high in fig fruit year-round, even though other foods are available. In contrast, in highly seasonal habitats with synchronous flowering and fruiting, the number of plant species consumed can fluctuate greatly throughout the year (Nunes, 1998) as preferred and staple resources come and go.

It is evident that primates are influenced by habitat quality, measured in terms of diversity and abundance, but it is also evident that other factors may also mediate the effects of habitat on food choice to some degree. For example, Dierenfeld and McCann (1999) reported an increase in feeding time for lion-tailed macaques (*Macaca silenus*) and for ring-tailed lemurs (*Lemur catta*) in connection with nutrient density in specific food items, rather than in general plant species density.

### **Phytochemical Effects on Food Selection, Behavior, and Population Characteristics**

Important factors in food selection by folivorous primates are the intrinsic phytochemical characteristics of plant products, such as protein, fiber, minerals, and toxins (Milton, 1980; Glander, 1981; Yeager et al., 1997). Each of these components varies in concentrations from

one species to another, between plants of the same species, and even within a single plant (Milton, 1979). Different plant parts (e.g. leaves and flowers) tend to vary in their constituent nutrients. For this study, I am interested in how generalist-folivores, such as howler monkeys, select food in the mangrove and how extrinsic and intrinsic factors of these plants influence their diet and survival.

Leaves have a high water content (c. 50-90%) yet also contain structural cells that are difficult to break down in the digestive systems of herbivores (Milton, 1980), marking them as low quality. According to Milton (1979), these structural components can be 30-60% of the dry weight of leaves. Thus, for herbivores without highly specialized gut morphology to break down structural cells (Strier, 2011), eating enough foliage to meet nutritional requirements must be cost/benefit effective in terms of searching for and digesting low-quality foods. Most primates include some insects and leaves in their diets for protein (ibid.).

Generally speaking, shoots, flowers, and fruits have lower fiber and higher sugar levels than leaves. Seeds are typically high in nutrients and are often easier to digest with intrinsic enzymes. These characteristics are marks of high-quality foods and thus are preferred food items because of their improved digestibility (Clutton-Brock, 1977a), but they are not always available.

Researchers have shown that protein to fiber ratios affect leaf choice for many primates that include a large portion of leaves in their diets (*Alouatta palliata*: Milton, 1979; Bilgener, 1995; *Colobus satanas*: McKey et al., 1981; *Nasalis lavartus*: Yeager et al., 1997; *Colobus guereza*: Chapman et al., 2004; Fashing et al., 2007). However, a high protein to fiber ratio is not always correlated with leaf preference or foraging behavior. Selection for low protein to fiber ratios and rejection of leaves with high protein to fiber ratios occurs in these same species and even within the same populations (Felton et al., 2009). Muñoz et al. (2006) found that

protein to fiber ratio was not a significant predictor of foraging effort in mantled howlers in Tabasco, and Serio-Silva et al. (2002) did not find any significant differences in this ratio between foods eaten and ignored for a population of mantled howlers in Veracruz, Mexico. In some cases, it may be levels of other compounds that determine leaf choice.

The presence and abundance of minerals in some plant species and parts may also affect food selection in primates. In a study of black-and-white colobus monkey (*Colobus guereza*) diet and abundance, Chapman et al. (2004) found that food selection was positively related to the amount of zinc and copper and negatively related to the amount of potassium in food items compared to nonfood items. Fashing et al. (2007) also found higher zinc levels in leaves selected as food by black-and-white colobus in Kenya. With respect to proboscis monkeys (*Nasalis larvatus*), Yeager et al. (1997) reported that selected food items contained more phosphorus and potassium and less calcium and magnesium than non-food items.

Despite numerous investigations into the effects of tannins and other secondary compounds on diet selection in primates, results remain conflicting and conclusions unclear in many cases (Milton, 1979; Davies et al., 1988; Waterman et al., 1988; Ganzhorn, 1989; Hagerman and Butler, 1989; Hagerman et al., 1992; Kool, 1992; Oftedal, 1991; Waterman and Kool, 1994; Bilgener, 1995; Chapman and Chapman, 2002; Rothman et al., 2006; Fashing et al., 2007; Felton et al., 2009). For example, in a study of *Colobus guereza* in Kenya conducted by Fashing et al. (2007), secondary compounds were low in most leaves selected as food, however, in the top ranking leaves selected as a food resource, condensed tannin concentrations were highest of all the leaves eaten. Kool (1992) found that fiber, not tannins or secondary compounds, had a negative influence on food selection by silver leaf monkeys (*Trachypithecus auratus*) and therefore were not the primary factors governing which plants were eaten.

Although it is preferable to define condensed tannin levels quantitatively in plant parts, the method for doing so can produce inaccurate results (Rothman et al., 2006). The acid-butanol spectrophotometric assay for estimating condensed tannin content is based on chemically breaking the interflavon bonds within the tannin molecules and producing a red color. This result is then compared with an external standard (e.g. Quebracho, Delphinidin). However, interflavon bonds release at different points in different tannins, producing different colors that cannot be compared with the external standard, depending on which types of tannins are present. In order to obtain accurate results, an internal standard of the plant species being tested should be created (Rothman et al., 2009) and is a direction for future research in this habitat.

Until methods are standardized and comparable data are available on tannins and other secondary metabolites, it is more useful to investigate nutrient availability and proportionate ratios, especially of foliage, that are already shown to influence the selection of food species over ignored species in primate diets (Felton et al., 2009), such as protein, fiber, and minerals.

In addition to studying phytochemical effects on food selection, several researchers have investigated the effects of plant phytochemistry on primate populations and behavioral responses to physiological deprivation of nutrients. For example, Ganzhorn (1992) and Chapman et al. (2004) found a positive correlation between protein to fiber concentrations of leaves eaten and primate biomass in colobines monkeys. Worden (1968) notes that malnutrition in young rats leads to delays in sexual and reproductive activity and limits social status within the group. In mature animals in the same study, malnutrition can also lower social status and reproductive success. Levels of sodium in the diet of red colobus when eating leaves in a mangrove forest correlated with the frequency of observations of the monkeys seeking out and drinking water (Nowak, 2008), a behavior in which many primates do not engage often because most of their

water intake comes from foods. Understanding various levels and forms of habitat limitations on primate populations and behavior is a fundamental part of foraging theory for herbivores.

### **Foraging Theory and Herbivores**

All animals have to make choices about what to eat. Plant and animal prey species alike have inherent nutritional value, but also each comes at a cost. This cost could be energy expenditure for the consumer or a defense mechanism the prey species has adopted to avoid predation. The goal of all animals when it comes to eating should be to balance their nutritional needs while keeping their cost to a minimum.

Classic studies utilized optimal foraging theory and focused on energy maximization and cost/benefit analyses of feeding and diet (MacArthur and Pianka, 1966; Schoener, 1971; Stephens and Krebs, 1986). The traditional view of optimal foraging theory is dynamic and is continually updated as new studies are published. As has been pointed out by researchers of primate diets and nutrition, different populations of the same species, and even different sympatric species, may not eat the same foods (species and parts), yet there is evidence to suggest that the nutritional quality of their diets is similar and that categorizing animal diets with food type (frugivory, folivory) is not useful when examining the nutritional quality of diets (Dierenfeld and McCann, 1999; Rothman et al., 2007). In the modern synthesis of foraging theory, researchers have moved away from energy maximization models to focus more on how dietary factors influence the morphology, physiology, and behavior of animals (Lambert, 2009).

Except for a few species, primates tend to be plant generalists and can incorporate all manner of plant parts in varying quantities into their diets (Lambert, 2007). This flexibility affords them the ability to survive and adapt in habitats and situations in which other, more

specialized animals cannot. However, in order to avoid direct competition with other life forms, primates, like other animals, fill different ecological niches. A niche includes where, when, and on what animals forage and spend their time. To negotiate the challenges of finding and extracting nutrients from food, primates have evolved morphological and behavioral adaptations to do so efficiently in their respective niches. For example, some Old World monkeys have highly specialized digestive systems to process foliage with the maximum benefit (Strier, 2011). In the New World primates, foregut morphology is less specialized, yet hindgut morphology is modified in some species to increase the retention time of leafy materials and allow more absorption of nutrients released by gut microflora (Milton, 1980). Behaviorally, primates adapted for taking advantage of leaves throughout the year tend to spend more time eating than other species that are more specialized for eating fruit. For example, howler monkeys (*Alouatta* spp.) and proboscis monkeys (*Nasalis larvatus*) are primarily folivorous and are highly selective feeders (Milton, 1980; Yeager et al., 1997; Silver et al., 2000). Being selective in food choice comes with costs, such as more energy spent traveling and increased exposure to predators, so primates must engage strategies that function to maximize nutrition and limit costs. Behaviors, such as search strategies, in conjunction with the abundance, density, and phytochemistry of food resources, are important factors to consider when measuring the effects of habitat on diet and behavior.

The mangrove habitat is different from all other forest types in that the plants therein are specially adapted to survive continual flooding and high salt levels. It is in this habitat that I studied, for the first time, a population of New World monkey isolated on an island of mangrove forest.

## **Mangrove Biology and Ecology**

The term “mangrove” refers to the association of tropical woody trees and shrubs that grow in tidal and saline wetlands (Ball, 1988), where land meets the sea. Mangroves are found in tropical and subtropical latitudes and are dependent upon four main conditions for their presence and distribution: soil type, tidal variability, saline water, and climate. Mangroves typically favor anaerobic soils, high salt levels, and fluctuating tidal inundation, and thrive under these harsh conditions, with adaptations in root structures, mechanisms to balance salt levels, and reproductive strategies. There are 36 families of plants and 50 species that form monodominant stands of mangroves or are frequently found in close association with mangroves (Tomlinson, 1986). Of these, few are “true” mangrove species, defined by Tomlinson (ibid.) as those: 1) occurring only in the mangrove environment, not in terrestrial environments; 2) having specialized morphology, such as vivipary and aerial roots; 3) having physiological specialization to excrete and/or exclude salt; and 4) and being isolated taxonomically from terrestrial relatives. In a recent study of morphological and phytochemical characteristics of true mangrove species, Wang et al. (2010) found that true mangrove species differed from mangrove associates (those species that do not meet requirements of true mangroves) in having lower specific leaf area and nitrogen concentrations, higher sodium and chloride accumulations (8-9 times), and higher potassium/sodium concentrations.

The mangrove forests near the Usumacinta River delta in Mexico are dominated by as few as 10 tree species (Thom, 1967), which are distributed in a typical pattern according to their salt tolerance. The only true mangrove species within the study site were red (*Rhizophora mangle*), white (*Laguncularia racemosa*), and black (*Avicennia germinans*) mangrove trees. These three species are commonly found in succession from the water line inward and work

together to stabilize soil, act as a buffer from storm surges, and trap tidal detritus and debris to provide a nursery, feeding, and breeding grounds for many aquatic organisms and birds (Haehle, 1999).

Because of the saline environment, concentrations of sodium and chloride in mangrove species are higher than in non-mangrove species, and therefore must be excreted from the plant tissues. Many mangrove tree species deposit salt onto stems and leaves through special glands while others accumulate salt in their bark or eliminate salt from their root systems (Tomlinson, 1986). Chemical defenses of mangrove species are primarily polyphenolics (i.e. carbon-based). Polyphenolics in leaves, such as condensed tannins and other flavonoids, plus high carbon to nitrogen ratios effectively deter insects and other herbivores from preying on mangrove trees (Tomlinson, 1986; Feller, 1995; Hogarth, 1999; Kandil et al., 2004). For example, the mature leaves of red (*Rhizophora*) and black (*Avicennia*) mangrove trees contain carbon to nitrogen ratios well beyond the upper limit of 17:1 for sustainable animal nutrition (91-98:1 and 47:1, respectively, meaning that carbon is high relative to nitrogen, and both are needed but in limited amounts) (Cundell et al., 1979; Twilley et al., 1986; Miller, 2000; Skov and Hartnoll, 2002). As a comparison, consider that alfalfa hay, a common food for cows, has a carbon-nitrogen ratio of 12:1 (Miller, 2000), meaning that carbon content is high relative to nitrogen content.

Additionally, limited plant-animal interactions occur in mangroves, as mangroves are nearly “exclusively dispersed by water; fruits and seeds are not attractive to animals” (Tomlinson, 1986:11). Until now, studies of the diets of primates in mangrove include them feeding on resources in other habitats or being provisioned, as in studies of crab-eating macaques (*Macaca fascicularis*) and non-naturally occurring vervet monkeys (*Cercopithecus aethiops*) in the Florida Keys (Supriatna et al., 1989; Hyler, 1995).

Secondary compounds in mangrove plant leaves have been the focus of many studies, as this habitat is rich in tannins (Janzen, 1973). For example, in a study of several mangrove tree leaves by Basak et al. (1996), the authors found that secondary compounds had a negative correlation with protein, so that as protein content increased, the level of toxins decreased. I discuss the findings of other researchers who have published on the toxic compounds of mangrove products in Chapter Four.

### **Primates in Mangroves**

There are reports of primates in mangroves, but few have been studied in detail. In Asia, the most well studied mangrove primates are crab-eating macaques (*Macaca fascicularis*) and proboscis monkeys (*Nasalis larvatus*). Macaques are able to extract high quality food resources from the mangrove in the form of animal materials (two-thirds annually of overall diet), such as shellfish, amphibians, crustaceans, and insects (Supriatna et al., 1989; Son, 2003). In contrast, proboscis monkeys, which do not exploit animal materials and eat primarily leaves, use the mangrove for food and shelter when resources are scarce in other forest or when adjacent forest is being disturbed (Bennett and Sebastian, 1988; Agoramoorthy, 2007). In Kalimantan National Park, a population of proboscis monkeys spends much of its time in degraded mangrove forest due to human encroachment and were reported to eat leaves, shoots, spores, and fruits of the mangrove apple tree (*Sonneratia alba*), the red mangrove tree (*Rhizophora apiculata*), mangrove fern (*Acrostichum aureum*) and the smallflower brugiera (*Brugiera parviflora*) (Agoramoorthy, 2007). Unfortunately, percentage of time spent feeding on mangrove plants was not reported in this publication. Other researchers have noted that some populations of proboscis monkeys do not use the mangrove for feeding, but rather for resting and as a way to move between lowland

freshwater swamps, where plant diversity is higher (Meijaard and Nijman, 2000). Researchers report seven other Old World primates that use mangroves for refuge: Temminck's red colobus (*Procolobus badius temmincki*), Zanzibar red colobus (*Procolobus kirkii*), Guinea baboons (*Papio papio*), green monkeys (*Cercopithecus (Chlorocebus) sabaesus*), patas monkeys (*Erythrocebus patas*), and silvered langurs (*Trachypithecus cristatus* and *T. auratus*) (Kool, 1989; Supriatna et al., 1989; Bennett and Davies, 1994; Gippoliti and Dell'Omo, 2003; Galat-Luong and Galat, 2005; Nowak, 2008; Gonedelé Bi et al., 2009; Nowak and Lee, 2011). Nowak (2008) conducted a study on the drinking behavior of red colobus in mangrove and reported that the group that spent the most time in the mangrove (85.4%) also drank (rain) water more frequently than groups spending less time in the mangrove. The red colobus groups in Nowak's study were observed to eat young leaves from *Sonneratia alba*, fruit from black mangrove (*Avicennia marina*), and leaves from red mangrove (*Rhizophora mucronata*). In a later publication, Nowak and Lee (2011) described the population characteristics of the Zanzibar red colobus in mangrove and coral rag thickets and found that in the species-poor habitat of the mangrove, red colobus had larger group sizes, increased infant survival, and a more stable population when compared with red colobus living in more seasonal and diverse coral rag nearby. Even with these publications, little is known about the behavior and ecology of many primate populations reported to utilize African and Asian mangroves.

Despite brief reports of more than ten species of New World monkeys in mangrove (Table 1.2), including four species of howler monkeys (*Alouatta palliata*: Milton and Mittermeier, 1977; Snarr, 2006; *A. pigra*: Serio-Silva et al., 2006; *A. belzebul*: Fernandes and Aguiar, 1993; and *A. seniculus*: Scott et al., 1976; Phillips and Abercrombie, 2003), there are no

published studies describing the behavior or ecology for any of these species *solely* in mangroves.

CERCOPITHECINAE – Old World Monkeys

Species	Common name	2012 IUCN status	Habit	Diet	Range	Refs
<i>Chlorocebus sabaues</i>	Green monkey	Least Concern	Terrestrial	Omnivore	West Africa	1, 20
<i>Erythrocebus patas</i>	Patas monkey	Least Concern	Terrestrial	Omnivore	Northern Africa	2, 21
<i>Macaca fascicularis</i>	Crab-eating macaque	Least Concern	Terrestrial	Omnivore	Southeast Asia	3
<i>Nasalis lavartus</i>	Proboscis monkey	Endangered	Arboreal	Folivore	Indonesia	4
<i>Papio papio</i>	Guinea baboon	Near Threatened	Terrestrial	Omnivore	Northwestern Africa	5
<i>Procolobus badius</i>	West African red colobus	Endangered	Arboreal	Folivore	West Africa	6
<i>Procolobus kirkii</i>	Zanzibar red colobus	Endangered	Arboreal	Folivore	Zanzibar, Tanzania	7
<i>Trachypithecus auratus</i>	Javan lutung	Vulnerable	Arboreal	Folivore	Indonesia	8
<i>Trachypithecus cristatus</i>	Silvery lutung	Near Threatened	Arboreal	Folivore	Indonesia, Malaysia	9

CEBINAE – New World Monkeys

Species	Common name	IUCN status	Habit	Diet	Range	Refs
<i>Alouatta caraya</i>	Black-and-gold howler	Least concern	Arboreal	Folivore		10
<i>Alouatta palliata</i>	Mantled howler	Least concern	Arboreal	Folivore	Meso- and South America	11
<i>Alouatta pigra</i>	Yucatán black howler	Endangered	Arboreal	Folivore	Mexico, Guatemala	12
<i>Alouatta seniculus</i>	Colombian red howler	Least concern	Arboreal	Folivore	Central South America	13
<i>Ateles geoffroyi</i>	Geoffroy's spider monkey	Endangered	Arboreal	Frugivore	Mesoamerica and Colombia	14
<i>Callithrix jacchus</i>	White-tufted-ear marmoset	Least concern	Arboreal	Frugivore/gumnivore	Brazil	15
<i>Cebus apella</i>	Guianan brown capuchin	Least concern	Arboreal/terrestrial	Omnivore	Northern South America	16

Species	Common name	IUCN status	Habit	Diet	Range	Refs
<i>Cebus capucinus</i>	White-throated capuchin	Least concern	Arboreal/terrestrial	Omnivore	Central America and Colombia	17
<i>Chiropotes satanas</i>	Black bearded saki	Critically endangered	Arboreal	Frugivore	Brazil	18
<i>Saimiri sciureus</i>	American squirrel monkey	Least concern	Arboreal	Frugivore	Northern South America	19

1) Kingdon and Gippoliti, 2008. 2) Kingdon et al., 2008. 3) Ong and Richardson, 2008. 4) Meijaard et al., 2008. 5) Oates et al., 2008a. 6) Oates et al., 2008b. 7) Struhsaker and Siex, 2008. 8) Nijman, and Supriatna, 2008. 9) Nijman and Meijaard, 2008. 10) Fernandez-Duque et al., 2008. 11) Cuarón et al., 2008a. 12) Marsh et al., 2008. 13) Boubli et al., 2008a. 14) Cuarón et al., 2008b. 15) Rylands et al., 2008b. 16) Rylands et al., 2008a. 17) Causado et al., 2008. 18) Veiga et al., 2008b. 19) Boubli et al., 2008b. 20) Gron et al., 2007. 21) Cawthon Lang, 2006.

**Table 1.1.** Primate species reported in mangroves.

A comparison of the protein and fiber content of leaves eaten by howlers in lowland tropical forest (Oftedal et al., 1991; Silver et al., 2000) with leaves eaten by the crab-eating macaque and the Javan langur in Vietnamese and Indonesian mangroves (Supriatna et al., 1989; Son, 2003), shows that lowland forest protein content is 4x higher and fiber content is 8x higher than in mangrove plants. From these data I infer that protein and fiber content is low in mangrove, meaning that the study howlers may be forced to ingest relatively more foliage, rely more on seasonal resources, and incorporate novel food items when compared to conspecifics in more diverse forest.

## Background and Previous Investigations

### *Howler monkeys, genus Alouatta*

Howler monkeys are relatively large (c. 10 kg) diurnal primates that are found only in the Neotropics. They are arboreal and prefer the middle to upper canopy of the forest, but will come

to the ground if necessary. Howlers are described as folivorous based on behavioral and morphological characteristics (Sussman, 2000), but prefer fruit when it is available (Di Fiore et al., 2010). Two outstanding traits of howler monkeys are their prehensile tails, which they use primarily for support whilst eating and resting (Bergeson, 1998), and the enlarged hyoid bones in their throats that give them one of the loudest long calls of any terrestrial mammal on the planet.

There are currently fourteen recognized species in the genus *Alouatta* that are widely distributed in the tropical Americas from southeastern Mexico (about 18° North) through Central America, and into much of South America to southeastern Brazil and northern Argentina (about 31° South) (Di Fiore et al., 2010; IUCN, 2012). Howler species data used for comparison in this dissertation include species found throughout their range in both Mesoamerica and South America. *Alouatta palliata mexicana* (the Mexican mantled howler) shares a distribution border with *A. pigra* in southeastern Mexico and southern Guatemala. The mantled howler monkey (*Alouatta palliata*) can be divided into two further subspecies in Central America and ranges from northern Honduras to Panama and Peru in South America (Rylands et al., 2006). *Alouatta seniculus*, the red howler, ranges in the northwest of the continent (Gron, 2007). *Alouatta belzebul*, the red-handed howler, is distributed in the northeast of Brazil (Veiga et al., 2008a). The black-and-gold howler, *Alouatta caraya*, is centrally located on the continent (Fernandez-Duque et al., 2008). The distribution of *Alouatta guariba*, the black-and-red howler, is along the border of northeastern Argentina and southeastern Brazil.

*Alouatta* is an excellent example of primates in which there is a considerable amount of inter- and intra-specific variation in both morphology and behavior (Crockett and Eisenberg, 1987; Di Fiore et al., 2010). Morphological variation is in pelage coloration, body size, hyoid bone size (Crockett and Eisenberg, 1987), sexual and age-related dichromatism, and degree of

sexual dimorphism. There is a degree of sexual dimorphism in body size, the hyoid bone, and canine teeth (Kay et al., 1988). Howlers live in cohesive social groups that range in size from only a few to dozens of individuals (Di Fiore et al., 2010). Social structure within the genus ranges from bisexual pairs to unimale and multimale groups; variation in social grouping also occurs within the same species and may depend on group size, habitat size and quality and on population density (Glander, 1980; Van Belle and Estrada, 2006; Bezanson et al., 2008).

Howlers spend over half of the daylight hours resting. Species means for resting range from 54.2% in *A. belzebul* (Bonvicino, 1989; Pinto, 2002; Pinto et al., 2003) to 78.5% in *A. seniculus* (Gaulin and Gaulin, 1982). Feeding behavior, which includes foraging effort, is lowest in *A. seniculus* at 12.7% (ibid.) and highest in the subspecies *A. palliata mexicana* at 27% (Estrada et al., 1999; Cristóbal-Azkarate and Arroyo Rodriguez, 2007)<sup>1</sup>. Locomotion, including both movement and travel behaviors, is highest in *A. belzebul* with 23.9% (Bonvicino, 1989; Pinto, 2002; Pinto et al., 2003) and lowest in *A. seniculus* with 6.2% (Gaulin and Gaulin, 1982). Howler monkeys spend little time engaging in social behavior. *A. belzebul* has the highest species mean for social behavior with 5.5% (Bonvicino, 1989; Pinto, 2002; Pinto et al., 2003) and the lowest mean is for *A. p. mexicana* with 0.5% (Estrada et al., 1999; Cristóbal-Azkarate and Arroyo Rodriguez, 2007).

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<sup>1</sup> This subspecies is included in this study because of its evolutionary and geographical proximity with *A. pigra*.

Species	% Feed Mean	SD±	% Rest Mean	SD±	% Locomote Mean	SD±	% Social Mean	SD±
<i>A. pigra</i> <sup>a</sup>	19.0	3.4	69.0	5.4	7.0	2.3	2.0	1.4
<i>A. palliata</i> <sup>b</sup>	18.0	3.4	67.0	5.4	12.0	6.4	4.0	3.6
<i>A. p. mexicana</i> <sup>c</sup>	27.0	20.1	59.0	20.0	7.0	4.6	1.0	0.0
<i>A. caraya</i> <sup>d</sup>	15.0	0.7	59.0	3.6	21.0	4.1	4.4	0.7
<i>A. belzebul</i> <sup>e</sup>	16.0	6.3	54.0	4.2	24.0	5.9	5.5	7.7
<i>A. guariba</i> <sup>f</sup>	18.0	0.9	64.0	7.1	14.1	3.6	3.0	2.6
<i>A. seniculus</i> <sup>g</sup>	12.7	-	78.5	-	6.2	-	2.5	-

<sup>a</sup> Silver et al., 2007; Pavelka and Knopff, 2004; Behie and Pavelka, 2005; Pozo-Montuy and Serio-Silva, 2007. <sup>b</sup> Milton, 1980; Teaford and Glander, 1996; Palacios and Rodriguez, 2001; Clarke et al., 2002; Williams-Guillén, 2003. <sup>c</sup> Estrada et al., 1999; Cristóbal-Azkarate and Arroyo-Rodríguez, 2007. <sup>d</sup> Bicca-Marques, 1993; Prates and Bicca-Marques, 2008. <sup>e</sup> Bonvicino, 1989; Pinto 2002a, 2002b; Pinto et al., 2003. <sup>f</sup> Mendes, 1989; Chiarello, 1993; de Marques 1995, 1996. <sup>g</sup> Gaulin and Gaulin, 1982.

**Table 1.2.** Activity pattern means from pooled data (see references below) and standard deviations (SD±) for several *Alouatta* species.

Although there is considerable variation in group size and composition between species and even within a population, trends are apparent for the genus. In general, both males and females disperse from their natal groups upon becoming of reproductive age to enter other groups or form new groups of their own (Di Fiore et al., 2010). Males are typically dominant over females within howler society and a hierarchical dominance relationship between females in a group is common (ibid.). Male-male competition has been documented both within groups, and between groups whose home ranges overlap. Competition is usually over access to females and is associated with group take-over attempts (ibid.). This competition is a generality and is not always the case, however (Wang and Milton, 2003), and it is proposed that direct male-male competition decreases as group size increases (Di Fiore et al., 2010).

### *Howler monkey feeding ecology*

Among the New World primates, howler monkeys (*Alouatta* spp.) are known to subsist in an assortment of habitats in various states of degradation and size (Crockett and Eisenberg, 1987). Howlers are considered generalist folivore-frugivores, with a large part of their annual diets consisting of leaves. They consume more leaves when fruits are not available, either due to seasonal changes or to habitat structure (Serio-Silva et al., 2002; Di Fiore et al., 2010), and may rely heavily on flowers and/or seeds at some point throughout the year (Chapman, 1987; Neves and Rylands, 1991). An important facet of the adaptability of howlers is their ability to obtain adequate nutrition from such a low quality diet while managing toxins. Howlers possess several morphological adaptations to assist in the efficient digestion of leafy plant material and avoid toxicity.

Howlers have sharp shearing crests on their molars to shred leaves into small pieces to begin the digestive process. The digestive passage is slow, particularly in the hindgut, where specialized bacteria assist in the fermentation of foliage (Milton, 1984). The caecum is somewhat enlarged to house this material while it is fermenting, allowing the absorption of more nutrients. However, howlers lack many of the anatomical specializations for digestion compared to other leaf-eating mammals and must also employ behavioral strategies for dealing with a diet comprised primarily of leaves (Milton, 1980, 1993). Most notably, howlers have adopted a somewhat sedentary lifestyle, resting for most of the day in between meals, in order to aid in the digestion process. Additionally, many researchers have shown that howlers eat from a combination of numerous tree species over an annual cycle (c. 60, range 7-109) and are selective in the particular parts of the plants consumed (Smith, 1977; Milton, 1978, 1980; Glander, 1978;

Bicca-Marques and Calegario-Marques, 1994b; Chiarello, 1994; Galetti et al., 1994; Silver et al., 1998; Solano et al., 1999; Santamaría-Gómez, 2000; Serio-Silva et al., 2002; Pinto et al., 2003; Pavelka and Knopff, 2004; Rivera and Calme, 2006). In order to obtain proper nutrients and avoid toxicity, howlers must select the right combination of a variety of plant species and parts (Glander, 1978; Milton, 1980, 1993).

The mantled howler subspecies *Alouatta palliata mexicana* is closest phylogenetically and shares the same geographic region with *A. pigra* (Rylands et al., 2006), as their respective distributions are primarily divided along the Usumacinta river system in southeastern Mexico. Thus, studies of the Mexican mantled howler in this region can provide important comparative data which is lacking in the region for black howlers. For example, Muñoz et al. (2006) demonstrated that protein to fiber ratios influenced the selection of young versus mature leaves on an agroforest plantation for cacao in Tabasco. The plantation is small (12 ha) and contains only 32 tree species, limiting food choices for the howlers. The howlers used 15 species for food, including two species of epiphytes and one species of vine. The two plant families most used for food were Moraceae (57%) and Fabaceae (32%). The plantation mantled howlers had an annual diet consisting of 60% leaves, 35% fruit, and 5% flowers and other items. Three of the five most used species were fig (*Ficus*) trees, which are an important food resource for howlers in general (Serio-Silva et al., 2002; Rivera and Calme, 2006). In another study conducted by Serio-Silva and colleagues (2002) on a small island study site (57 ha), a population of *A. p. mexicana* used just over half of the 63 plant species on the island. *Ficus* represented the most important food resource for these howlers, who chose fig products in 64% of feeding bouts.

Howlers can subsist effectively in forest fragments (high diversity, small area) and in areas of agro-forestry (low diversity, small area), such as cacao and coffee plantations (Limeira,

1997; Williams-Guillén, 2003; Estrada et al., 2006b) and researchers of howler diets report that although many tree species in the diet are important, only a few (5-15) species account for over half the diet on an annual basis (Estrada, 1984; Garcia del Valle et al., 2001; Sussman, 2000; Serio-Silva et al., 2002; Muñoz et al., 2002; Rivera and Calme, 2006; Ludwig et al., 2008). Yet other researchers of howlers in low diversity habitats have proposed that habitats without much variety in terms of tree diversity, density, and abundance affect the presence and behavior of those populations (e.g. Limeira, 1997; Cristóbal-Azkarate, 2005).

#### *Yucatán black howlers (Alouatta pigra)*

The Central American black howler, hereafter referred to as “black howlers”, has a restricted distribution in southeastern Mexico, Guatemala, and Belize (Wolfheim, 1983; Crockett and Eisenberg, 1987; Rylands et al., 2006).

Black howler monkeys, of all ages and both sexes, have black fur and black faces. Males of this species generally weigh an average of 11 kg and females an average of 6.4 kg (Ford and Davis, 1992; Smith and Jungers, 1997). Researchers suggest this species is the largest of the *Alouatta*, has the largest hyoid bone (and thus, the loudest call), but does not have the highest sexual dimorphism index for the genus (Kay et al., 1988).

Information about the black howler comes primarily from three sites in Belize: the Community Baboon Sanctuary, Cockscomb Basin Wildlife Preserve, and Monkey River, where habitat fragmentation is prevalent (Bolin 1981; Silver et al., 1998, 2000; Marsh, 1999; Ostro et al., 1999, 2001; Silver and Marsh, 2003; Pavelka and Knopff, 2004; Pavelka and Chapman, 2006). A few studies of the black howler were conducted in Tikal National Park, Guatemala in the mid-1970s through the early 1980s (Coelho et al., 1976; Schlicte, 1978; Bolin, 1981). Other

researchers in Mexico and Guatemala investigated black howler populations more recently, adding distribution, population and foraging data in both fragments and continuous forest to our knowledge of this species (Estrada et al., 2002a, 2002b, 2003, 2004a, 2004b, 2006a, 2006b, 2006c; Rodríguez-Luna et al., 2003; Luecke and Estrada, 2005, 2006; Mandujano et al., 2006; Rivera and Calme, 2006; Serio-Silva et al., 2006; Van Belle and Estrada, 2006; Pozo-Montuy and Serio-Silva, 2007).

Black howlers studied at the sites referenced above spend a majority of the daylight hours resting (mean 69.1%, range 62-77%). Feeding is generally the second most frequent activity, averaging 19.1% (range 15-24%). Locomotion averages 7% (range 4.5 to nearly 10%) of activity budgets. Social behavior for this species ranges from less than 1% to 3.7% and averages 1.9%. In comparison with the activity patterns of other howler species means reported in the literature, black howlers fall within the genus range for resting, feeding, locomotion, and social behavior, indicating that black howlers generally adhere to the activity patterns typical of the genus (Table 1.1). (Milton, 1980; Gaulin and Gaulin, 1982; Bonvicino, 1989; Mendes, 1989; Bicca-Marques, 1993; Chiarello, 1993; Galetti et al., 1994; Teaford and Glander, 1996; Palacios and Rodriguez, 2001; Clarke et al., 2002; Pinto, 2002; Pinto et al., 2003; Williams-Guillén, 2003; Cristóbal-Azkarate and Arroyo Rodriguez, 2007; Prates and Bicca-Marques, 2008) black howlers are in the upper end of the range for resting (range 8-80%, median 65.5%) and in the normal range reported for feeding (7.5-85%, median 18.7%) and locomotion (0.7-29%, median 10.2%) and social behaviors (0-16.9%, median 2.5).

My dissertation research adds invaluable information on the range of howler monkey adaptability to different habitats and food resources, if the population is doing well. If this is the case, mangroves may prove to be viable resources in the conservation of many primate species.

If the mangrove howler population does not show signs of thriving and the mangrove plants prove to be nutrient poor, then we may gain information on environmental limitations on howler monkeys and primates in general.

## **Content and Organization of the Dissertation**

The organization of my dissertation follows a progression of the causal chain from resource base to its effect on the howler population in terms of density, social structure, general activity, and feeding ecology. In the chapter descriptions below, I present general material, hypotheses, and predictions.

In Chapter Two, I describe the reserve in which the study site is located and define the study population of howlers. I outline the basic methodologies used for the collection and analysis of behavioral and vegetation data throughout the dissertation. Specific methodologies relevant to each chapter are provided therein.

An understanding of species diversity, richness, and structure in the study site is vital to the base and construction of hypotheses in later chapters. Therefore, I present ecological data on the forest, such as structure, biomass, canopy cover, density, and richness, to erect a framework upon which I build subsequent analyses.

Given that mangroves are considered a specialized, low quality, and low-diversity habitat, I hypothesize that significant differences exist regarding habitat qualities among the mangrove study site and floristically diverse habitats in which primates are found. After a literature review of biodiversity in other tropical forest habitats, I predict that tree diversity will be low (in overall species present) and that species richness (species per hectare) will also be low when compared with other primate habitats. I also predict that the mangrove in Arroyo Polo

varies significantly from biologically diverse habitats in forest structure (canopy height, density, and volume) and food availability (basal area and above-ground biomass).

Based on the ability of howler monkeys to survive in many different habitats, my second hypothesis is that the vegetation characteristics of the mangrove study site will affect howler monkey population grouping patterns, population demographics, and population density. I predict that if the mangrove habitat is not significantly different from biologically diverse habitats in terms of diversity and richness, then the howler population density, group sizes, and density will be similar to other populations of black howlers in similar habitat conditions, such as low diversity and richness. If the mangrove is significantly lower in diversity and richness and small group sizes, low densities, and skewed population demographics are expected in low-quality habitats, then the mangrove howlers should have significantly smaller mean group sizes, low population density, low adult male to female ratios, and low adult female to immature ratios than howlers in diverse habitats.

In Chapter Three, I describe the activity patterns, substrate use, and diet composition of the five howler study groups. I begin with hourly/daily activity patterns, present results for monthly and seasonal changes in activity patterns, and then give a general overview of activity. I analyze substrate use by the howlers during each behavior for information on which trees are used most often for daily behaviors. I then examine and present information on the diets of the howlers – general, age/sex differences, seasonal, and life form (tree or liana) – and map the results onto vegetation characteristics from Chapter Two.

If there are no differences in habitat vegetation characteristics among the mangrove and other howler monkey habitats, I hypothesize that significant differences will not exist in activity budgets among the mangrove howlers and howlers in more diverse habitat types. However, if

differences do exist, I predict that the howlers confined to mangrove will exhibit behavioral patterns more similar to howlers in low-diversity habitats than either are to conspecifics in diverse habitats. Because of the apparent effect of poor habitats, such as dry forest or disturbed fragments, on the amount of time needed to travel in search of low abundance food resources, I predict that search time (travel) will be significantly higher than travel time for howlers in diverse habitat with more food trees.

If there are significant differences between the island mangrove site and other howler study sites, I hypothesize that the diet of the mangrove howlers will vary significantly from other howler populations in terms of diet composition, number of species eaten, and plant parts consumed. The diet of mangrove black howlers should be composed primarily of young leaves throughout the year and they should exploit seasonal resources, such as flowers and fruits, when they are available. I predict that the mangrove howlers will eat from significantly fewer plant species and incorporate novel food items into their diets than do howlers in diverse habitats. If the mangrove is low in diversity and food availability, I predict that the mangrove howlers will have a similar diet to other howler populations in landscapes where diversity and abundance are low.

In Chapter Four, I recap dietary preferences of the mangrove howlers from Chapter Three and define the study of nutritional ecology to introduce the phytochemical analyses of mangrove plants. The phytochemical analyses include proximate (e.g. protein, fiber, carbohydrates) and minerals, and also include ratios that index quality, such as protein to fiber and calcium to phosphorus. I describe the proximate and mineral components of the howler diets and the mangrove plants in general. I then make comparisons among plant parts, foods and non-foods, life forms (trees and lianas), and seasonal variation.

I proposed several null hypotheses regarding phytochemical content of mangrove plants. The first hypothesis is that there is no difference in nutritional content between plants selected and ignored as food items by the howlers. Because there may be seasonally preferred items and novel foods available, I predict that mangrove foods selected by the howlers will be higher in quality than items ignored. The second and third hypotheses are that mangrove plant phytochemistry will not vary seasonally or between life forms (trees and lianas). I predict that levels and ratios of nutrients will vary from wet to dry seasons if seasonal foods are available. The fourth hypothesis is that nutritional content of mangrove plants selected for food will not vary significantly in phytochemical content from food plants in other primate studies. I predict that mangrove plants will be higher in sodium and be of lower quality than non-mangrove plants. Comparisons with food plants selected by other primate populations may reveal similarities in nutrients and show that the mangrove howlers select foods to balance nutrient intake.

Chapter Five is a summary of the findings from Chapters Two, Three, and Four and a discussion of what the findings mean in relation to other primate studies and to theoretical frameworks for understanding relationships between ecology and behavior. Before bulleting my overall conclusions for the dissertation, I briefly discuss what the findings might mean for primate conservation and include a summary of the ethnobotany of the local Chontal Maya descendants who inhabit and use the mangrove in the study site.

## **CHAPTER TWO**

### **METHODS, BLACK HOWLER POPULATION, AND VEGETATION CHARACTERISTICS**

#### **Introduction**

In this chapter, I describe the study area and site and lay out a general overview of methods used to collect data common to all the chapters. More detailed methodological descriptions of behavioral and phytochemical data collection and analysis can be found in Chapters Three and Four, respectively. Howler monkey population characteristics, forest structure, and vegetation analysis are also presented in this chapter to provide information referenced in later chapters.

#### **Study Area: Pantanos de Centla Biosphere Reserve, Tabasco, Mexico**

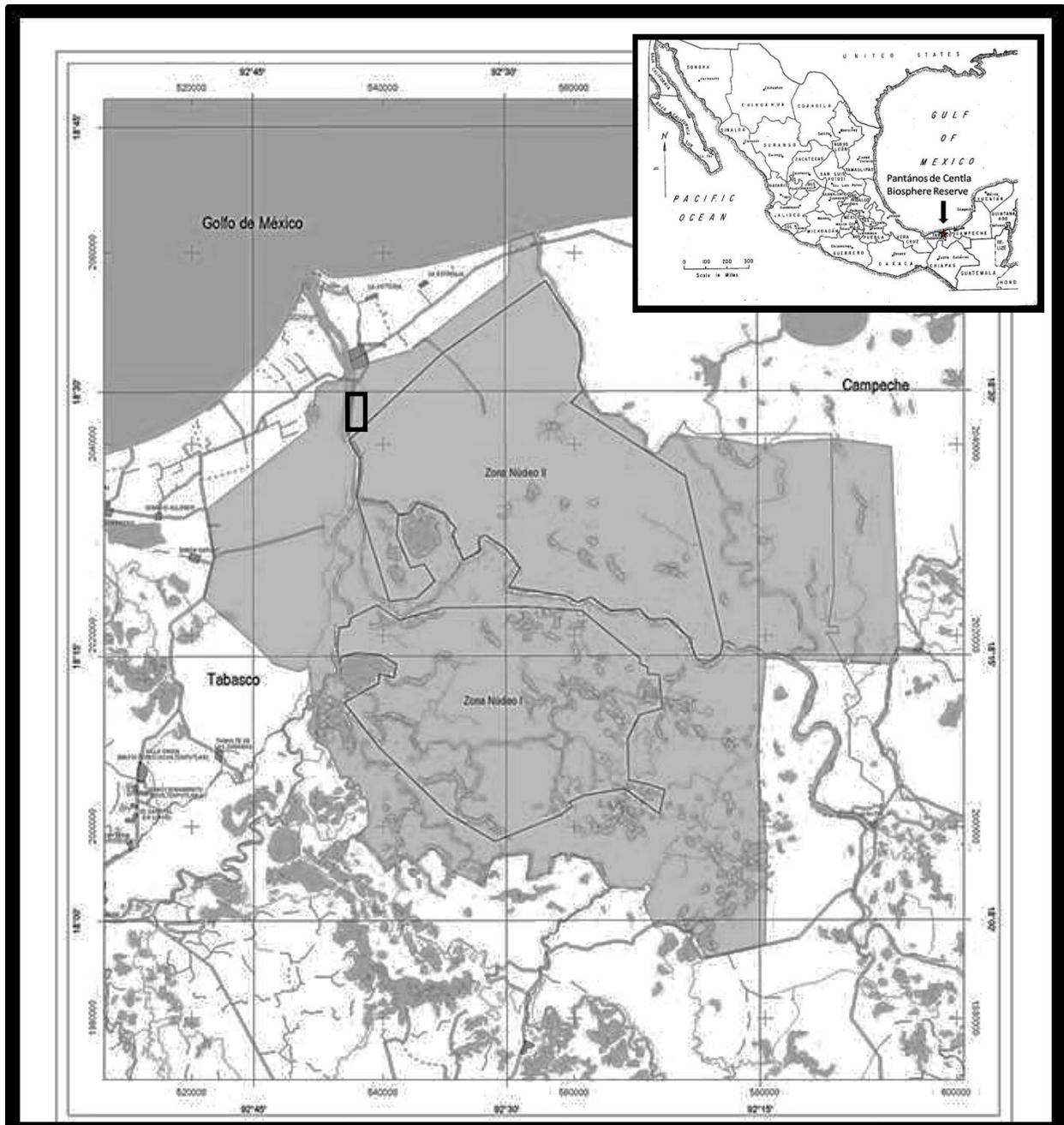
Pantanos de Centla is a wetlands biosphere reserve located in Tabasco, Mexico on the southern rim of the Gulf of Mexico on the Isthmus of Tehuantepec between the states of Veracruz and Campeche (Figure 2.1). Centla covers just over 300,000 hectares (3,000 km<sup>2</sup>) between 17° 57'53" and 18° 39'03" N, and 92° 06'39" and 92° 47'58" W (Figure 2.1). Northern Tabasco is a deltaic floodplain containing one of the most important river systems in Central America (Ramsar, 2001). Three rivers make up the Usumacinta River system: the Usumacinta, the San Pedro, and the Grijalva. The rivers flow north in the floodplain and converge approximately 13 km south of the field site and 18 km south of the river mouth into the Gulf. The river resulting from the convergence retains the name Grijalva. Elevation on the reserve ranges from 1-6 meters above sea level.

The climate is hot and humid, with a mean annual temperature of 26°C. Annual precipitation ranges from 1500 – 2000 mm. There is a short dry season each year in the spring (March-May) (ParksWatch-Mexico, 2003).

Pantanos de Centla was officially designated a biosphere reserve in August 1992. In June 1995, the Ramsar Convention recognized the reserve as a wetland of international importance (site #733). The Ramsar List was established in response to Article 2.1 of the Convention on Wetlands (Ramsar, Iran, 1971) with the purpose:

To develop and maintain an international network of wetlands which are important for the conservation of global biological diversity and for sustaining human life through the ecological and hydrological functions they perform (Ramsar 2012:1).

The Ramsar Convention selects wetland sites worldwide for recognition to encourage conservation and sustainable use. Wetlands function as ecosystems that contribute not only to biological diversity but also to economies, science, and culture.



**Figure 2.1.** The Pantanos de Centla Biosphere Reserve in Tabasco, Mexico (modified from [www.simec.conabio.gob.mx](http://www.simec.conabio.gob.mx)) with inset showing the location of the reserve within the country and an outline of the study site location (small box).

The reserve has a variety of wetland habitats. Permanently flooded freshwater swamps are the most common habitat. Other wetland habitats include rivers, lakes, brackish lagoons, seasonally flooded saltmarshes and freshwater swamps, mangrove swamps, estuaries, seasonally flooded agricultural land, and man-made water storage areas and canals. Combined, there are 110 bodies of freshwater in the reserve (Ramsar, 2001).

The 2001 Ramsar report describes the main plant associations in the reserve as *Bucida buceras* forest (known locally as *pucteales* because the local name for this species is *puckte*), *Haemotoxylum campechianum* (Caesalpiniaceae) forest (local name *tinto*), riparian and coastal mangrove forest (*manglares*) (Rhizophoraceae, Combretaceae, Avicenniaceae), *Dalbergia brownii* (Fabaceae) thickets (*muco*), and palms from the genera *Acoelorrhaphe* and *Sabal* (Arecaceae). Furthermore, the reserve contains 13 species of plants that are classified as rare or threatened (Ramsar, 2001).

There are fifteen dominant plant families documented on the reserve by Guadarrama (2000). She reports that the most abundant family is the Leguminosae with nearly 90 species, followed by Poaceae and Cyperaceae with c. 50 species each. In the Centla District, in which much of the biosphere reserve is located, Guadarrama recorded 110 families, 363 genera, and 637 species. The study area contains monodominant stands of red mangrove (*Rhizophora mangle*) near the water edges and monodominant stands of white mangrove (*Laguncularia racemosa*) further inland, with several other tree species interspersed.

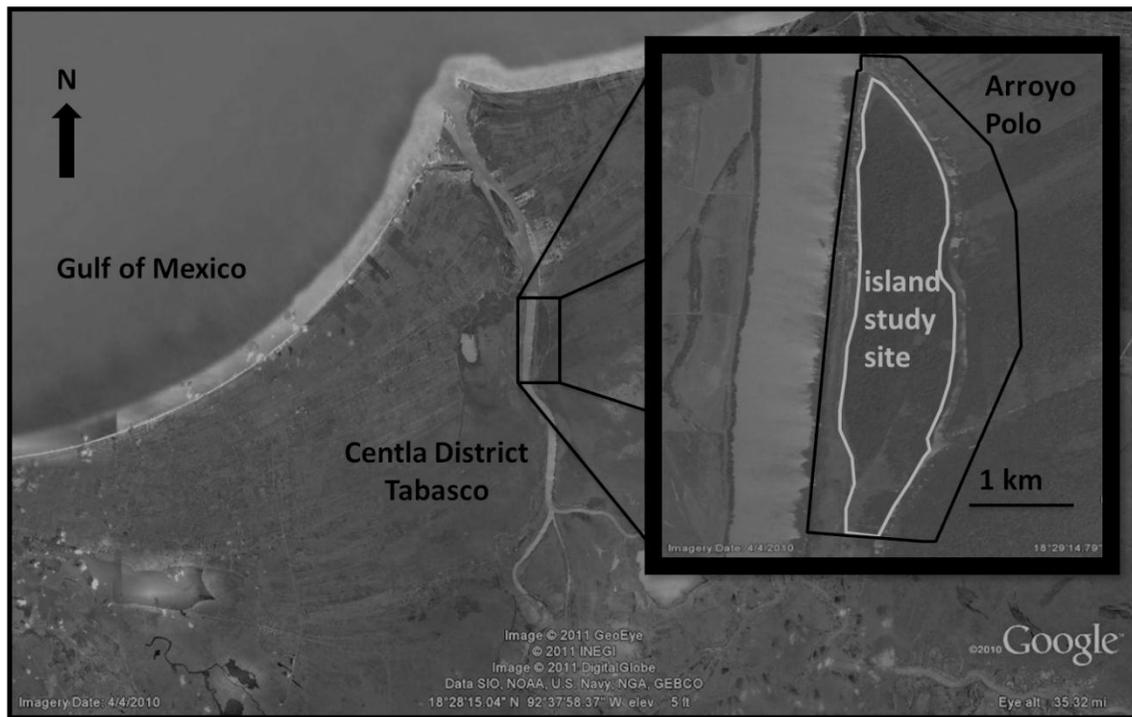
According to the Ramsar report, the fauna in the reserve include 72 species of reptile, 60 species of fish, 25 species of amphibians, 86 species of mammals, and 191 species of birds, both migratory and resident. The Instituto Nacional de Ecología (National Institute of Ecology of Mexico) reports slightly different numbers: 68 reptile species, 52 fish species, 27 amphibian

species, 104 mammal species, and 255 bird species (INE, 2000). In either case, a high level of animal biodiversity on the reserve is evident. One hundred and twenty-three of these species are endangered or vulnerable and are nationally protected, including the peregrine falcon (*Falco peregrinus*), the jabiru stork (*Jabiru mycteria*), the Morelet's crocodile (*Crocodylus moreletii*), the jaguar (*Panthera onca*), the West Indian manatee (*Trichechus manatus*) (Ramsar, 2001; ParksWatch-Mexico, 2003), and only two species of primates: Mexican mantled and Yucatán black howler monkeys (*Alouatta palliata mexicana* and *Alouatta pigra*) (Luecke and Estrada, 2005).

Although many animals use the mangrove, there are few mammals that live in it exclusively. Besides the monkeys, other arboreal mammals observed in the mangroves at the study site include the coati (*Nasua narica*) and the zorro espino, or Mexican hairy porcupine (*Sphiggurus mexicanus*). Coatis are both terrestrial and arboreal and frequently use the ground to travel and search for insects and small vertebrates to eat during the day. Coatis may also exploit the crustaceans and snails found in abundance in the mangroves. The Mexican hairy dwarf porcupine, uncommon in lowland wet forests, is arboreal and nocturnal (Reid, 1997). Its diet consists of both leaves and fruit. The tamandua or anteater (*Tamandua mexicana*) was spotted on one occasion during the field study. Tamanduas eat mainly termites and ants, are both arboreal and terrestrial, and prefer habitats with many vines and epiphytes near water. Encounter rates for these animals were very low over the course of both field seasons (three coatis, two spiny porcupines, and one tamandua), leading to the conclusion that their densities are also low in the mangrove habitat.

## Study Site: Arroyo Polo, Centla District

The study site is located near the northern border of the reserve and is an island formed by an estuary that empties into the Grijalva River (Figure 2.2). The site is within a fishing community and shared land called Arroyo Polo (18°29'10.10" N, 92°39'00.48" W).



**Figure 2.2.** The island study site in Arroyo Polo, Centla District, Tabasco, Mexico.

## Field Methods

Research was conducted from July-October 2009 and from March-May 2010 to collect data through both the wet and dry seasons. Because of my previous pilot studies and familiarity with the area and the animals, only the first few weeks of the study were devoted to locating, censusing, and habituating the howler study groups and holding informal meetings with local community leaders for permission to work on the island. I spent one week habituating the study groups who were already used to seeing people (fishermen) in the mangrove.

Inter-observer reliability was tested during behavioral data collection while habituating the monkeys in the first few weeks (92% reliability achieved). Behavioral data collection was conducted four days a week, beginning in mid-July 2009 and continuing through both field seasons until the end of May 2010.

Vegetation plots were undertaken once a week for four weeks in the 2009 season. Three additional plots and a Gentry transect (Gentry, 1982) were performed during the 2010 season. One day per week during both field seasons was dedicated to the collection and processing of vegetation samples. Local guides were hired to assist with vegetation plots and with the transect. Guides provided initial plant identifications with local names and information on local uses. Plants were later identified with their scientific names using field guides and confirmed by botanists at the herbarium on the campus of the Universidad Juárez Autónoma de Tabasco, División Académica de Ciencias Biológicas (UJAT) in the capital city of Villahermosa.

Daily temperatures and rainfall were collected in the village of Arroyo Polo. Temperatures were recorded in Celsius degrees using a Taylor® Wireless Weatherguide™ station and precipitation in millimeters using a Productive Alternatives® All-Weather Rain Gauge. For comparative purposes, 29 years of temperature and rainfall data (1971-2000) were downloaded from the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) website for the northwest portion of the reserve (SEMARNAT, 2010).

### *Study animals*

The monkeys in this study are *Alouatta pigra* (Lawrence, 1933), known colloquially as Yucatán black howler monkeys in English and as *saraguatos* or *monos aulladores* in Spanish (Figure 2.3). In the study area, the monkeys are *changos* or simply *monos* (monkeys). Black

howlers are endemic to southeastern Mexico, Belize, and throughout northern Guatemala (Rylands et al., 2006). The site in this study is on the westernmost edge of this species distribution, which ends at the eastern bank of the Grijalva River in this region.



**Figure 2.3.** *Alouatta pigra* adult female in the study site.

Subjects selected for the study included five groups of black howlers (N=29 individuals in total) on the mangrove island in the fishing community of Arroyo Polo (Table 2.1). Age classifications follow Carpenter (1965) and Glander (1980). The demographics of the study population were 6 adult males, 12 adult females, 4 male juveniles, 2 female juveniles, 4 male infants, and 1 female infant. The adult male to adult female ratio was 1:2. Adult female to infant ratio was 2.4:1 and adult female to immature (juveniles and infants) ratio was 1.1:1. Average group size was 5.8 individuals. Groups had an average of 1.2 adult males (ADM), 2.4 adult females (ADF), 1.2 juveniles (JUV), and 1 infant (INF). The five groups were identified by

composition, location, and individual distinguishing characteristics, such as scarring. Most were named according to each group's core area, except for the group closest to the bridge, in which the adult male was very vocal most of the time (Cranky Group).

Group	ADM	ADF	JUV	INF	Total
Cranky	1	2	0	1 (m)	4
Island	1	3	2 (m,f)	1 (m)	7
Letty's	1	3	1 (m)	1 (f)	6
Fence	2	2	2 (m,f)	1 (m)	7
End	1	2	1	1 (m)	5
Total	6	12	6	5	29

**Table 2.1.** The study subjects: *Alouatta pigra* (black howler monkey) groups and demographics.

ADM=Adult male, ADF=Adult female, JUV=Juvenile, INF=Infant; (m)=male, (f)=female.

### *Behavioral observations*

Quantitative behavioral and feeding data were systematically collected using focal-animal sampling (Altmann, 1974) to document and compare activities and feeding behavior within and between species. General behaviors representing the typical activities of howler monkeys were recorded. These included feeding, resting, locomotion, and social behaviors. Feeding behavior included actual chewing and ingestion of food items and every effort was made to identify plant part and species eaten. Plant part categories were defined as leaves, fruit, flowers, seed pods, stems, bark, and roots. Resting was scored as active, inactive, or neither if visibility prevented determining if the focal animal was awake and attentive or if its eyes were closed and seemed to be sleeping. Locomotion involved movement either within the same tree (move) or between trees (travel). Social behavior records included the nature of the social

interaction (affiliative or aggressive), with whom the interaction occurred, and whether the focal animal was the performer or recipient of the interaction. Affiliative social behaviors were further noted as grooming, resting-in-contact, play, touch/contact, and copulation. Aggressive social behavior was noted as displacement, charge, chase, and vocalize (including only vocalizations directed at another individual that elicited an evasive reaction). Table 2.2 is an ethogram further outlining these behaviors.

Behavior	Definition
Feed	The act of placing a piece of food material into the mouth and chewing. Includes both active rest and eating, together.
Locomote	The distance an individual or group moves that is greater than its own body length, but is within the same tree.
Travel	The distance an individual or group moves that involves moving from one tree to another tree.
Rest	An individual is completely without activity. Can be resting inactively (eyes closed, sleeping) or actively (eyes open, alert).
Social	Any purposeful behavior that involves interaction with another individual.
Affiliative	Behavior which is intended to make or maintain peaceful social bonds between individuals. May include touching (through contact of any part of the body), proximity, grooming, and play behaviors.
Aggressive	Behavior which is intended to increase the social dominance of one individual relative to the dominance position of other individual. May include displacement, hitting, vocalizations paired with posture indicating some sort of conflict. Conflicts are usually over status or access to resources.

**Table 2.2.** Ethogram: definitions of behaviors collected during this study. Modified from Marsh (1999).

### Focal animal sampling

Focal-animal sampling (Altmann, 1974) is the collection of behaviors for an individual during a sample period. With this method, one can collect data from selected individuals of several behaviors by watching one focal individual at a time. This method of data collection can accurately provide information on frequencies of behaviors (Lehner, 1996). All-day follows (0600-1800 hrs) with one-hour focal animal sample periods were used to collect the behavior of individuals.

Age and sex of focal animals were rotated for hour-long sample session when possible to achieve equal sampling for each throughout each collection day. Focal animals were chosen at random and were according to individuals visible at the time. If a focal animal went out of view during the sampling period for more than 10 minutes, collection on that animal terminated and a new focal animal was selected. All recorded out-of-view data were subsequently removed from the dataset before analysis.

### Instantaneous sampling

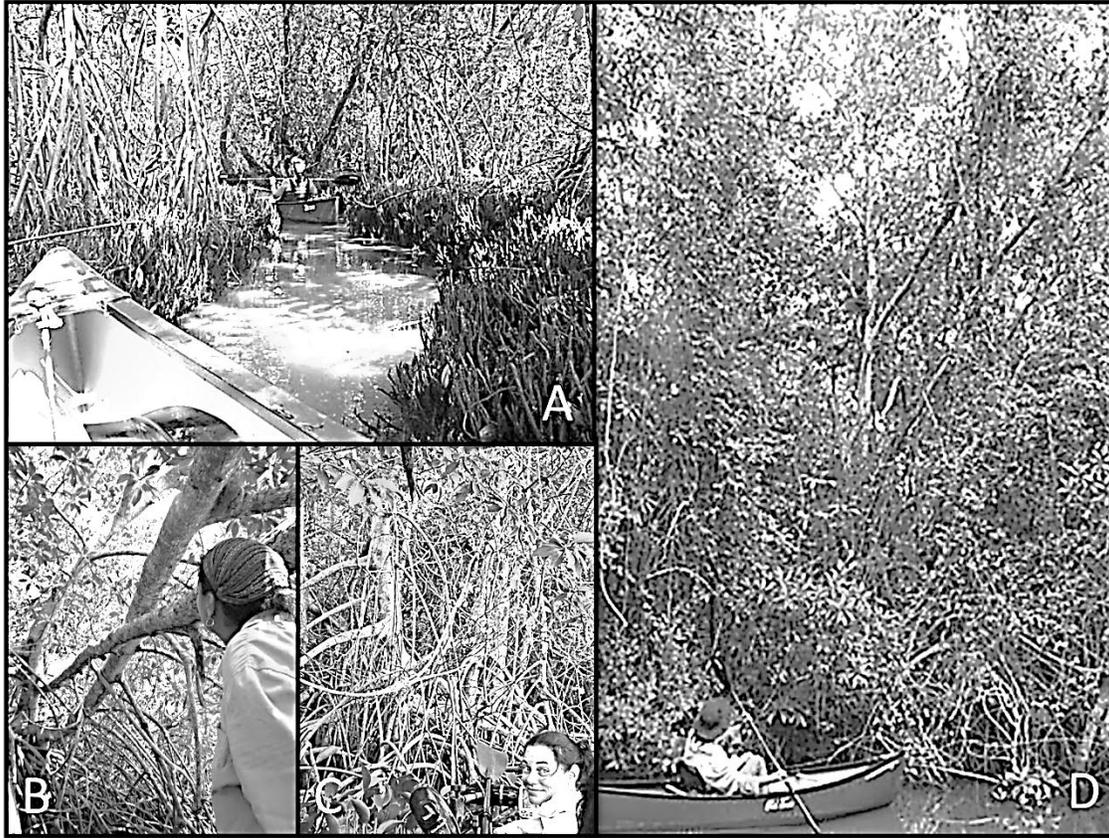
Instantaneous sampling involves the recording of the focal animal's behavior at predetermined points in time. This is an appropriate method for determining time (activity) budgets (Lehner, 1996). Behaviors of focal animals were recorded at five-minute intervals during each one-hour sample.

### Group scans

Group scans, in which the behaviors of all group members are recorded, were collected at 10-minute intervals in hour-long samples. Group scans were conducted when all group members

were within visible range. If an individual was not visible at the 10-minute interval mark, it was recorded as out of view.

Focal groups were followed four days a week from canoes or a motorboat. Groups were watched opportunistically. Some groups were much easier to observe than others and so were watched more frequently than other groups. It is possible that this bias could affect my results in terms of number of different individuals sampled and substrate used, due to a higher density of red mangrove near the water's edge, but not likely to affect data collected on food choices and general behavior, as food resources were fairly evenly distributed throughout the site (see results later in this chapter).



**Figure 2.4.** Collecting behavioral data. A. Paddling on a natural path through the mangrove following monkeys. B. Watching a group high up in red mangrove. C. Watching a group lower to the ground from the motorboat. D. Looking for monkeys along the water's edge.

### *Forest structure and community*

The influence of different habitat components on the survival and reproduction of individuals is important to our understanding of proximate and ultimate forces shaping primate adaptive behaviors and life history traits. Thus, the description of forest type and structure is fundamental to making inferences about environmental effects on the morphological, physiological, and behavioral traits of the animals inhabiting them. In this study, I sampled the vegetation on the island using two different methods and collected data in order to describe the

structure of the mangrove forest and its diversity. Structural components include measurements of the trees and lianas. Habitat diversity measures include tree species density, richness, and evenness. These descriptions allow for direct comparison of the vegetation at the mangrove study site with published data on other habitats.

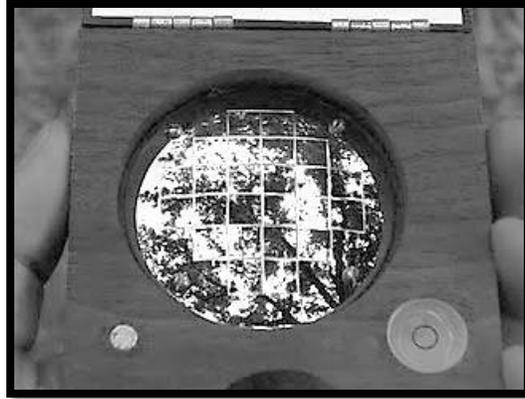
#### Vegetation sampling plots

A circular plot method was used to sample vegetation for diversity and richness and to describe forest structure within the mangrove island. Each plot had a 5 m radius and sampled a total area of 78.5 m<sup>2</sup>. A 10 m x10 m grid system was overlaid onto a georeferenced map of the study area and plot locations were randomly selected using Microsoft Excel® random numbers generator. The center of each selected plot was marked as a waypoint in a Garmin® III Plus™ GPS handheld satellite receiver and subsequently located on foot by the field team to an accuracy of within 5 m.

Tree data were collected from 16 circular plots within the study area (Figure 2.6). Trees greater than 10 cm DBH (diameter at breast height—c. 1.3 m from ground level) or GBH (girth at branching height—above the uppermost stilt root on red mangrove) were included in the sample. If a qualifying tree trunk was at least halfway inside the 5 m radius, it was included in the sample. Other variables collected from each tree within the plots were bole height, crown height, total height in meters, and distance to nearest neighbor trees >10 cm DBH/GBH (Gentry, 1982). I used a metric DBH tape from Forestry Suppliers® for measuring tree trunk diameters. Using a 50 m retractable tape and two people, crown area was approximated as the distance between opposite extremes of the crown along perpendicular axes from below. Tree height was estimated using the “person method”. In this method, a person of known height in meters stands at the base of the tree. A second person moves as far away as is needed to see the tree top.

Then, using their hands scaled to the size of the person by the tree, the second person counts how many “people” there are to the top of the tree. Bole height (BH), or the height at the first branching, was estimated using the same method. Distances between trees in the sample were also measured in meters. Identification of sample trees came first from our guide in local terminology and then by the field team in scientific names using a text on vegetation in the area (Novelo Retana, 2006). I made an estimate of above-ground biomass of mangrove trees, using an algorithm based on DBH/GBH, developed by Soares and Schaeffer-Novelli (2005). As a measure of tree volume and stand competition, I calculated basal area (BA) for trees in square meters.

Canopy cover is an estimation of ground surface area covered by shade, using a spherical densiometer (Figure 2.5), and produces a measure of connectivity of large trees which form the canopy, and in which howlers tend to travel. A spherical densiometer allows accurate, one-person measurement of tree canopies. Instruments are a spherical-shaped convex mirror engraved with a cross-shaped grid of 24 1/8" x 1/8" squares. Each square represents an area of canopy cover or canopy opening when the area overhead is reflected onto the sphere. To take readings, the instrument is held level, 12" to 18" in front of body and at elbow height, and the number of squares that are open are counted. If some squares are only partially open, they are added together to make a complete open square count. The total count is then multiplied by 4.17 to obtain the percent of overhead area not occupied by canopy. The difference between this and 100 is an estimation of overstory density in percent (California Dept. of Pesticide Regulation, 2004). Densiometer readings were taken in each quadrant of the circular plots and at 20 m intervals along the transect.



**Figure 2.5.** Spherical densiometer used to estimate canopy cover.

### Gentry Transect

A 1 km line transect was conducted through the center of the study area, west to east, to record floristic transitions across the island from water's edge to water's edge (Figure 2.6).

Gentry transects incorporate 2 x 50 m sampling plots along a straight line (Gentry, 1995). We conducted six of these plots along the transect and avoided autocorrelation and non-independence by spacing each plot 50 m apart (Ganzhorn, 2003).

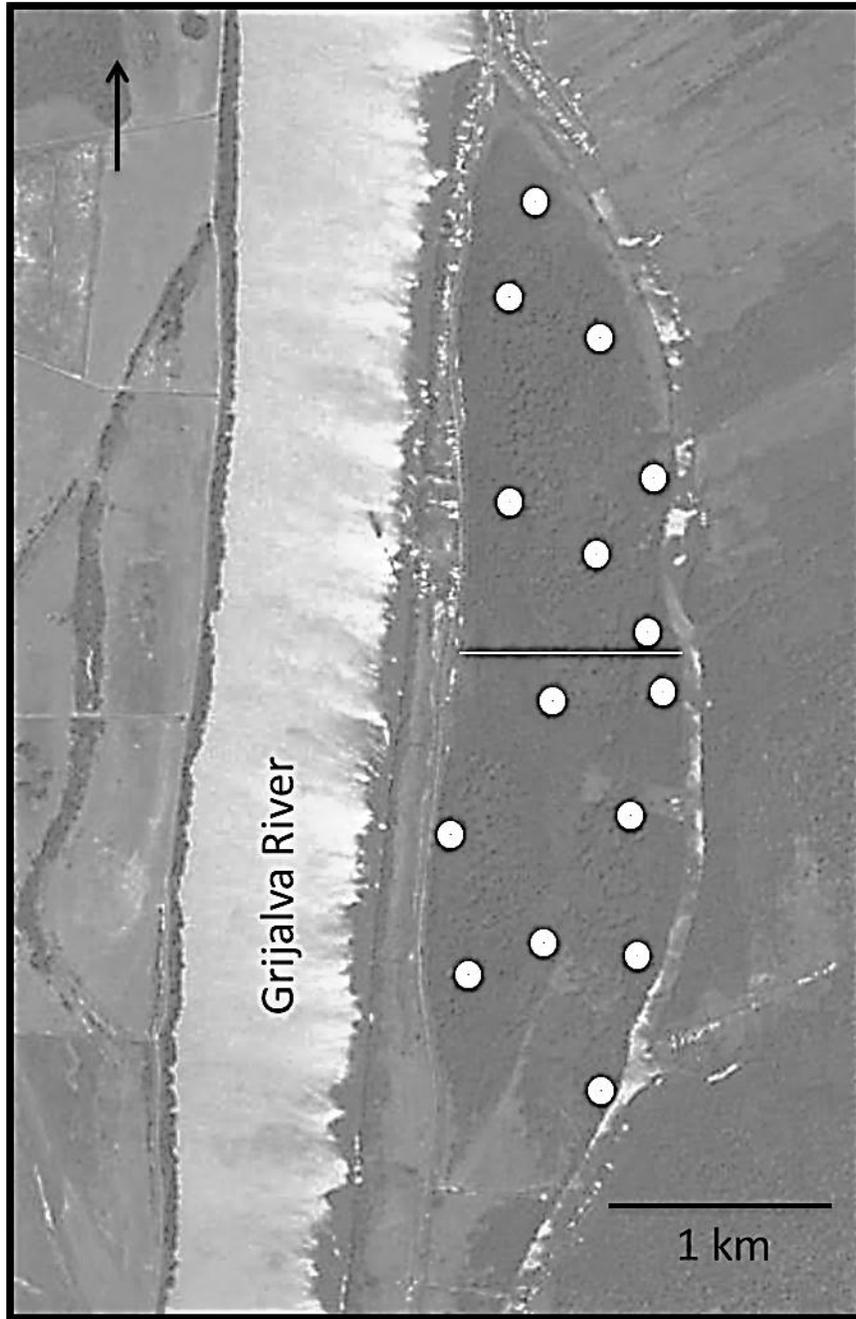
The beginning point of the transect was selected according to accessibility and authorizations by the local governing committee. The transect team included two local guides and six field team members. Each team member was assigned a specific job; the guides measured and ran the line while another person checked the bearings on a compass to keep the transect line due east across the island. The remaining three people measured and marked plot edges, took measurements, recorded vegetation data, and collected samples.

Liana censuses were conducted within the plots along the Gentry transect but not within the circular plots, as transect sampling provides a better estimate of liana above ground biomass (Schnitzer et al., 2006). Lianas are strictly defined as

...climbing plants that produce true wood (i.e. xylem tissues derived from vascular cambium) and that germinate on the ground but lose their ability to support themselves as they grow, so they have to rely on external physical support to ascend to the canopy (Gerwing et al., 2006:257).

Lianas are a significant component of tropical forests and can make up 10-45% of forest species (Schnitzer, 2006). These important plants are often overlooked in the census of forest species because of the difficulty involved in identification and measurement (ibid.). There is much debate over which climbing plants should be included in a census of lianas because climbing monocots and fibrous “subwoody” dicots (ibid:257) also contribute to forest structure, biomass, and diversity.

Lianas were sampled using a standard protocol (Gerwing et al., 2006) in which all individuals within the 50 x 2 m plots were identified and measured for DBH where the liana stem crossed a horizontal plane 130 cm above ground. This method was chosen because of the difficulty in finding where exactly lianas were rooted within the plots (many were underwater). Above ground biomass (AGB) was estimated for lianas using an allometric equation developed by Schnitzer et al. (2006).



**Figure 2.6.** Location of the 16 circular vegetation plots and the 1 km Gentry transect in the field site (indicated by the white line).



**Figure 2.7.** Vegetation sampling. A. Taking measurements for a circular plot. B. Taking measurements for the transect. C. Liana thicket along the transect. D. Climbing red mangrove roots to take a girth measurement.

### Vegetation collection

For each plant sample collected for deposit into the herbarium or for analysis, several data points were recorded in the field. First, the sample was given a collection number which reflected the date, the type of plant (e.g., tree or liana), followed by the sequential number for that type of specimen that day. For example, if two tree samples were taken on October 23, 2009, the first would be T102309-1 and the second T102309-2, and so on. If more than one sample was taken from the same individual plant, (flowers from T102309-2, for instance), the

collection number would be T102309-2a. If the species was identifiable, it was recorded. The plant part and collector were also recorded. Geographic coordinates (waypoints) for each sample were documented using a handheld GPS receiver (Garmin III Plus®). Specimens were either wrapped in newspaper or secured in plastic Whirlpak® bags for transport out of the field. Plant samples generally were 100g wet weight, although for some plant samples, we could only obtain part of this goal weight due to access and/or availability. Plant samples for identification, herbarium deposition, and nutrient analysis were taken back to the plant laboratory in the village for processing.

I took photographs of the specimens either *in situ*, against a scale in the lab, or both. Fresh weights of plant samples were measured using a Pesola Micro Line® spring scale. These data were recorded on the collection bag and in a notebook by hand, and then entered into a Microsoft® Excel database. The specimens and their corresponding data were transferred to brown paper bags for drying. Bags were closed and left inside the lab for several weeks to dry. After drying, the samples were weighed again using the same scale to estimate water content (in mg). If the plant was unknown or not verified, a voucher specimen was prepared to take to the herbarium at the Universidad Autónoma de Tabasco in Villahermosa (UJAT) for identification and deposition into the herbarium.



**Figure 2.8.** Vegetation collection. A. Sometimes getting a food sample involves a lot of climbing. B. Preparing a sample in the field for pressing and drying. C. *In situ* photo of *Urechites andrieuxii*. D. Plant sample in photo C dried and pressed for the herbarium collection.

Plant samples slated for the herbarium were prepared according to guidelines (Liesner, 1992) provided by Dr. James Solomon, curator of the herbarium at the Missouri Botanical Garden in St. Louis, Missouri. These samples were stored in sealed dry boxes until the next trip to UJAT, located a 1.5-hour drive southwest of the field site. Protocol for storage of plants to bring back to the United States for analysis included sealing the samples in Whirlpak® bags after sampling and storing them in an airtight dry box until USDA inspection at the border and

transportation back to Missouri was complete. Samples were then processed by re-drying in paper bags for two weeks indoors, re-weighing to get a final dry weight, and grinding each sample into a powder using a coffee mill in a sterile environment to prepare them for analysis.

## **Analyses**

### *Howler population and biomass on the island*

I assessed the howler population on the mangrove island during field seasons from 2005, 2006, 2009 and 2010. I conducted censuses in which the primary foci were group counts and demographics (Luecke and Estrada, 2005, 2006). I used the same methods described in said reports to evaluate the population again after three years and before behavioral data collection began. I express demographics on a population and a per-group basis. I present ratios of females to males, infants to adult females, and immatures (infants and juveniles) to adult females on a population basis.

The density and biomass of primates in area are functions of population estimates, average primate weights, and the size of the area sampled. I calculated primate density using methods described in the National Research Council's (NRC) 1981 publication on the study of animal populations:

$$\text{Density: } \frac{\text{estimated animal population}}{\text{census area}}$$

Density is expressed as individuals per square kilometer (ind/km<sup>2</sup>). For biomass, I used Smith and Jungers' (1997) body weights for adult male and female *A. pigra* and multiplied them by the numbers for all adults in the population. I estimated juveniles to weigh half of the adult weights

and infants to weigh 1 kg each then multiplied these figures by the number of juveniles and infants in the population. I then summed the quotients and divided the total by the sample area to give biomass in kilograms per square kilometer (kg/km<sup>2</sup>) and compared these data with earlier studies of biomass and density of black howlers (Luecke, 2004).

### *Vegetation*

Basic statistical descriptions of forest structure from data collected on trees and lianas in the field, including mean calculations for DBH/GBH, canopy area, canopy cover, height, and bole height were constructed using Minitab® statistical software.

To describe the diversity of the vegetation and make comparisons with other primate habitats, I calculated standard diversity indices (Simpson's Diversity Index and the Shannon-Weiner Index) to estimate richness and density for the mangrove island species. These indices are used in many studies of primate habitats to describe these characteristics.

### Species richness (trees): Simpson's Diversity Index

Simpson's Diversity Index is a calculation of the number of species in an area and is used as a measure of diversity (Simpson, 1949). Simpson's Diversity Index has been used frequently in studies of species richness and evenness. Indices calculated in this study follow:

$$\sum \left( \frac{n_i(n_i - 1)}{N(N - 1)} \right)$$

Where  $n_i$  represents the number of individuals (in this case, trees) belonging to the  $i$ th species and  $N$  represents the total number of individuals (trees, all species) in the dataset. This

measurement takes into account not only the number of species present, but also the relative abundance of each species. The Simpson index represents the probability that two randomly selected individuals in the habitat will belong to the same species. The index output is between 0-1, with 0 characterized as having no diversity and 1 as having infinite diversity.

*Species diversity (trees): Shannon-Weiner Index*

The Shannon-Weiner diversity index is widely used for comparing diversity between various habitats (Clarke and Warwick, 2001). The equation is:

$$H' = - \sum_{i=1}^s p_i \log(p_i)$$

(Chao and Shen, 2003).  $H'$  represents the Shannon Index of observed diversity,  $s$  represents richness or the total number of tree species in the community, and  $p_i$  represents the proportion of  $s$  made up of  $i$ th species. However, Shannon's original equation does not take into account species that may be rare and are not included in the sample. Chao and Shen (2003) proposed an alternate equation for which a better estimate of species richness and diversity can be estimated. The new algorithm is based on examining diversity as a whole using plot-based data, then dividing those data into groups of rare and abundant in the dataset. The default number for the cut-off between rare and abundant species is 10, so that species with records lower than 10 are rare and it is these species that are the base of the estimation of how many species are likely to be missed during censuses. I downloaded the program SPADE (Species Prediction and Diversity Estimation (Chao, 2010) and used it to test how many species might be missing from my plot and transect data.

### Above-ground biomass (AGB) and basal area

Above-ground biomass (AGB) is a good indicator of plant productivity and food abundance in a forest (Chapman and Pavelka, 2005; Tombak et al., 2011). Soares and Schaeffer-Novelli (2005) proposed models for estimating AGB for both *Rhizophora mangle* and *Laguncularia racemosa*, which are the two most prevalent tree species in my study site. The authors base their models on direct field data from two sites in Brazil, one of which (Bertioga, São Paulo) is similar in structure, density, and community composition to my site in Arroyo Polo (Table 2.10). In their study, total biomass includes prop roots, trunks, leaves, twigs, branches, and reproductive parts. Biomass is measured in dry weight (kg). I used the regression models from Bertioga in my analysis of the two true mangrove species used by the howlers in Arroyo Polo. For *Laguncularia*, the regression is:

$$Biomass = -441.05021 + 464.47815 (DBH)^2 - 645.89716 (height)$$

For *Rhizophora*, the regression is:

$$\ln(biomass) = 4.89219 + 2.61724 \ln(GBH)$$

Foresters and researchers alike use diameter at breast height (DBH/GBH) as an indicator of leaf biomass (Catchpole and Wheeler, 1992). In addition to biomass estimates using the methods outlined above for red and white mangrove trees, I calculated indices of potential food biomass above ground for all tree species found in the plots and transect using cumulative DBH/GBH along with density of trees per hectare.

The equation for estimating AGB of lianas in this study required the conversion of DBH at 130 cm above the ground to the estimated DBH of the liana stem at 130 cm above the root.

This equation is:

$$D_{130} = 0.07 + 1.02 (D_{passing} 130)$$

where  $D_{130}$  is the stem diameter at 130 cm above the root and  $D_{passing} 130$  is the diameter of the stem at 130 cm perpendicular to the ground. Following conversion, I estimated AGB using the following allometric equation described in Schnitzer et al. (2006):

$$AGB = \exp[-1.484 + 2.657 \ln(D)]$$

In this equation, AGB is the predicted above ground biomass of oven-dried weight (kg) and D is the diameter of stems at 130 cm from the root of lianas.

The basal area of trees per square meter in the plots and transect was calculated for each species using the following metric equation:

$$BA = \frac{\pi}{4 * 10000} * DBH^2$$

Where DBH was an average of all trees of each species <10 cm DBH within the plots and transect samples. To calculate the basal area of tree species per hectare, the basal area per square meter was multiplied by 10,000.

## Statistical analyses

Comparisons of the primate population and forest characteristics with other sites were made using nonparametric Kruskal Wallis H tests and significance was set at  $p < 0.05$ . Minitab<sup>®</sup> Statistical Software, version 16 (Minitab Inc., 2012) was employed for statistical testing.

## **Results**

### *Howler population*

In previous surveys of the island, I detected eight groups of howlers through sightings and triangulation of morning and evening choruses (see Luecke and Estrada, 2005, 2006). During the present study, I came into visual contact with six of the groups and auditory contact with two others. My estimation is that there are still eight groups. We regularly encountered five of the groups which were the groups included in data collection. Mean group size was calculated from counts of the known groups and was then multiplied by the total number of groups on the island to estimate population density for howler in the mangrove. I propose there are between 46-50 black howlers on the island study site, giving a density of  $15.3 \text{ ind/km}^2$ . Using weight data for *A. pigra* from Smith and Jungers (1997) and average demographics per group, I estimate the primate biomass to be  $97 \text{ kg/km}^2$ .

I made comparisons among the study howlers in the mangrove and other populations of howler monkeys (Table 2.3). When compared with black howlers in other locations, the average group size for the mangrove black howlers was not significantly different ( $z = -0.17$ ,  $p = 0.862$ ). Likewise, when population density was compared with black howler populations in other habitats, there was no significant difference ( $z = 0.32$ ,  $p = 0.752$ ). Significant differences did not exist in mean group sizes among different *Alouatta* species in the sample dataset ( $H = 8.18$ ,  $df = 5$ ,

p=0.119), however, mean densities reported for populations of *A. palliata* (26.7 ind/km<sup>2</sup>), *A. caraya* (180.5 ind/km<sup>2</sup>), *A. guariba* (117 ind/km<sup>2</sup>), and *A. seniculus* (68.5 ind/km<sup>2</sup>) in South America were significantly higher than densities for *A. pigra* (15.2 ind/km<sup>2</sup>), including the mangrove population (z= -3.22, p=0.023).

Species	Site	Group size mean	Density (ind/km <sup>2</sup> )
<i>A. pigra</i>	PCBR, Mexico <sup>1</sup>	5.8	15.3
<i>A. pigra</i>	Calakmul, Mexico <sup>2</sup>	7.5	15.2
<i>A. pigra</i>	Palenque, Mexico <sup>3</sup>	6.7	23.0
<i>A. pigra</i>	Yaxchilán, Mexico <sup>2</sup>	6.6	12.8
<i>A. pigra</i>	Tikal, Guatemala <sup>2</sup>	8.7	17.8
<i>A. pigra</i>	Lachuá, Guatemala <sup>3</sup>	5.6	15.8
<i>A. pigra</i>	Lacantún W, Mexico <sup>4</sup>	5.5	14.4
<i>A. pigra</i>	Lacantún E, Mexico <sup>4</sup>	5.1	13.3
<i>A. pigra</i>	El Tormento, Mexico <sup>3</sup>	6.7	12.7
<i>A. pigra</i>	Bermuda Landing, Belize <sup>5</sup>	4.4	8.1
<i>A. palliata</i>	Los Tuxtlas, Mexico <sup>6</sup>	9.1	23.3*
<i>A. palliata</i>	HLP, Costa Rica <sup>7</sup>	10.2	30.0*
<i>A. palliata</i>	CSWR, Honduras <sup>12</sup>	6.3	78.0*
<i>A. caraya</i>	Rio Richuelo, Argentina <sup>8</sup>	6.4	81.0*
<i>A. caraya</i>	Isla Guascára, Argentina <sup>8</sup>	10.2	280.0*
<i>A. guariba</i>	Caratinga, Brazil <sup>9</sup>	6.8	117.0*
<i>A. seniculus</i>	Hato el Frio, Venezuela <sup>10</sup>	7.6	25.0*
<i>A. seniculus</i>	Hato MSGL, Venezuela <sup>11</sup>	10.5	112.0*

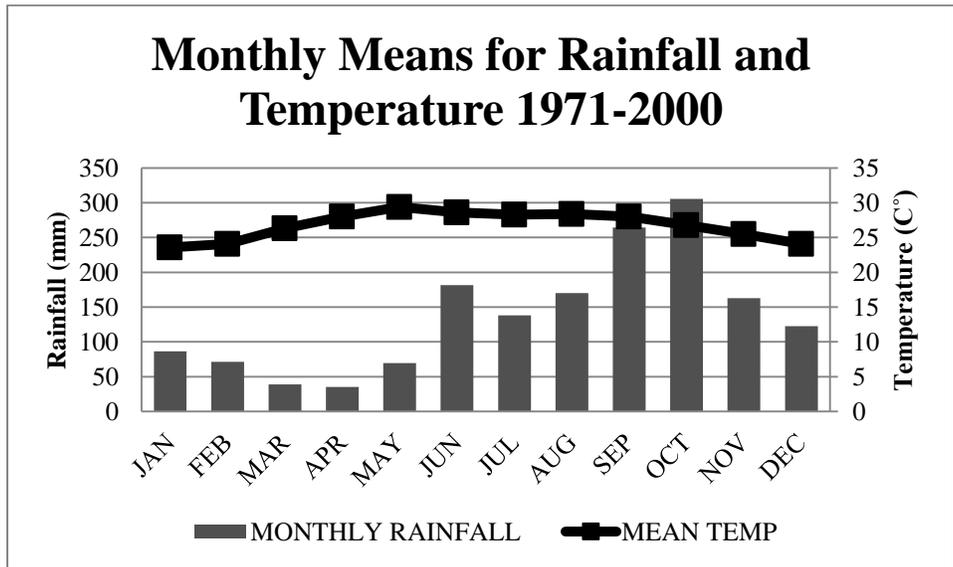
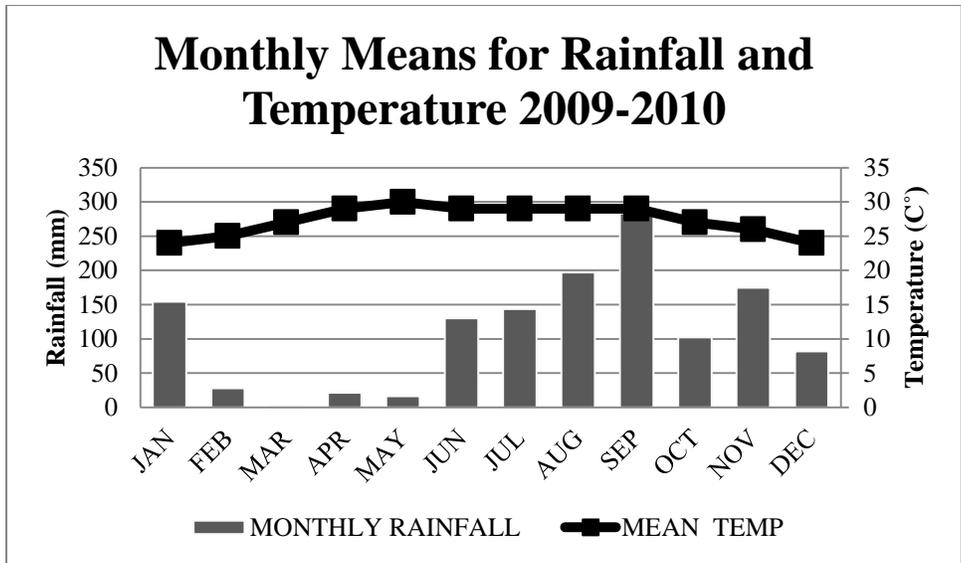
<sup>1</sup>This study. PCBR = Pantanos de Centla Biosphere Reserve. <sup>2</sup>Estrada et al., 2004a. <sup>3</sup>Van Belle and Estrada, 2006. <sup>4</sup>Estrada et al., 2004b. <sup>5</sup>Bolin, 1981. <sup>6</sup>Estrada, 1982, 1984. <sup>7</sup>HLP = Hacienda La Pacifica. Clarke et al., 2002. <sup>8</sup>Rumiz, 1990. <sup>9</sup>Mendes, 1989. <sup>10</sup>Braza et al., 1981 <sup>11</sup>Hato MSGL = Hato Masaguaral, Venezuela. Crockett, 1984. <sup>12</sup>Cuero y Salado Wildlife Refuge, Honduras. Snarr, 2006.

**Table 2.3.** Average group sizes and population densities of *Alouatta*. \*Significantly higher densities than black howlers (z= -3.22, p=0.023).

### *Weather patterns*

Over the course of the study period from July 2009 to June 2010, precipitation totaled 1,334.1 mm, with rain falling on 134 days. Rainfall was highest in the late summer through the autumn months and into winter from June through January, with monthly totals averaging above 100 mm (range 102.3-283.4 mm) and nearly half the days each month having rain. September had the highest amount of rainfall with 283.4 mm. In contrast, the dry season during the study period, from February through May, averaged 16.9 mm of rain (2.5-27 mm) and just 7 days of rain per month. March saw the lowest amount of rainfall for the year with just 2.5 mm. The mean high temperature over the annual cycle was 32 °C (89.1° F), the mean daily temperature was 27 °C (81.2° F), and the mean low temperature was 23 °C (73.3° F). April and May had the highest mean temperatures and December and January had the lowest mean temperatures.

There were no significant differences ( $H=4.0$ ,  $df=4$ ,  $p=0.443$ ) in daily max, mean, and low temperatures between the present study period and data pooled over a 29-year period from 1971-2000 (SEMARNAT, 2010). The number of days with rainfall did not differ significantly annually between the two datasets. Total rainfall for the study period was lower than the average for the long-term dataset, but this result was not significant ( $z=-1.0$ ,  $p=0.317$ ) (Figure 2.9).



**Figure 2.9.** Mean monthly temperature (in Celsius) and monthly rainfall (in millimeters) at the study site from July 2009-June 2010 (top) and from 1971-2000 (bottom).

*Forest community characteristics and structure*

Thirty-five species of trees, lianas, shrubs, aquatic plants, herbaceous monocots, and epiphytes were identified during vegetation sampling (circular plots, Gentry transect, and plant

collection for the herbarium and analysis) and behavioral data collection in the mangrove (Appendix A). Twenty-two families and 34 genera were represented in the site. Tree species numbered 17 in 11 families. Families with more than one tree species represented were *Arecaceae*, *Fabaceae* and *Combretaceae*. We identified 10 species of liana in 7 families. Families most represented for lianas were *Apocynaceae* and *Malvaceae*. Shrubs were represented by two species of the genus *Randia* (*Rubiaceae*), aquatic plants by the genera *Hymenocallis* (*Amyrillidaceae*) and *Eichhornia* (*Pontederiaceae*), and epiphytes by the genera *Selenicereus* (*Cactaceae*), *Polypodium* (*Polypodiaceae*), *Aechmea* (*Bromeliaceae*), and *Anthurium* (*Arecaceae*). Herbaceous monocots found on the island were from the genera *Sagittaria* (*Alismataceae*) and *Thalia* (*Marantaceae*).

#### *Circular plots and Gentry transect*

We collected vegetation data from 16 circular plots for a total area of 1,256 m<sup>2</sup> (Table 2.3) and sampled an area of 600 m<sup>2</sup> along the Gentry transect, representing a total of c. 20% of a hectare (Table 2.4). Many of the species encountered opportunistically while collecting samples during behavioral data collection were not encountered or were too small to be counted in the plot or transect sampling. Only trees larger than 10 cm in diameter (N=77) were counted in the circular plots. Trees larger than 10 cm in diameter and lianas larger than 1 cm in diameter were recorded in the Gentry transect plots (trees N=22, lianas N=110).

I estimated the average height of the forest was 8.7 m (c. 28 ft.) and the average DBH/GBH was 25.7 cm (c. 10 inches). Crown area averaged 47.1 m<sup>2</sup>. Canopy cover averaged 58% in the forest plots and 48% in the transect plots. Results for tree species densities (density

per hectare, relative density per hectare for the entire site, and total site density) are presented in Table. 2.6.

Plot	# Trees	# Species	CC%	Most Abundant Tree Species
1	5	2	64	<i>Rhizophora mangle</i>
2	5	3	69	<i>Laguncularia racemosa</i>
3	1	1	70	<i>Laguncularia racemosa</i>
4	3	1	75	<i>Laguncularia racemosa</i>
5	5	3	54	<i>Laguncularia racemosa, Rhizophora mangle</i>
6	4	1	59	<i>Laguncularia racemosa</i>
7	7	3	61	<i>Laguncularia racemosa</i>
8	2	1	61	<i>Laguncularia racemosa</i>
9	6	2	58	<i>Laguncularia racemosa</i>
10	8	1	58	<i>Laguncularia racemosa</i>
11	5	2	24	<i>Laguncularia racemosa</i>
12	8	3	53	<i>Laguncularia racemosa</i>
13	2	2	44	<i>Laguncularia racemosa, Bucida buceras</i>
14	6	1	49	<i>Rhizophora mangle</i>
15	5	3	69	<i>Lonchocarpus hondurensis</i>
16	5	4	59	<i>Laguncularia racemosa</i>
Total	77	4	58*	<i>Laguncularia racemosa</i>

**Table 2.4.** Tree data from circular plots. Each plot covered an area of 78.5 m<sup>2</sup>. CC% is the estimated percentage of canopy cover from an average of four measurements taken within each plot with a spherical densiometer. \*The average canopy cover percentage of all plots.

Transect Plot	# Trees	# Species	CC%	Most Abundant Tree Species
1	8	3	68	<i>Rhizophora mangle</i>
2	4	3	55	<i>Rhizophora mangle</i>
3	5	2	58	<i>Laguncularia racemosa</i>
4	2	2	40	<i>Bucida buceras</i> <i>Lonchocarpus hondurensis</i>
5	2	1	51	<i>Laguncularia racemosa</i>
6	1	1	19	<i>Laguncularia racemosa</i>
Total	22	5	48.5*	<i>Laguncularia racemosa</i>

**Table 2.5.** Tree data from Gentry transect. Each of the six plots covered a 100 m<sup>2</sup> area. CC% is the mean percentage of canopy cover from eight readings along each plot. \* is the average of all plot means.

Species	N/0.19 ha	Per ha	Relative Density Per ha/300 ha	Site Density Per ha x 300 ha
<i>Avicennia germinans</i>	1	5	0.02	1,500
<i>Sabal mexicana</i>	2	10	0.03	3,000
<i>Bucida buceras</i>	5	25	0.08	7,500
<i>Lonchocarpus hondurensis</i>	8	40	0.13	12,000
<i>Pachira aquatica</i>	10	50	0.16	15,000
<i>Rhizophora mangle</i>	21	105	0.35	31,500
<i>Laguncularia racemosa</i>	52	260	0.86	78,000
TOTAL	99	495	1.65	148,500

**Table 2.6.** Estimated densities of the most abundant tree species in combined data from sample plots and Gentry transect (Per hectare = N x 5).

### Top five tree species

#### Rank 1: Mangle blanco / white mangrove (*Laguncularia racemosa* Gaert.)

The white mangrove belongs to the Combretaceae (Indian almond), a family of trees, shrubs, or vines which can be found in a number of different habitats. This pan-tropical family is composed of between 14 and 22 genera and approximately 500 species (Tomlinson, 1986; Novelo Retana, 2006). In Mexico there are five genera and 18 species recorded, and on the reserve, there are four genera and five species recorded (Novelo Retana, 2006). Of these, *Laguncularia* is specially adapted to thrive in flooded and brackish environments, such as estuarine habitats, and tends to grow on the landward side where the substrate is more stable. *Laguncularia racemosa* is the only species of this genus found on the reserve or in the state of Tabasco.



**Figure 2.10.** White mangrove (*Laguncularia racemosa*) in the study site. A. Fruits. B. Foliage. C. Flowers.

White mangrove (Figure 2.10) is evergreen and typically 4-10 m tall with numerous pneumatophores radiating from the base of the trunk. The trunk is generally straight and its leaves are simple, elliptical, and opposite. Leaves are approximately 3-13 cm long and 1.5-4.5 cm wide. The leaf petioles have two prominent glands and the leaves are leathery and without visible veins. Some flowering may occur throughout the year, but has a peak in springtime (Allen, 2004). The fruit is a drupe with a single seed with a thin fleshy covering, which is dispersed as a propagule when mature by water. Typical uses for the hard and strong wood include firewood, fence posts, tool handles, and for making charcoal (Little and Wadsworth, 1964 cited in Allen, 2004).

White mangrove was the combined most abundant species with an estimated density of 260 individuals per hectare (ind/ha). Mean DBH in the vegetation plots was 33 cm, mean height was nearly 10 m, and crown area averaged 52 m<sup>2</sup>. White mangrove trees made up 41% of the trees recorded in the circular plots and 56% of the trees recorded along the transect. White mangroves tend to grow on the landward side of the water's edge where the supporting stratum is more stable, and beyond the red mangrove trees that fringe the banks. White mangrove forest dominates the middle of the island but areas of secondary growth or pasture dot the landscape where people removed the trees for firewood or grazing cattle.

Rank 2: Mangle rojo / red mangrove (*Rhizophora mangle* L.)

According to Novelo Retama (2006), the family Rhizophoraceae has approximately 16 genera and 120 species across the tropics worldwide. Four of these genera are adapted to saltwater and are found in mangrove forests. In Mexico, red mangrove is represented by two genera and three species, and on the reserve by one species – *Rhizophora mangle* (ibid.) (Figure

2.11). The genus *Rhizophora* has seven species that are commonly found in mangroves worldwide. Red mangrove wood is important socioeconomically as it is a durable wood used for construction of homes and furniture, is used in households as firewood for cooking, and has medicinal uses to “cure” diabetes (Novelo Retana, 2006:155).



**Figure 2.11.** Red mangrove in the study site. A. Stilt roots of the red mangrove under the canopy. B. Leaves and flowers. C. Propagated fruit.

This species can grow up to 25 m tall and has a straight trunk with many aerial stilt or prop roots, which provide support in the soft substrate for its massive trunk and limbs and oxygen for the roots buried in the anaerobic soil. Its leaves are simple and opposite and oblong in shape with a thick, leathery texture and measure 6-19 cm in length and 2-5 cm in width. The flowers have 4 lobes, are yellowish-white, and are in groups of 2-3. The flowers may be self-pollinated or wind-pollinated. The flower lobes are small at 0.5-1.5 cm in length. The fruits, actually embryonic root structures called propagules, of the red mangrove are germinated on the

parent tree (vivipary), and when ready, drop into the water and float to a new location and implant into a suitable stratum. The propagules can float and remain viable for at least a year before implantation.

Red mangrove is the second most abundant tree on the island growing mostly along the water's edge and where it can withstand shifting salt levels and continuously flooded conditions. Red mangroves have evolved to exclude salt when absorbing water through their roots. Red mangroves have an estimated density of 105 ind/ha and are the dominant trees that ring the island and waterways within the mangrove. Red mangrove accounted for 18% of trees recorded in the plots. Along the transect, 32% of the trees were red mangrove, and combined they made up 21% of both plot and transect data.

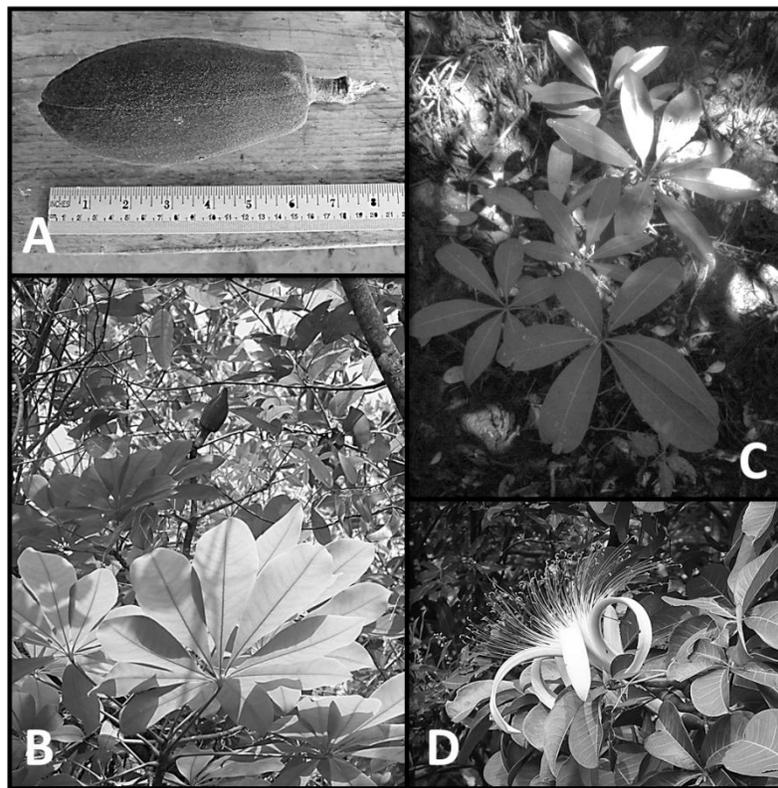
Rank 3: Zapote de agua / Guianan chestnut (*Pachira aquatica* Aubl.)

This pan tropical genus in the Malvaceae family has approximately 40 species, with a major concentration in South America. There are only two species described in Mexico. On the reserve, *P. aquatica* is the only species reported (Novelo Retana, 2006).

*P. aquatica*, seen in Figure 2.12, prefers flooded conditions and does especially well in areas where inundation is varied. These trees are relatively small ranging in size from 5-15 m in general and make up the understory canopy in my study site. They have straight trunks and composite 5-8 palmate leaves measuring 15-35 cm in length. The flower buds are 14-25 cm long and resemble pods. When the pod breaks open, it peels back like a banana and exposes a showy 5-petaled white-yellow flower of the same length. There are c. 100 bright orange-red colored stamen. This tree belongs to a family of plants that are known to be pollinated by bats (from their flower shape). The fruit of *P. aquatica* resembles a football in shape and can grow to be 30

cm long and 12 cm in diameter (Floridata, n.d.). There are several seeds inside the fruit, growing to about 4 cm each (Novelo Retana, 2006). The seeds are edible raw or cooked and can be ground into flour to make bread, although this is not common practice in Arroyo Polo.

*Pachira aquatica* trees were the third most abundant tree on the mangrove island, according to my censuses, with an estimated 50 trees per hectare. Because these trees were under the canopy of the larger red and white mangrove trees, they averaged nearly 6 m tall, with a mean DBH of 12.4 cm. Crown area was also relatively small at 7.4 m<sup>2</sup>.



**Figure 2.12.** *Pachira aquatica* in the study site. A. Mature fruit. B. Young tree leaves and fruit. C. Seedlings. D. Flower.

Rank 4: Gusano / swamp dogwood (*Lonchocarpus hondurensis* Benth.)

*Lonchocarpus* is a pan tropical genus in the family Fabaceae with approximately 130 species (all in the Americas, except for one in Africa). There are 67 species recorded in Mexico, and 12 in the state of Tabasco (Novelo Retana, 2006).

Gusano trees are typically 18-30 m in height, with a straight trunk and branches that rise then stretch out and bend down toward the ends (Alvarado et al., 2004). The leaves are dark green, paripinnate, and alternate. *L. hondurensis* flowers are small and purple, in axillary panicle form, and are pollinated by insects, primarily bees (Figure 2.13). The fruits are small fleshy pods 4-6 cm long containing one or two seeds. The wood of the gusano is considered a hardwood and is generally used in heavy construction, furniture, flooring, wagons, tool handles, transoms, pilings, and boats (ibid.).

In the study site, *L. hondurensis* density was estimated to be 40 ind/ha. Although gusano trees were not as tall on average as *P. aquatica* trees, they contributed more crown area to the lower canopy, with an average of 24.3 m<sup>2</sup>. Mean DBH was 13.7 cm.



**Figure 2.13.** *Lonchocarpus hondurensis* budding flowers.

Rank 5: Puckte / black olive (*Bucida buceras* L.)

The puckte tree belongs to the Combretaceae family, as does the white mangrove. The genus *Bucida* has four species distributed in the Americas from Florida through Central America and the Antilles (Novelo Retana, 2006). There are two recognized species in Mexico but only one of these is found in Tabasco and on the reserve (ibid).

*B. buceras* trees can grow to approximately 35 m in height but average about 15 m (Novelo Retana, 2006; USDA plants database) and have medium salt tolerance. The branches have 3-5 cm spines with clusters of leaves towards the end (Gilman and Watson, 2007). Its leaves are dark bluish-green, alternate, simple, 3.5-14 cm in length and 1.5-5 cm wide. This species is evergreen and produces leaves year-round. Flowers are inconspicuous and small and are only produced in the spring. The flowers are green-yellow and have a sweet scent (Figure 2.14). Fruits of the puckte tree are tiny (1.5 cm) seeds covered with a black flesh that have a high tannin concentration (ibid.). People use the wood for construction and at times for

firewood, but the fruit and seeds are not palatable (United States Department of Agriculture PLANTS Database, n.d.).

The density of puckete trees on the mangrove island site was estimated to be 25 ind/ha. They were the largest trees on average with a mean DBH of 67.7 cm and a mean height of nearly 11 m. They produced a lot of shade in the upper canopy with their large dense crowns, at an average of 191 m<sup>2</sup>.



**Figure 2.14.** *Bucida buceras* in the study site. Left, flowers just starting to bloom. Right, an example of the dense foliage with flowering at the apex of branches.

#### *Forest structure*

Overall, the mean height of trees in the mangrove was 8.7 m, the mean DBH was 25.7 cm, and the average bole height was 3.5 m. In Kruskal-Wallis H-tests, there were significant differences among tree species in DBH ( $H=35.7$ ,  $df=6$ ,  $p<0.01$ ), height ( $H=24.7$ ,  $df=6$ ,  $p<0.01$ ), and crown area ( $H=29.64$ ,  $df=6$ ,  $p<0.01$ ). In pairwise analysis, it became apparent that puckete trees (*B. buceras*) were significantly larger in terms of DBH and crown area than other tree species. White mangrove trees were the next largest in terms of DBH and height, followed by the Rio Grande palmetto (*Sabal mexicana*) and red mangrove trees.

The dominant trees in this mangrove were the white and red mangroves. In white mangrove forest, the mean DBH was 33 cm and the mean height was nearly 10 m. Bole height had a mean of 4.3 m and crown area averaged 52 m<sup>2</sup> that ranged from 5-150 m<sup>2</sup>. In stands of red mangrove, the mean GBH was 19.8 cm and the mean height 7.8 m. Crown area average for red mangrove trees was 52.3 m<sup>2</sup>, and ranged from 17 to 90 m<sup>2</sup> (Table 2.7).

GENUS	N	DBH (cm)	H (m)	BH (m)	CA (m <sup>2</sup> )	DENS (ind/ha)
<i>Laguncularia</i>	43	33.0	9.9	4.3	52.1	260
<i>Rhizophora</i>	14	19.8	7.8	3.2	52.3	105
<i>Pachira</i>	9	12.4	5.9	3.3	7.4	50
<i>Lonchocarpus</i>	6	13.7	4.7	1.8	24.3	40
<i>Bucida</i>	2	67.7	10.8	2.8	191.0	25
<i>Sabal</i>	2	32.8	7.0	4.3	20.5	10
<i>Avicennia</i>	1	10.2	3.0	0.5	20.0	5

**Table 2.7.** Mean structural data for trees in the 16 plots.

#### *Diversity and richness measures*

Alpha biodiversity for both transect and plots, estimated using Simpson's Diversity Index, was 0.334. This value indicates that biodiversity in the study site, on a scale from 0-1, was relatively low. However, this number is based on only the tree data collected in the plots and the transect (N=7 species). When I estimated how many species I might have missed in my enumerations using Chao's SPADE program, the result was that there were between 7-8 species that were unaccounted. This result is verified by the fact that I identified (and collected voucher specimens for) 15 species of tree on the island, eight of which did not appear in my plot and transect collection (Appendix A).

The result of the Shannon-Weiner Index (log) was 1.98 for the plots and transect data, a comparatively low index (Table 2.8). Lower numbers mean less diversity; for example, in communities where there is only one species, the index would be zero.

Site	<i>Alouatta</i> spp.	Forest type	Shannon- Weiner Index
Tabasco, Mexico <sup>a</sup>	<i>A. pigra</i>	Mangrove	1.98
CSWR, Honduras <sup>b</sup>	<i>A. palliata</i>	Mangrove/lowland swamp forest	1.20
Mombacho Volcano, Nicaragua <sup>c</sup>	<i>A. palliata</i>	Coffee plantation	2.88
Los Tuxtlas, Mexico <sup>d</sup>	<i>A. palliata</i>	High evergreen rainforest	3.25
Barro Colorado Island, Panama <sup>e</sup>	<i>A. palliata</i>	Lowland, moist forest	3.80
Santa Rosa NP, Costa Rica <sup>f</sup>	<i>A. palliata</i>	Tropical dry forest	2.15-4.95
Paraná, Brazil <sup>g</sup>	<i>A. caraya</i>	Mainland, semi-deciduous sub-montane	2.68
Paraná, Brazil <sup>g</sup>	<i>A. caraya</i>	Island, riparian	1.97-2.24

<sup>a</sup>This study. <sup>b</sup>Snarr, 2006. <sup>c</sup>Williams-Guillén, 2003. <sup>d</sup>Cristóbal-Azkarate et al., 2005.

<sup>e</sup>Milton, 1979. <sup>f</sup>Sorensen and Fedigan, 2000. <sup>g</sup>Ludwig et al., 2008.

**Table 2.8.** Comparisons of diversity indices for the mangrove with other habitats of howler monkey sites. All other sites were significantly different in this index from the mangrove sample (T=7.19, p<0.001).

Community Characteristic	This Study	Makandé Forest	Barro Colorado	Los Tuxtlas	CSWR
Tree Density	495/ha	469/ha	195/ha	633/ha	-
Number of Tree Families	13	34	-	23	17
Number of Tree Species	15	125	135	36	20
Relative Density (Top 5 species)	52.0	23.9	6.27	-	33.6
	21.0	13.6	4.21	-	25.7
	10.0	8.1	4.12	-	18.6
	8.0	4.9	3.76	-	6.2
	5.0	4.8	3.49	-	6.2
% (Top 5) of Tree Families	38.0	55.3	-	-	77.5*
% (Top 5) of Tree Species	33.0	24.5	23.9	-	-

**Table 2.9.** Comparison of tree species diversity and abundance in this study with a study of colobines and cercopithecines in a rainforest in central Gabon, Africa (Brugiere et al., 2002), Milton's 1980 study of mantled howlers on Barro Colorado Island, Panama, data from Los Tuxtlas in Veracruz, Mexico (Cristóbal-Azkarate et al., 2005), and mangrove/lowland swamp forest data from northern Honduras (Snarr, 2006). \* top three tree species.

#### *Above-ground biomass and basal area of trees and lianas*

Using linear equations developed for red and white mangrove trees (Soares and Schaeffer-Novelli, 2005), I estimated total above-ground biomass (AGB) for the dominant mangrove species on the island to be in excess of 52 million kilograms in dry weight (Table 2.10). This estimation of AGB for the two mangrove species is similar to those presented for mangrove forest in Bertioga, Brazil (ibid.).

	Mean Height (m)		AGB (kg)		EST. AGB PCBR	
	PCBR	Bertioga	PCBR	Bertioga	kg/ha	kg/300ha
<i>Laguncularia racemosa</i>						
DBH 10 cm	12	8.7	43	36	810	243,000
DBH 15 cm	7.5	10.4	99	95	5,285	1,585,500
DBH 20 cm	9	10.7	188	193	7,400	2,220,000
DBH >25 cm	6.6	-			22,620	6,786,000
<i>Rhizophora mangle</i>						
DBH 10 cm	4.5	9	54	61	855	256,500
DBH 15 cm	5	11	151	168	2,880	864,000
DBH 20 cm	4.4	7.6	296	310	6,815	2,044,500
DBH>25 cm	11	-			127,680	38,304,000

**Table 2.10.** Comparison of structural data and AGB of the Pantanos de Centla (PCBR) mangrove and a mangrove forest in Bertioga, São Paulo, Brazil (Soares and Schaeffer-Novelli, 2005) and above-ground biomass estimates for the study area in PCBR. AGB (kg) is the estimated above-ground biomass in kilograms per tree based on diameter at breast height (DBH) in centimeters and tree height in meters. The EST. AGB PCBR is the estimated total biomass per size and species of mangrove tree per hectare (ha) and for the entire study site (300 hectares) on the Pantanos de Centla Biosphere Reserve.

The estimated AGB for the liana *D. brownei* was 525 kg dry weight per hectare and 157,000 kg dry weight for the entire 300 ha island. There were no comparative AGB estimates for lianas in other howler monkey or mangrove sites.

Tree density and volume estimates in individuals/ha, basal area/ha and cumulative DBH/ha are presented in Tables 2.11 and 2.12. The most abundant species, *Laguncularia*, had a density of 260 ind/ha, the highest CDBH at 8,051.5 cm/ha, and the largest in basal area at 28.5 m<sup>2</sup>/ha. *Rhizophora* were second in terms of density (105 ind/ha) and CDBH (2,103.5 cm/ha), but third in basal area (3.5 m<sup>2</sup>/ha). Density of *Pachira aquatica* was 50 ind/ha, CDBH was 631

cm/ha, and ranked number six in BA at 0.65 m<sup>2</sup>/ha.. *Lonchocarpus* density was 25 ind/ha, CDBH was 611 cm/ha, and was 5<sup>th</sup> in volume of BA with 0.75 m<sup>2</sup>/ha. Cumulative DBH for *Bucida* trees was 958 cm/ha, its density was low at 25 ind/ha, and yet its BA ranked second at 5.0 m<sup>2</sup>/ha. *Sabal* palm density was 10 ind/ha, CDBH was 327.5 cm/ha, and was fourth in BA at 1.0 m<sup>2</sup>/ha. *Avicennia* had the lowest density, CDBH, and basal area (5 ind/ha, 10.2 cm/ha, 0.04 m<sup>2</sup>/ha, respectively). These seven species are the only trees (>10 cm DBH) I encountered during the plot and transect sampling. Other tree species were encountered opportunistically, and are listed in Appendix A and discussed in Chapter Four.

Genus	Density (ind/ha)	CDBH (cm/ha)	Basal Area (m <sup>2</sup> ) per tree	Basal Area (m <sup>2</sup> /ha)
<i>Laguncularia</i> *	260	8,051	5.7	28.5
<i>Rhizophora</i> *	105	2,103	0.7	3.5
<i>Pachira</i>	50	631	0.1	0.65
<i>Lonchocarpus</i> *	40	611	0.2	0.75
<i>Bucida</i> *	25	958	1.0	5.0
<i>Sabal</i>	10	328	0.2	1.0
<i>Avicennia</i>	5	51	0.0	0.04

**Table 2.11.** Tree densities, cumulative diameter at breast height (CDBH), and basal area calculations from plot and transect data for each species. Basal area in square meters is the sum of basal area for each species in the sample for the total sampled area of 0.2 of a hectare. Basal area in square meters per hectare is the previous calculation multiplied by 5 to extrapolate basal area in one hectare.

Site	Forest Type	Basal Area (m <sup>2</sup> /ha) of canopy trees	Density (trees/ha)	Reference
PCBR	Mangrove	39.4	495	This study
CSWR <sup>1</sup> Honduras	Mangrove/lowland swamp	36.4	760	Snarr, 2006
Santa Rosa NP Costa Rica	Tropical dry forest	14.9	828	Sorensen and Fedigan, 2000

**Table 2.12.** Comparison of basal area and density among howler and capuchin (*Cebus* spp.) study sites in low and high diversity habitats. <sup>1</sup>Data from the western section of the study site.

## Discussion

The mangrove community in Arroyo Polo is significantly lower than other habitats in terms of tree species diversity and richness. I predicted the mangrove howler population would have smaller group sizes and lower density than other howler populations in higher diversity sites. Lower population density was reported by Supriatna et al. (1989) for silver leaf monkeys (*Presbytis aurata*) in a western Java mangrove, where densities were less than half than populations in lowland tropical forest. Although plant diversity on the island was low, group sizes and howler monkey density were within the ranges found for black howlers in other sites with varying diversity. As is reported by several researchers and depicted in Table 2.3, black howler group sizes and densities tend to be lower than other howler species. I found that mean group size and density were most similar to those black howler populations a Lachuá, Guatemala (Rosales-Meda et al., 2008) and along the Lacantún River in Chiapas, Mexico (Estrada et al., 2004b). These habitats were not similar to the mangrove in composition, diversity, or density.

The proportion of males, females, and immatures in a population can give an indication of population health (Altmann, 1985). In the mangrove, adult male to female ratio was higher

(1:2) than for Lachuá (1:1.3) or Lacantún (1:1.3, 1:1.3). The adult female to immature ratio is used as a measure of the stability of a population, albeit constrained by group size (Zucker and Clarke, 2003), yet can give an indication if the population at the time of census is stable or not (Clarke et al., 2002, Cristóbal-Azkarate et al., 2005). Adult female to immature ratios in Arroyo Polo were most similar to those of a stable black howler population at the Lacantún east site (1:1.1 compared with 1:1.0), which were both higher than Lacantún west and Lachuá. Forest types and general habitats were not similar among the sites. I suggest that the even ratio of adult females to immatures in the mangrove indicates that the population is relatively stable at this time, and has been since my initial censuses in 2005.

The historical mean annual temperature reported for the reserve was 26°C. During the study year, the mean annual temperature was 27°C and monthly means were within the range of means for historical records. Rainfall for the study year was 300 cm lower than the average 1,667 cm reported for the area, yet 1,334 cm of annual rainfall is within the normal range for the past 30 years.

Of the 54 confirmed true mangrove species, only three are on the island. The forest is best described as medium height, evergreen, true mangrove forest. Red mangrove (*Rhizophora mangle*) lines the fringe of the island and expands like capillaries inward along waterways created by tidal inundation. Inland, white mangrove forest (*Laguncularia racemosa*) dominates the landscape with few black mangrove trees (*Avicennia germinans*). The white mangrove forest is dense with thickets of the ubiquitous liana Indian rosewood (*Dalbergia brownii*), inhibiting travel on foot, even with a machete. Other recorded species on the island are described as mangrove associates, yet diversity is low compared with diversity indices reported for other sites in varied habitats (Tables 2.7 and 2.8).

The Arroyo Polo mangrove island site differs from most other locations where howlers have been studied in two primary ways: 1) the howlers do not have access to other forest types and are isolated on the island, and 2) the low diversity and domination of the forest by only two species of tree. My site is also different in that the dominant tree species are adapted to high levels of salt tolerance and perpetual inundation. I propose that the mangrove habitat does not limit the health or the general characteristics of the howler population, judging from my population demographics and density estimations. While the mangrove may not affect population characteristics, it may affect behavior patterns, foraging strategy, and competition for resources within the howler population. I investigate the possible effects of tree density and abundance of feeding trees on the howlers' behavior and diet in the following chapter.

Both white and red mangrove trees have strategies for dealing with excess salt yet likely provide animals with necessary amounts of sodium that other, drier locations lack. Mangrove trees may provide other essential nutrients in sufficient amounts to meet the howlers' daily requirements. If the mangrove trees comprise a large portion of the howlers' diet, and if this diet is sufficient, then I expect to see a decrease in time spent traveling because of the high density of mangrove trees. If feeding trees have low density, then the howlers should increase travel time in comparison with howler populations with more diversity and possibly more food choices. If the howlers rely heavily on species with low density, then I expect to see competition, either within groups or between them, or both. If direct competition is not evident, then behaviors mitigating direct competition may be evident. If the howlers favor seasonal items, as is seen with other howler populations (Glander, 1978; Milton, 1980), then seasonal changes in resource use are likely to affect the behavior and ecology of the howler population in the mangrove. In order to evaluate the effects of the mangrove habitat on howler behavior, I examine the activity

and foraging patterns, the diet, and the relationships of forest characteristics to these environmental factors.

## CHAPTER THREE

### ACTIVITY PATTERNS AND FEEDING BEHAVIOR

#### Introduction

I described the tree community composition and forest structure of the study site at Arroyo Polo in Chapter Two. Tree density and species richness were lower in the mangrove forest in comparison with most other howler study sites, but were comparable to a few studies of howlers living in similar or altered habitats, such as mangrove/lowland swamp and agro-forest croplands like cacao. The low diversity and density of the mangrove, limited by excessive salt levels and tidal inundation, provide an opportunity to explore the relationship between a low-diversity environment and howler daily activity and feeding behavior. According to Milton (1980) and Juan et al. (2000), feeding patterns of *A. palliata* are dependent upon habitat-specific availability of resources. I suggest that *A. pigra* on the mangrove island will differ in their dietary composition and behavior patterns from howlers in other, more diverse, habitats. I predict that the mangrove howlers will exhibit less overall dietary diversity, use only a few species as staple foods, rely heavily on seasonal food items, incorporate more leaves into their diets than howlers in more diverse habitats, and exploit novel food resources, such as colony insects.

If food plant species are less abundant than at moderate to high diversity sites where *A. pigra* have been studied, then the mangrove black howlers will rely on those food species more heavily than black howlers at other sites. If food species are rare in geographic and/or temporal distribution, then the mangrove howlers may exhibit behavioral competition for preferred resources. If seasonal resources are used heavily, such as flowers and fruits, then time spent traveling during availability of seasonal items is expected to increase. If the mangrove howlers

eat more leaves, then I expect them to spend more time resting and digesting than howlers ingesting fewer leaves. In order to explore the relationship between activity patterns and the mangrove environment, I will define 1) the species and parts that make up the diet, 2) seasonal variation in food selection and availability, 3) feeding time spent on food species in relation to abundance and quality (quality is based on nutritional characteristics related to digestibility). Also in this chapter, I outline the activity patterns of the mangrove howlers on monthly, seasonally, and annual bases. I then compare the results with studies of black howlers in other sites and to studies of different species of howler monkeys in general in order to discuss how forest composition, forest structure, and food distribution influence the population and behavior of howler monkeys and possibly other folivorous primates.

## **Methods**

### *General behavior and diet*

The black howler monkeys observed in the study were 29 individuals in five cohesive groups. Groups had an average of 5.8 members, with 1.2 adult males, 2.4 adult females, 1.2 juveniles, and 1 infant. Detailed information on each of the groups and on the mangrove field site can be found in Chapter Two.

Behavioral data were collected from July – November 2009 (rainy season) and March – June 2010 (dry season). The field team consisted of 2-6 members, who varied throughout both field seasons. A combined total of 2,000 person-hours were spent in contact with the monkeys. Behavioral data collection was scheduled for four days a week for 32 weeks. Each behavior collection day began at 0600 in canoes or a motorboat and ended at 1800. The study area is a 300 ha island and therefore only accessible by water. It took five minutes by boat to arrive at the

beginning of the 8 km loop around the island. This loop was usually in a clockwise rotation, but varied somewhat depending on the direction of the tidal flow. For the most part, we maintained a 1 km/hr pace in the canoes, and a 3-4 km/hr pace in the motorboat. These speeds were variable due to environmental factors (i.e. wind, current).

Monkey groups were located at all times during the day, and occasionally no groups were located. Visual contact was usually made after movement was detected, either visually or audibly. Contact with a monkey group ranged from a few minutes to several hours. The mangrove habitat is difficult at best to maneuver through with its tangle of aerial roots, making it next to impossible to track monkey groups inside the mangrove unless they follow a natural waterway (Figure 3.1). Although it is possible that this limitation may have skewed my data on feeding behavior, I show with vegetation data that differences in forest composition across the island varies little, and thus may have no impact on the general behavior of the howlers that I observed.



**Figure 3.1.** Maneuvering through the mangrove by boat (left) or on foot (right) poses many challenges.

Each individual in a contacted group was counted by all members of the field team until a consensus on group size was met. Each individual was also sexed and assigned to an age group, according to size, following Carpenter (1965) and Glander (1980). The ethogram for the howlers in this study included the behaviors rest, feed, locomote (movement and travel), and social (either affiliative or aggressive). Definitions for each behavior are presented in Chapter Two.

Because the habitat prevented extended observations, focal animal scan sampling was the method chosen to collect behavioral data (Altmann, 1974). One-hour samples were conducted on focal animals; behaviors were recorded every five minutes. The one-hour samples continued on individuals unless the subjects went out of view for 10 minutes. After 10 minutes, a new focal animal was randomly chosen based on individuals visible at the time and a new hour of data collection began. Group scans of the activities of all group members were conducted every

10 minutes for one-hour time periods when all group members were generally in view. The substrate (tree or liana and species) used by the howlers during each behavioral data point collection was noted in order to examine species use in this manner.

When feeding activity was observed, the species and/or type (tree or liana) and the plant part consumed were recorded. Plant parts include leaves, fruits, flowers, seed pods, and stems. At times, the ages of leaves were discernible (new or mature) and recorded. Most mangrove seeds are contained in pods that are neither fleshy nor brightly colored. Seeds are primarily water or wind-dispersed in this habitat, so it is not necessary for fruits to be attractive to mammal or bird dispersers (Van der Pijl, 1982). Seeds in this study are defined specifically as seeds and their containing pods, not seeds inside fleshy fruit (see Figure 3.2). Food samples were collected for identification and nutritional analysis when possible either from the feeding tree or a nearby tree of the same species.



**Figure 3.2.** Typical water-dispersed seed pods in the mangrove: *Laguncularia racemosa*.

Observation time was not equivalent across groups because not all groups were accessible at the same rate due to difficulties following them in the mangrove. Observations were also not equivalent for both the wet and dry seasons. During heavy rain, the monkeys are not as active and are hard to locate because of our decreased ability to see and hear them. In order to correct for these incongruities, I present raw data results on each group's diets on a monthly and seasonal basis. The raw data consists of total feeding time for each food species and part, which are then summed in monthly increments and then calculated as percentage of the monthly diet. For the population as a whole, monthly diets are an average of the five groups. Annual diet is calculated as the mean of the annual diets of the five groups.

Presentation of plant parts in the diet of the mangrove howlers are as percentages of overall feeding observations. Because the sample size of leaf age (young vs. mature) was relatively small due to visibility problems, young (including leaf buds) and mature leaves were grouped together for analysis. For this same reason, the category of "stem/bark" was removed from the dataset for analysis. There could be differences in these specific plant parts which may be important, but I could not evaluate these at this time and must set it aside for future study.

To evaluate food species selection, I used the selection index described in Clutton-Brock (1977b) using the ratio of percentages of feeding records to individuals of tree species in the circular plots and transect plots. I did not include lianas because of the problems associated with assessing liana densities.

### *Activity patterns*

General activity patterns were constructed using different methods according to daily, monthly, seasonal, and annual descriptions. First, I pooled all observation data together from the

individual samples and parsed activities by time of day, expressed as a percentage of time each day devoted to each behavior by all individuals. I then constructed monthly activity budgets for each group using group scan samples, taken at 10-minute intervals, in which the activities of all group members were recorded. Activities for each scan were calculated as a percentage and activity budgets constructed by averaging all values for each behavior on a monthly basis. Seasonal budgets were calculated in the same way, but divided into wet and dry season months before averaging.

For general activity pattern analysis, each behavior was described as a percentage of the overall behaviors recorded. Activities for each age/sex category were analyzed by determining a percentage of each behavior for adult males, adult females, adult females with infants, juveniles, and infants. Measures of variance among age and sex categories were calculated. Behaviors were subsequently analyzed according to times of the day when they occurred and described as a percentage of the total observations for each behavior during two-hour increments throughout each day during the study period. These data are presented using descriptive and analysis of variance (one-way, two-way, and Tukey's multiple comparisons) statistics to alleviate the problem of uneven observations in time.

#### *Substrate use*

The species and type of substrate was noted for each behavior recorded to determine which trees were utilized the most for which behaviors. Descriptive statistics were calculated according to frequency of behaviors in plant species and life forms (trees or lianas).

## Results

Behavioral observations resulted in a total of 5,213 data points covering 500 hours of data collection on the five study groups of black howlers. Thirty-two percent of these observations were of adult females (1,645 data points, 137 focal sessions), 13.3% were of adult females with infants (694 data points, 58 focal sessions), 34% were of adult males (1,786 data points, 150 focal sessions), 7.3% were of juveniles (381 data points, 32 focal sessions), and 13.6% were of infants (707 data points, 59 focal sessions). There were more observations of adult activities because adults did not move in and out of sight, as the juveniles and infants often did.

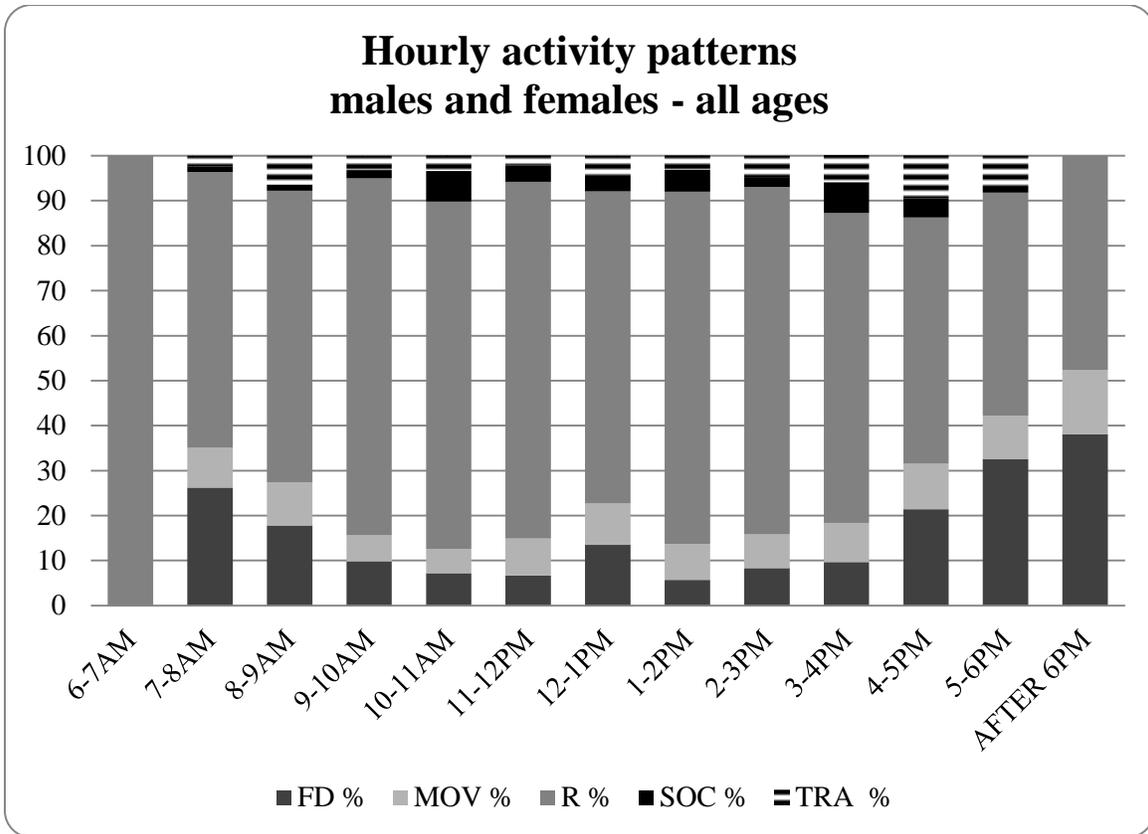
### *Activity patterns*

#### Daily/hourly

Resting behavior occurred most often during the mid-morning hours 0900-1100 for all ages and sexes, except juveniles, whose main resting period was during the hours of 1100-1300. Locomotory movement (moving about within the same tree) was highest for adult females with infants and adult males during the mid-afternoon hours from 1500-1700. The infants' most active time engaged in movement was in the early morning from 0700-0900. Ten percent of infants' movement behaviors focused on practicing gross and fine motor skills in the forms of self-play and object play. Travel behavior (locomoting between trees) varied between age and sex category. Traveling behavior was highest for juveniles in the early morning hours 0700-0900. Social behavior was engaged in most frequently in the afternoon hours from 1500-1700 for all age/sex classes. All but one of the social interactions observed between individuals (3.52% of overall activity budget or fewer than 0.01 occurrences per hour) were friendly in nature. The once instance of aggressive behavior observed between individuals involved two

adult females, in which one female made threatening noises and displaced the other for proximity access to an adult male, shortly after which the displacer and male copulated. Only 3 occurrences of intergroup contact was observed. These were in home range overlap areas and consisted of adult male vocalizations from each group and lasted less than 15 minutes each. We observed most feeding activity in the late afternoon hours during 1700-1800. This was the period of time when adult males, adult females, and infants fed most frequently. For adult females with infants, feeding occurred more frequently in the mornings during 0700-0900. Juveniles were most frequently observed feeding during the midday hours of 1100-1300.

In Figure 3.3, I present a summary of behaviors in 1-hour increments throughout a typical day. The mangrove howlers were relatively late-risers, moving about and feeding after sunrise at 0700 (their morning howling choruses began 0530-0600). Feeding peaks occurred in the early morning and evening with a smaller peak at midday. The highest frequency of social behavior occurred between peak feeding times. Resting was negatively correlated with feeding in that as feeding frequency increased, resting behavior decreased, but rose in frequency after feeding peaks. Group movements from one area to another were higher in the early- to mid-morning and in the late afternoon. Only three intergroup interactions, where different groups come into visual contact with each other, were observed during both seasons. As sunset neared, the monkeys were usually already in their sleeping trees and quite often feeding and moving around within the tree crowns until dark between 6-6:30 pm.



**Figure 3.3.** Average percentages on an hourly basis of activities by all individuals observed throughout each day. FD = feed, MOV = movement, R = rest, SOC = social, and TRA = travel.

#### Monthly

Behavioral data were collected from July-October 2009 and March-May 2010, the monthly results of which are presented in Table 3.1. Feeding behavior for all groups was highest during September (15.9%) and lowest in August (3.4%). The next lowest percentage occurred in May at 7.1%. In comparison with predicted values, a Chi-square test showed feeding behavior counts were lower than expected in March, May, and August, yet were higher than expected in April. Resting behaviors were very high in August at 90.5% and lowest in September at 64.8%, but only the high in August was significantly higher than the Chi-square prediction. Locomotion records were highest in September (17.9%) and lowest in October (6.0%). Locomotion

incorporated both movement within trees and between trees. Within tree movement was highest in April (8.5%) and lowest in October (2.6%; significantly lower than Chi-square prediction). Traveling between trees was highest in September (9.7%; significantly different from predicted count) and lowest in July (1.8%). The highest occurrence of affiliative social behavior was in July (8.0%; significantly higher than predicted) and lowest in August, a month in which no social behaviors were recorded (lower than predicted). Only one instance of aggressive social behavior was recorded; it was in April and occurred between two adult females around the time when copulations with the adult male of the group was observed. The male copulated with the female (without an infant) on several occasions. Aggressive behavior accounted for only 0.03% of observations in April and 0.02% of observations overall.

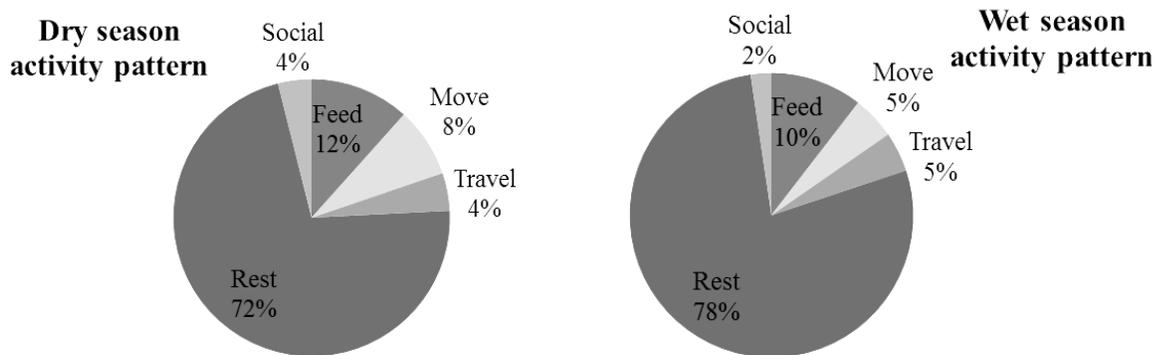
	STUDY MONTHS							
	MAR	APR	MAY	JUL	AUG	SEP	OCT	ANNL
FEED	*7.7	*13.1	*7.1	12.4	*3.4	15.9	12.9	11.5
REST	71.8	71.1	77.1	72.6	*90.5	64.8	79.3	73.2
LOC:MOV	7.7	8.5	6.6	5.3	*3.4	8.3	*2.6	7.5
LOC:TR	5.7	4.2	4.4	1.8	2.8	*9.7	3.5	4.4
SOC:AFF	*7.2	3.2	4.8	*8.0	*0	1.4	1.7	3.5
SOC:AGG	0	0.03	0	0	0	0	0	0.02

**Table 3.1.** Distribution of behaviors (percentage) by months when behavioral data were collected and summary for wet and dry seasons (ANNL). Chi-square test for independence:  $\chi^2=117.22$ ,  $df=24$ ,\*  $p<0.001$ .

### Seasonal

Seasonality had a significant effect on all behaviors, except for traveling between trees ( $\chi^2=12.811$ ,  $df=4$ ,  $p=0.012$ ) (Figure 3.4). Feeding, movement within trees, and social behavior

were higher than expected and resting was lower than expected for the dry season. Feeding, movement within trees, and social behavior were lower and resting was higher than expected for the wet season. Movement, resting, and social behavior had the highest impact and contributed the most to the Chi-square result. The aggressive social behavior category was removed from the analysis because the percentage was <5.



**Figure 3.4.** Percentages of behavior records by season for all age/sex categories combined.

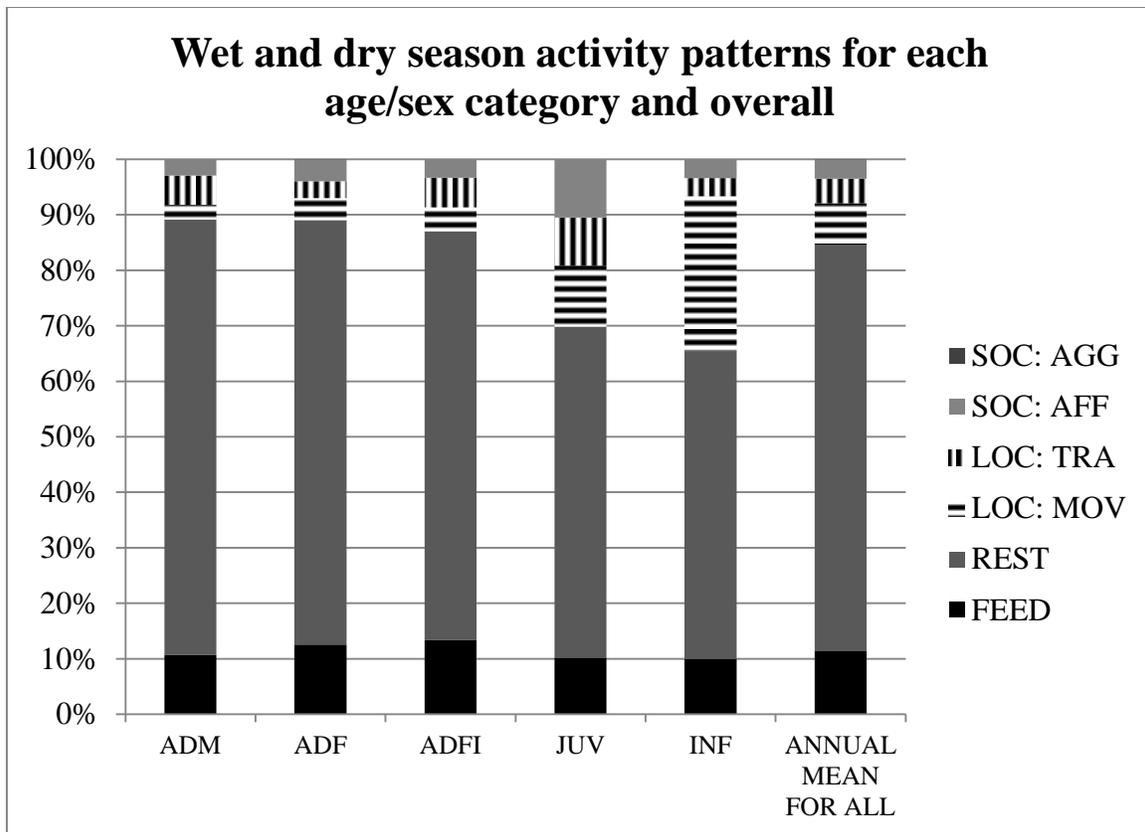
Combined wet and dry seasons

Results for behavioral observations for all sexes and ages (Table 3.2 and Figure 3.5) show that, over wet and dry seasons, the mangrove howlers spent most of their time resting (73.2%) followed by locomoting (11.9%). They spent more time moving about within trees (7.5%) than traveling between them (4.4%). Affiliative social behaviors were recorded in 3.5% of total observations while aggressive social behaviors were recorded in only 0.02%. Feeding activities occurred in 11.5% of observations. Behavioral categories differed significantly among

age and sex categories in a one-way ANOVA ( $F=15.11$ ,  $df=4$ ,  $p<0.01$ ), in that infants varied the most from the other age categories in a Tukey pairwise comparison ( $CI=99.36\%$ ) with a higher rate of locomotory behavior (most of it self-play movement) and lower rates of resting.

AGE/ SEX	N	$\pm$ SD	FEED %	LOCOMOTE		REST %	SOC/AF%	SOC/ AG%
				MOV %	TRA%			
ADF	1645	0.91	12.6	3.9	3.0	76.5	3.9	>.01
ADFI	694	1.03	13.4	4.3	5.3	73.6	3.3	0
ADM	1786	0.98	10.7	2.6	5.3	78.4	2.9	0
JUV	381	1.19	10.2	11.0	8.6	59.6	10.5	0
INF	707	0.94	9.9*	28.0	3.3	55.4	3.4	0

**Table 3.2.** Annual percentage of pooled observations spent in principal activities for each age/sex category. ADF=adult female, ADFI=adult female with infant, ADM=adult male, JUV=juvenile, INF=infant. \*Includes nursing.



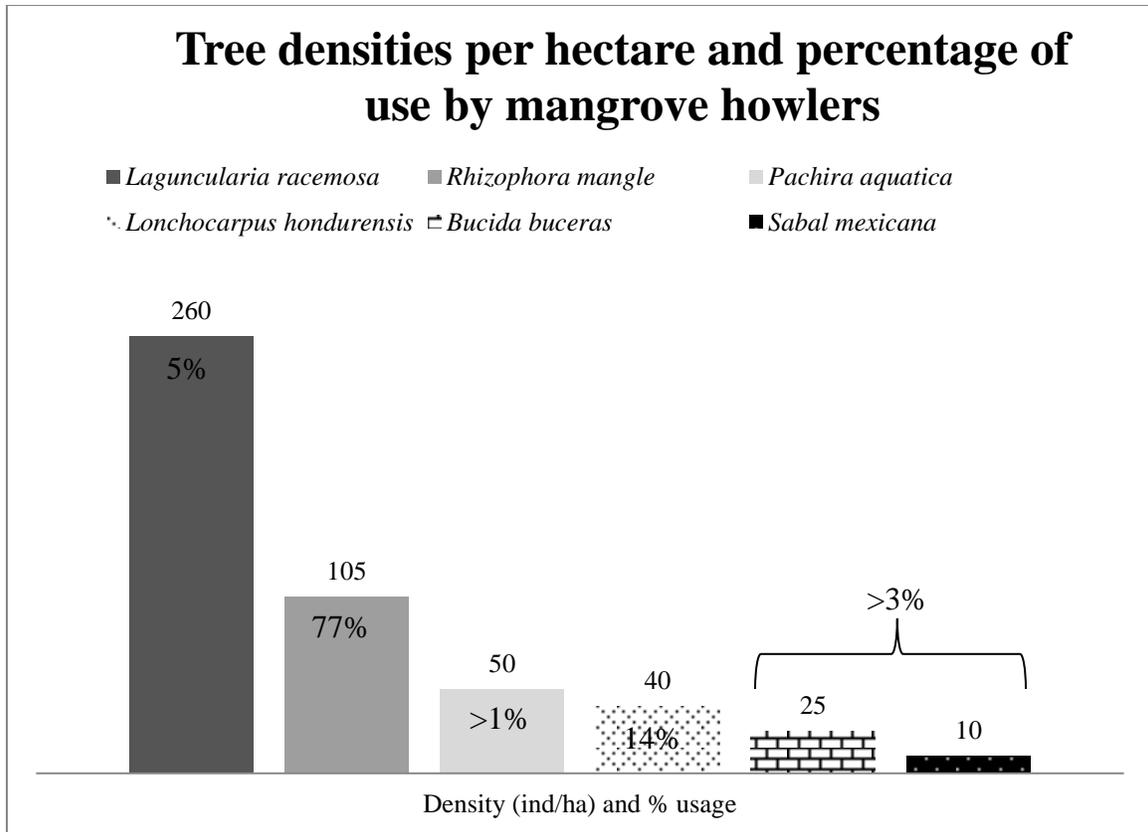
**Figure 3.5.** Average percentage of observations spent in principal activities over the study period. ADM=adult male, ADF=adult female, ADFI=adult female with dependent infant, JUV=juvenile, INF=infant. The percentage of infant time spent feeding includes nursing.

### *Substrate use*

Activity data also included the type and species of substrate used during each behavior recorded (Figure 3.6). Although these results are likely biased to some degree, based on the higher densities of red mangrove trees near the water's edge where we could more easily watch groups, the data do give us a picture of preferred substrates in these locations. The most-oft used tree most by the mangrove howlers for various activities was the red mangrove tree (*Rhizophora mangle*, 77%) This tree species had the second highest density on the island at 105 ind/ha. The two next most used trees were the *gusano* (*Lonchocarpus hondurensis*, 14%) and the white

mangrove (*Laguncularia racemosa*, 5%). *Gusano* trees were a major feeding source for the howlers and ranked number four in terms of tree species density at 40 ind/ha. White mangroves were the monodominant tree species covering most of the island, and had the highest density at 260 ind/ha. This disparity is likely due to a bias from the areas where we were most able to observe the groups, which was in areas near the water's edge where red mangrove tree density was higher. The two tree species with the lowest densities, *Bucida buceras* and *Sabal mexicana*, were used by the howlers in less than 3% of observations. The least used tree species (<1%), *Pachira aquatica*, had the third highest density on the island. This species, although prevalent, was relatively short and did not provide any food products or means of support for the howlers.

When feeding, substrate use was almost evenly divided between red mangrove and *gusano* trees (41.4% and 40.4%, respectively), however, while in red mangrove, the howlers usually ate from other trees or from lianas. Resting was mostly performed in red mangrove (more than 82% of resting observations), with another 10% in *gusano* trees. When traveling between trees, red and white mangrove trees were used most often (73.6% and 11.6%, respectively). Trees were used as a substrate in 98.5% of observations and lianas in 1.5%. Lianas were most commonly used as a substrate for traveling between trees. Of the lianas that were identified as a substrate, *muco* (*Dalbergia brownii*) was used most often for feeding, resting, and socializing.



**Figure 3.6.** Tree species and densities in individuals per hectare used as substrates (percentages) by the howlers.

#### *Feeding behavior and diet*

Of the total 5,213 observations, we recorded 600 instantaneous samples of feeding behavior for all ages and sexes. Of these, 191 were for adult males, 207 for adult females, 93 for adult females with infants, 39 for juveniles, and 70 for infants, which included instances of nursing.

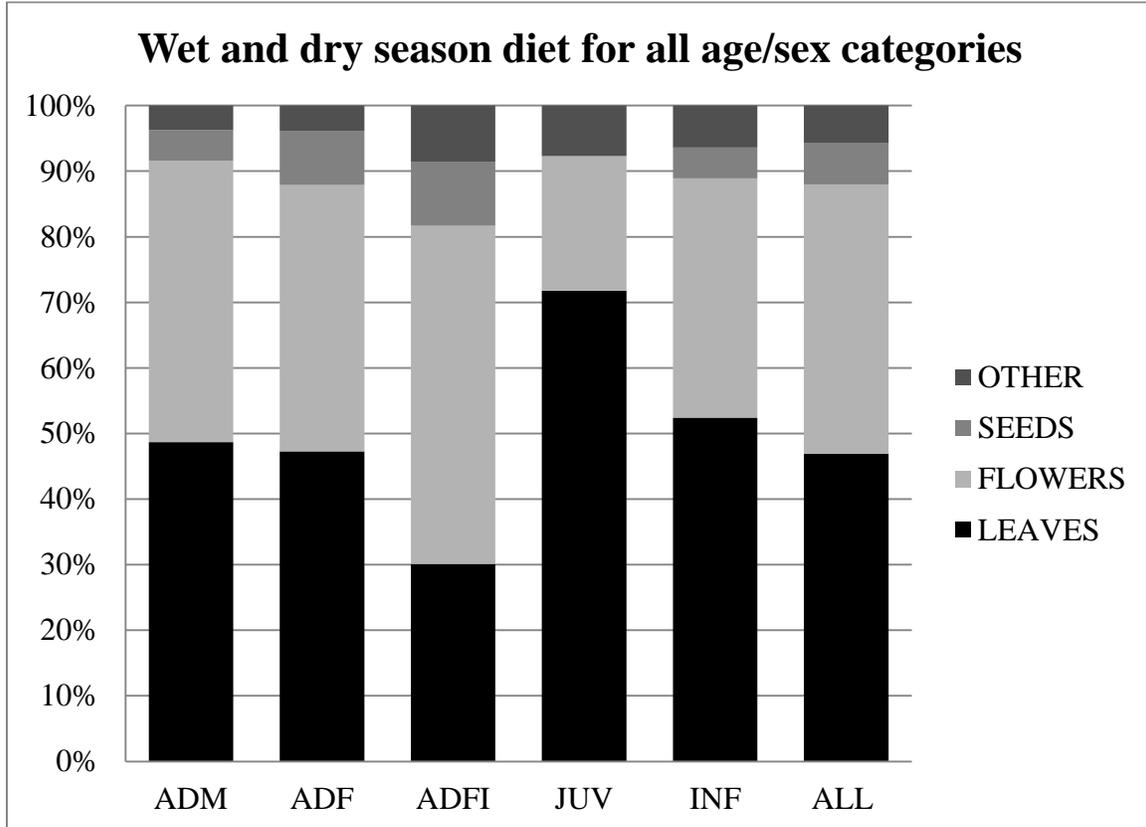
Due to small sample sizes for young and mature leaves, I grouped all leaves together into one category for analysis. When all of the feeding data were pooled, leaves made up 47.2% of the howlers' diet through both the wet and dry seasons. Where leaf age was discernible (19.4% of leaf records), mature leaves accounted for 8.8% and young leaves accounted for 91.2% of the

total. Flowers made up 41.3% of the diet. The howlers ate seed pods less often than leaves and flowers. Observations of seed eating occurred in 6.4% of feeding instances. Other occurrences of feeding made up 5.1% of observations and included drinking, eating stems, nursing by infants, and unidentifiable plant parts.

Percentages of food items in the diets of adults, juveniles, and infants are illustrated in Table 3.3 and Figure 3.7 below. In Chi-square tests for independence, the most striking deviations from expected means were in the diets of females with infants (ADFI) and juveniles (J). Adult females with infants ate seeds more frequently than expected and fewer leaves than expected. The average diet of juveniles differed in all part categories: more leaves, fewer flowers, and fewer seeds than expected. Inability to identify plant parts eaten by juveniles made the frequency of the “other” category higher than expected.

	# of species	Leaves %	Flowers %	Seeds %	Other %
Adult males	7	48.7	42.9	4.7	3.7
Adult females	10	47.3	40.6	8.2	3.9
Adult females w/inf	7	30.1*	51.6	9.7*	8.6
Juveniles	7	71.8*	20.5*	0*	7.7
Infants	4	52.4	36.5	4.7	6.4
Column Mean	-	<b>47.2</b>	<b>41.3</b>	<b>6.4</b>	<b>5.1</b>

**Table 3.3.** Number of plant species recorded as eaten and percentages of feeding observations for each age/sex category and plant part. The category “other” includes drinking, stems, unidentifiable plant parts, and nursing for infants. Chi-square test for independence of percentages:  $\chi^2=35.745$ ,  $df=12$ ,  $*p<0.001$ .



**Figure 3.7.** Percentages of items in the diet by age/sex class and pooled overall (“ALL”) throughout the wet and dry seasons. The category “other” includes drinking, stems, unidentifiable plant parts, and nursing (for infants).

Thirty-five prevalent tree and liana species were identified in the study site (see Chapter Two for detailed information). However, the howlers selected only 12 of these as food resources. Of the 600 instances of observed feeding behavior, we could not identify the species in 87 instances of leaf eating (trees and lianas combined), and another eight feeding instances were not on plant material (nursing, drinking water). We identified plant part and species in 478 instances of feeding. Species were identified in all instances of flower and seed eating, and in most cases of leaf consumption. Among the most important food resources were the leaves,

flowers, and seeds of the *gusano* tree (*L. hondurensis*) and the leaves and flowers of the prolific liana *muco* (*D. brownei*). Together, these two plants provided 68% of the monkeys' food over the wet and dry seasons. The foods ranking 3 and 4 are white mangrove leaves (*L. racemosa*) and the leaves of a liana (*Rhabdadenia biflora*) come in at 3.9% and 2.4%, respectively. Only four species make up 74% of the howlers' diet during the wet and dry seasons.

Genera	Total % in Diet	Rank	Leaves %	Flowers %	Seeds %	Other %
<i>Lonchocarpus</i>	44.69	1	17.86	68.98	100	26.67
<i>Dalbergia</i> *	23.44	2	27.86	24.90	-	-
<i>Laguncularia</i>	3.88	3	8.21	-	-	-
<i>Rhabdadenia</i> *	2.36	4	4.29	-	-	6.67
<i>Rhizophora</i>	1.69	5	3.57	-	-	-
<i>Tabebuia</i>	1.52	6	-	3.67	-	-
<i>Paullinia</i> *	1.18	7	2.50	-	-	-
<i>Bucida</i>	1.18	8	1.07	1.63	-	-
<i>Hippocratea</i> *	1.01	9	1.79	0.41	-	-
<i>Clytostoma</i> *	0.67	10	1.07	0.41	-	-
<i>Passiflora</i> *	0.34	11	0.36	-	-	3.33
<i>Malvaviscus</i> *	0.17	12	0.36	-	-	-
Unknown	17.88	-	31.07	-	-	63.33

**Table 3.4.** The 12 plant genera used as food resources by the black howlers in the mangrove site and the percentages of records each species and plant part contributed to the diet for both the wet and dry seasons in rank order. Percentages for each food item category were calculated using the totals for each food item by species. The category “Unknown” represents instances in which the plant type and species was not identifiable at the time the data were collected. \*Denotes liana species; tree species are unmarked.

### Selectivity index

Selection index values (Table 3.5) close to 1.0 indicate that a species is eaten in proportion to its abundance, above 1.0 indicate selection higher than its abundance, and lower than 1.0 indicate selection below its abundance.

Genus and part	Percentage of diet	Tree Density (ind/ha)	SI Annual	SI Wet Ssn	SI Dry Ssn
<i>Lonchocarpus</i> Leaves	8.4	40	0.21	0.85	0.16
<i>Lonchocarpus</i> Flowers	28.0	40	0.70	-	0.77
<i>Lonchocarpus</i> Seeds	6.4	40	0.16	-	0.17
<i>Laguncularia</i> Leaves	3.9	260	0.01	0.10	0.01
<i>Rhizophora</i> Leaf buds	1.7	105	0.02	0.06	0.02

**Table 3.5.** Selection indices of the top three tree genera and parts eaten by the mangrove howlers. “Percentage of diet” based on both wet and dry season calculations. Methods for determining tree density are in Chapter Two. SI=Selection Index. Ssn=Season.

### Seasonal feeding patterns

Seasonal differences in food resources were apparent in the number of species ( $H=115.29$ ,  $df=14$ ,  $p<0.025$ ) and in plant parts eaten ( $H=37.42$ ,  $df=4$ ,  $p<0.025$ ), as is seen in Table 3.6 and Figure 3.8. During the wet season from July to November, leaves were selected in 95% of feeding records. Five percent of feeding records went unidentified in terms of plant parts. Based on observations made by the field team, there were few to no flowers or seeds on any plants, but ample fruits (propagules) present on most red mangrove trees. However, we did

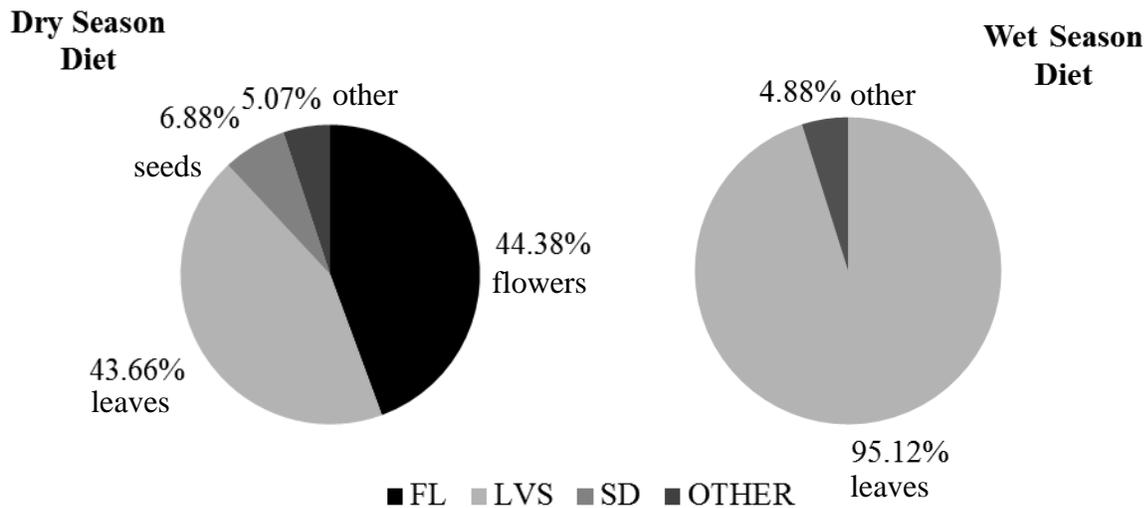
not observe the howlers eating this fruit, most likely because the fruits are woody, not fleshy and succulent. In all wet season observations in which the plant part was identified, 100% were leaves. In cases where tree species eaten were identifiable, leaves from three (*L. hondurensis*, *L. racemosa*, and *R. mangle*) made up 63% of all leaves eaten during the wet season. Leaves from three liana species (*D. brownei*, *Malvaviscus arboreus*, and *R. biflora*) and unidentified species feeding occurrences on leaves made up 36% of the wet season diet. Unidentified species and plant parts were the remaining 1%.

Genus	Dry Season %	Dry Season Parts	Wet Season %	West Season Parts
<i>Lonchocarpus</i>	45.5	LVS, FL, SD	34.2	LVS
<i>Dalbergia</i> *	24.8	LVS, FL	4.9	LVS
<i>Laguncularia</i>	2.2	LVS	26.8	LVS
<i>Rhabdadenia</i> *	2.2	LVS, ST	4.9	LVS
<i>Rhizophora</i>	1.6	LVS	2.4	LVS
<i>Tabebuia</i>	1.6	FL	-	-
<i>Paullinia</i> *	1.3	LVS	-	-
<i>Bucida</i>	1.3	LVS, FL	-	-
<i>Hippocratea</i> *	1.1	LVS, FL	-	-
<i>Clytostoma</i> *	0.7	LVS, FL	-	-
<i>Passiflora</i> *	0.4	LVS	-	-
<i>Malvaviscus</i> *	-	-	2.4	LVS
Unknown spp.	17.4	81% LVS**	24.4	90% LVS**

**Table 3.6.** Observed plant genera used as food resources by the mangrove howlers in the wet and dry seasons. LVS=leaves, FL=flowers, SD=seeds, ST=stems. \* denotes lianas, unmarked genera are trees. \*\*of the feeding records where we could not identify plant species, this was the percentage in which leaves were eaten by the howlers; for example, in the dry season, plant species were unidentified in 17.4% of feeding records. Of the 17.4% , 81% were instances of leaf-eating.

During the dry season, flowers and seeds were more prevalent and contributed largely to the howlers' diet from March through May. The flowers of three tree species and three liana species represented 44.4% of the howlers' observed diet during this time. Dry season food resources also consisted of leaves from 10 species (29.5%; 43.7% if unidentified plant species are included) and seeds from the *Lonchocarpus* tree (6.9%).

The diversity of species used as food resources was low during the wet season, consisting of only six species. Species used in the dry season increased to 11. Overall, the mangrove howler population used just 12 plant species for food, considered low for howlers (Milton, 1980; Glander, 1981), as howlers tend to eat from an average of 60 different species annually (Smith, 1977; Milton, 1978, 1980; Glander, 1978; Bicca-Marques and Calegaro-Marques, 1994b; Chiarello, 1994; Galetti et al., 1994; Silver et al., 1998; Solano et al., 1999; Santamaría-Gómez, 2000; Serio-Silva et al., 2002; Pinto et al., 2003; Pavelka and Knopff, 2004; Rivera and Calme, 2006).



**Figure 3.8.** Comparison of percentages of mangrove howler diets during the wet and dry seasons.

### Feeding patterns by life form

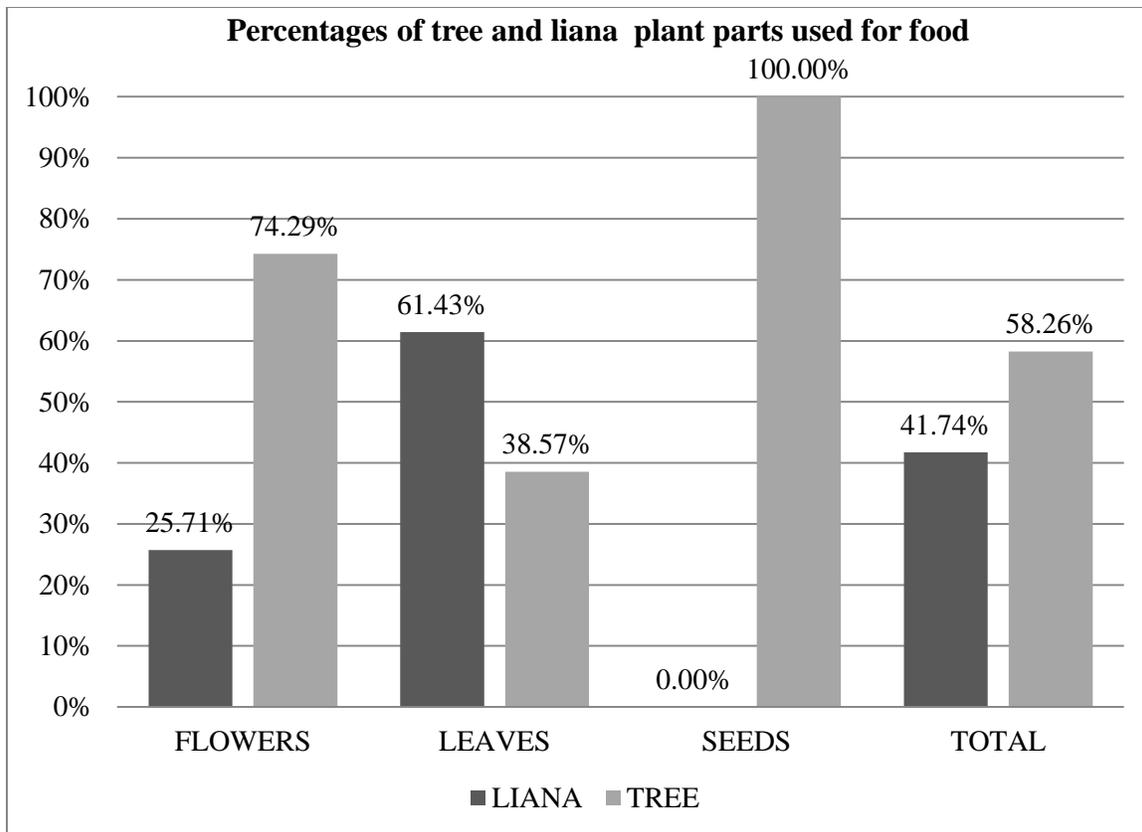
In the mangrove, lianas were just as important a food resource as trees for the monkeys (Table 3.7 and Figure 3.9). Overall, tree products constituted over half of the howlers' diet at 58.3%, while liana products provided 41.7%. Tree leaves constituted 38.6% and liana leaves made up 61.4% of the overall leaf consumption. Leaves from a total of six tree species were observed to be eaten by the howlers, including two species specially adapted to saline conditions; the red mangrove (*R. mangle*) and the white mangrove (*L. racemosa*). The howlers selected seven identifiable liana species for leaf consumption.

The majority of flowers eaten were from trees (74.3%). Of the tree flowers, 96.8% were from the *gusano* tree (*L. hondurensis*). Liana flowers were eaten in 25.7% of flower feeding observations. Of the liana flowers, 98% were from one species (*D. browni*). All seed-eating occurrences were from *L. hondurensis*, even though other seeds were available at the same time on both lianas and trees (e.g. *Dalbergia*, *Haemotoxylum*<sup>2</sup>, *Bucida*).

	Number of Tree Species	Number of Liana Species	TOTAL
Leaves	4	7	11
Flowers	3	3	6
Seeds	1	0	1
Overlap	2	3	5

**Table 3.7.** Number of different tree and identifiable liana species eaten.

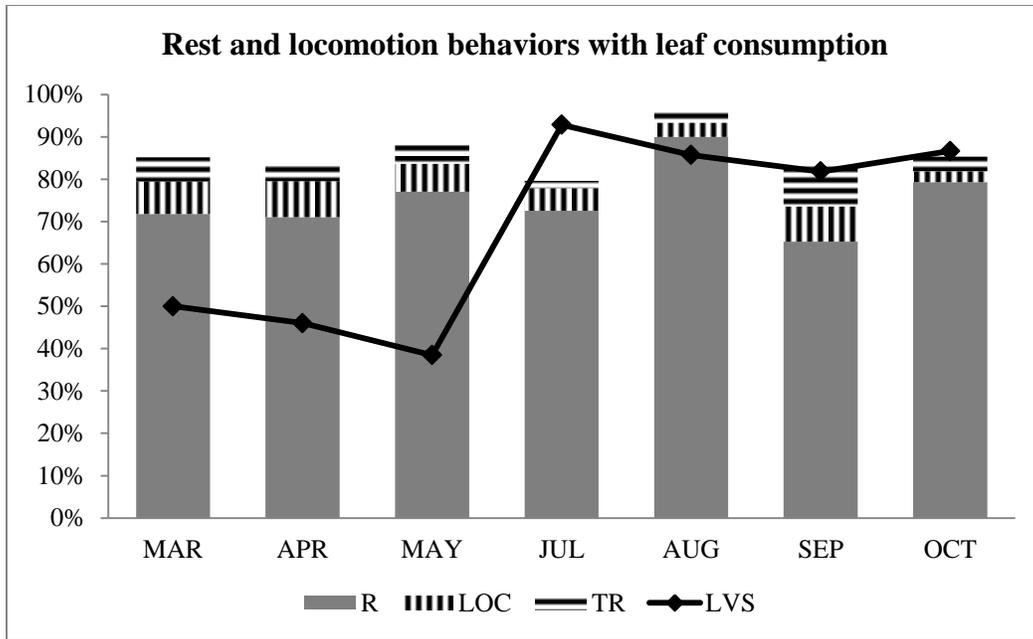
<sup>2</sup> For more information on this, and other, plant genera not eaten by the howlers, see Chapter Four and Appendix A.



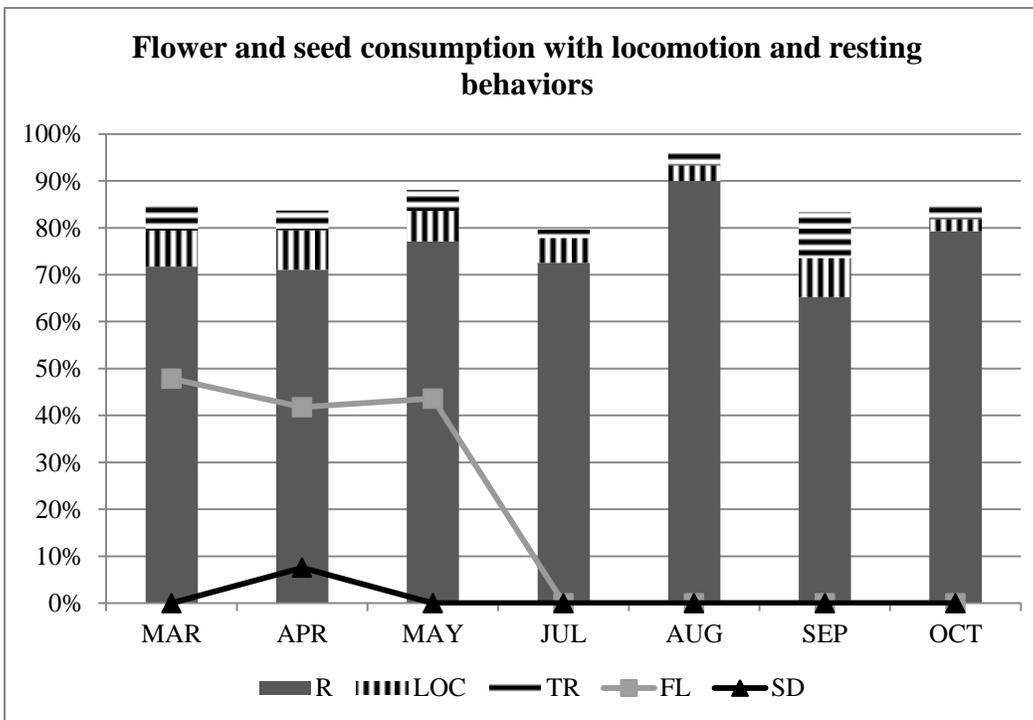
**Figure 3.9.** Comparison of the percentages of plant parts from trees and lianas in the diet of the mangrove howlers. Liana leaves were preferred over tree leaves, tree flowers were preferred over liana flowers, and tree seeds were preferred over liana seeds.

*Feeding and activity patterns*

I examined relationships of monthly locomotion and resting patterns with feeding behavior for seasonal and non-seasonal foods (Figures 3.10, 3.11). There were no correlations among the amount of leaves in the diet of the mangrove howlers and how much they rested or locomoted on a monthly basis. As with leaves, there were no correlations among resting and locomotory behaviors and the consumption of seasonal food items.



**Figure 3.10.** Behaviors and leaves in the mangrove howler diet during the study months.



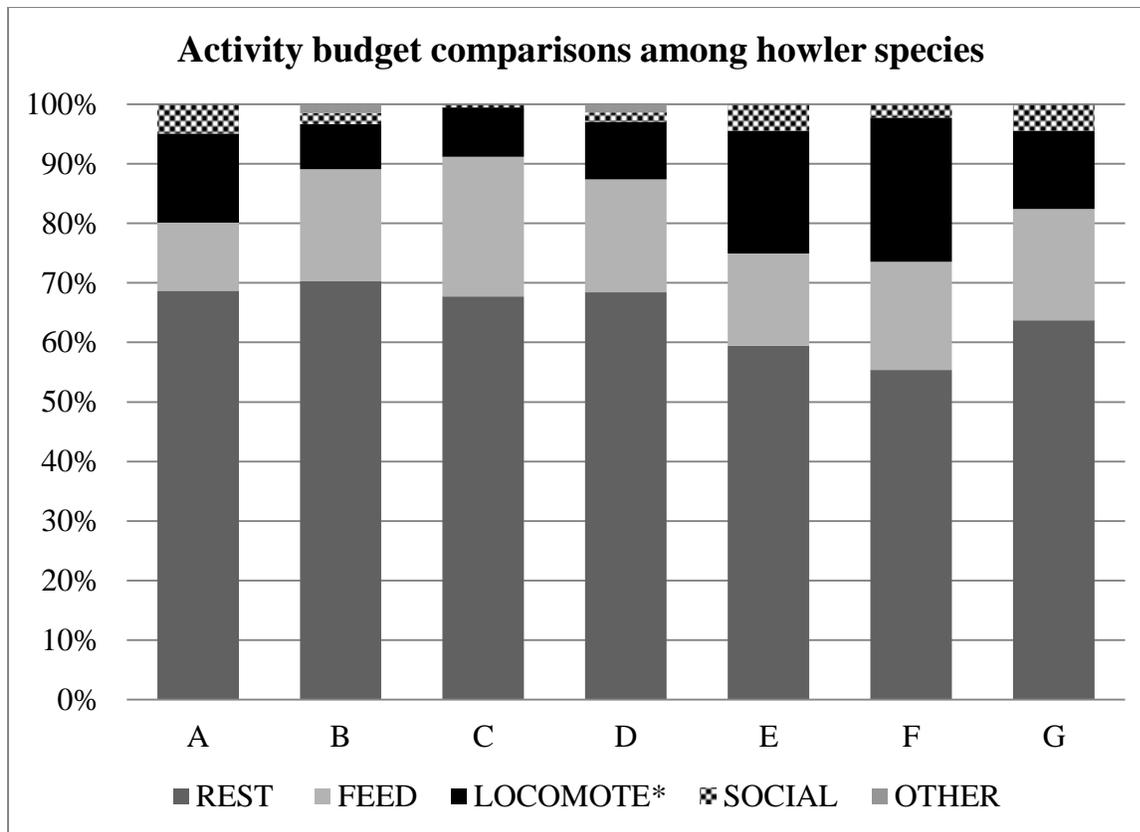
**Figure 3.11.** Behaviors and seasonal plant items in the diet of the mangrove howlers.

## Comparisons With Other Howler Monkey Populations

### *Activity patterns*

The mangrove howler annual activity patterns were not significantly different from the activity patterns of other conspecific populations (Table 1.1, Figure 3.9), but differed from some congeneric populations.

Although species means for feeding time were not significantly different from each other ( $H=6.16$ ,  $df=6$ ,  $p=0.406$ ), the mean for the mangrove howler population was the lowest (11.4%) of all species compared (range: 15.4-22.7%). The population mean for resting behavior in the mangrove howlers (68.7%) was within the range for conspecifics and congenics (range: 54.8-69.5%). The mangrove howler mean for travel was 4.4% and was within range for the comparative species (0.6-8%). Notably, the mean for mangrove howler social behavior is higher than the range for the comparative populations at 4.9% (range: 0.5-4.4%), but was not significant in Kruskal-Wallis nonparametric testing ( $H=5.77$ ,  $df=6$ ,  $p=0.236$ ). Movement within trees was significantly different between species ( $H=15.28$ ,  $df=6$ ,  $p<0.025$ ). *Post hoc* analysis revealed the mangrove population within the range for *A. pigra*, *A. palliata*, and *A. guariba* (7.4-13.2%), and that these three species were significantly different from *A. caraya* and *A. belzebul* (20.5% and 24%, respectively) ( $z=1.26$ ,  $2.76$ ,  $p<0.01$ ).



A. *A. pigra* in this study. B. *A. pigra* (Silver et al., 1998; Pavelka and Knopff, 2004; Behie and Pavelka 2005; Pozo-Montuy and Serio-Silva, 2007). C. *A. palliata mexicana* (Estrada et al., 1999; Cristóbal-Azkarate and Arroyo Rodríguez, 2007). D. *A. palliata* (Teaford and Glander, 1996; Palacios and Rodríguez, 2001; Clarke et al., 2002). E. *A. caraya* (Bicca Marques, 1993; Prates and Bicca Marques, 2008). F. *A. belzebul* (Bonvicino, 1989; Pinto 2002a,b; Pinto et al., 2003). G. *A. guariba* (Mendes, 1989; Chiarello, 1993; de Marques, 1996).

**Figure 3.12.** Activity budget comparison among several howler species. Kruskal-Wallis H tests reveal a significant difference in the average percentage of locomotion ( $H=15.28$ ,  $df=6$ ,  $p=0.018$ ) among the mangrove howlers and the howler species denoted in **bold** above.  $*p<0.025$ .

#### *Comparative feeding patterns*

I compared feeding data from several studies of Yucatán black howlers (*A. pigra*) with the black howlers from the mangrove in this study (Table 3.8). These other sites include the

Community Baboon Sanctuary, Monkey River, and Cockscomb Wildlife Preserve in Belize (Silver et al., 1998; Marsh, 1999; Pavelka and Knopff, 2004; Behie and Pavelka, 2005).

Percentages of plant parts in the diets of the study species were compared with pooled data on other populations of the same species and other howler monkey species (Table 3.8 and Figure 3.13) using Kruskal-Wallis H tests. While the amount of leaves in the diet of the mangrove howlers (47.2%) is within the range of leaf consumption for other howlers ( $H=12.95$ ,  $df=7$ ,  $p=0.073$ ), flowers and seeds make up a significantly greater proportion of the mangrove howlers' diet compared with other howler populations (flowers 41.3% ( $H=17.44$ ,  $df=7$ ,  $p=0.015$ ) and seeds 6.4% ( $H=49$ ,  $df=7$ ,  $p<0.025$ )). Notably, other howlers spend on average 25-57% of their feeding time eating fruits; the mangrove howlers in this study were never observed to eat fruit.

Closer inspection using *post hoc* pairwise comparisons (one-sample z tests, with significance set at  $p<0.025$ ) revealed significant differences between the black howlers in the mangrove and other populations of black howlers. The mangrove study groups ate fewer leaves ( $sd=21$ ,  $z=2.21$ ,  $p=0.027$  (approaching *post hoc* significance)); more flowers ( $sd=5$ ,  $z= -18.51$ ,  $p<0.01$ ); more seeds ( $sd=1$ ,  $z= -5.7$ ,  $p<0.01$ ); and less fruit ( $sd=18$ ,  $z=4.64$ ,  $p<0.01$ ). The number of plant species in the annual diet of the study population was significantly fewer ( $sd=21$ ,  $z=3.2$ ,  $p<0.001$ ) than in the comparison populations of *A. pigra*.

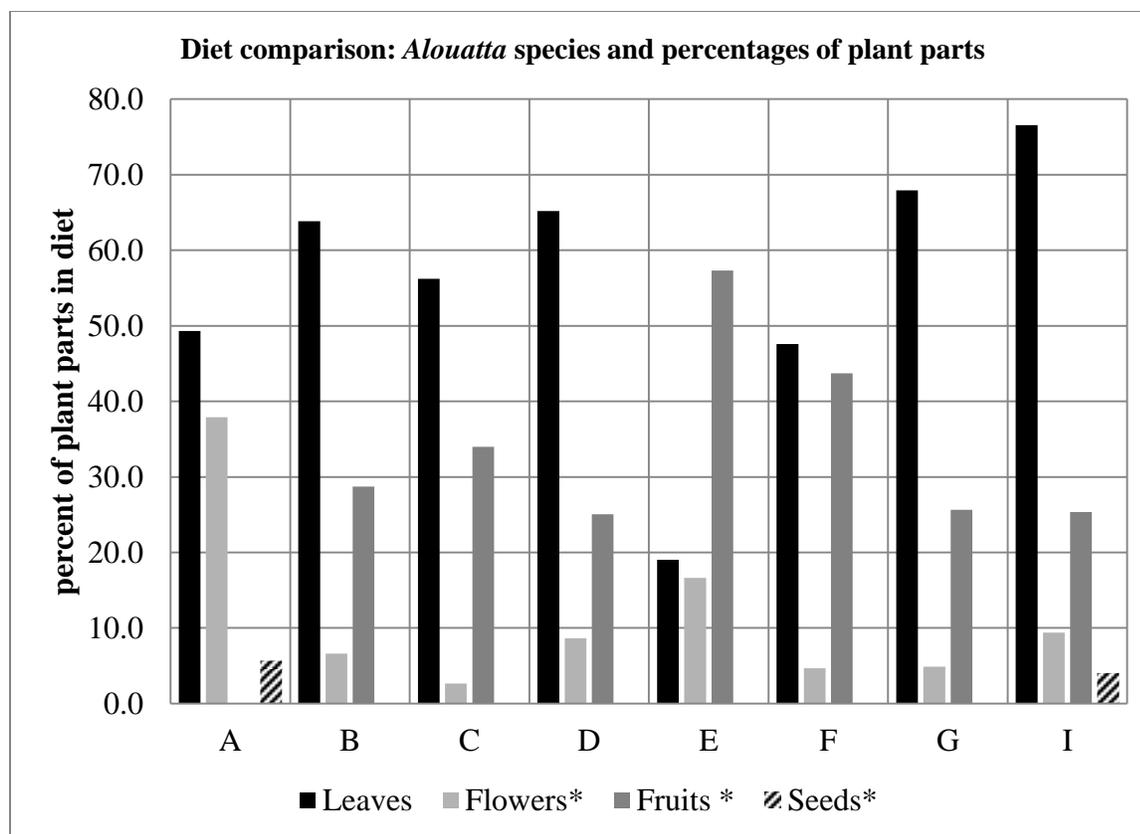
A one sample z-test of the percentages of leaves in the diets of the mangrove howlers compared with each of the howler species revealed that mantled howlers ate significantly more leaves ( $sd=12$ ,  $z=2.58$ ,  $p=0.01$ ) and red-handed howlers ate significantly fewer leaves ( $sd=1$ ,  $z= -27.7$ ,  $p<0.01$ ) over an annual period. Except for the black-and-gold howler, the black howlers in the mangrove ate significantly more flowers than all the other howler groups in the comparison

( $z = -27.89$ ,  $p < 0.01$ ). The mangrove howlers ate significantly more seeds than all other howler groups ( $z = -5.7$ ,  $p < 0.01$ ). All other howler groups, except for black-and-gold howlers, included more fruits in their diets than the study howlers ( $z = 12.7$ ,  $p < 0.01$ ). In terms of the number of plant species in the diet, the study howlers selected significantly fewer species than all other howler groups in the comparison ( $z = 7.26$ ,  $p < 0.01$ ).

Species	Leaves	Flowers*	Seeds*	Fruits*	Other	No. species*
<i>A. pigra</i> <sup>1</sup>	47.2	41.3	6.4	0.0	5.1	12
<i>A. pigra</i> <sup>2</sup>	63.9	6.6	0.0	28.7	0.0	40
<i>A. palliata mexicana</i> <sup>3</sup>	56.2	2.7	0.0	34.0	7.1	35
<i>A. palliata</i> <sup>4</sup>	65.2	8.6	0.0	25.1	1.2	66
<i>A. belzebul</i> <sup>5</sup>	19.1	16.7	0.0	57.3	7.0	67
<i>A. seniculus</i> <sup>6</sup>	47.6	4.7	0.0	43.7	4.1	-
<i>A. caraya</i> <sup>7</sup>	68.0	4.9	0.0	25.6	1.2	16
<i>A. guariba</i> <sup>8</sup>	76.6	9.4	4.0	25.4	5.1	-

<sup>1</sup>This study. <sup>2</sup>Silver et al., 1998; Marsh, 1999; Pavelka and Knopff, 2004; Behie and Pavelka, 2005. <sup>3</sup>Estrada and Coates-Estrada, 1984; Estrada et al., 1999; Solano et al., 1999; Serio-Silva et al., 2002; Fuentes et al., 2003; Muñoz et al., 2006; Cristóbal-Azkarate and Arroyo-Rodríguez, 2007; Dunn et al., 2009. <sup>4</sup>Smith, 1977; Glander, 1978; Milton, 1980; Chapman, 1987, 1988; Tomblin and Cranford, 1994; Stoner, 1996; Fuentes et al., 2003; Ramirez-Orjuela and Cadena, 2003; Williams-Guillén, 2003. <sup>5</sup>Pinto, 2002a; Pinto and Setz, 2004. <sup>6</sup>Gaulin and Gaulin, 1982; Neves and Rylands, 1991; Julliot and Sabatier, 1993; Mendes Pontes, 1997; Palacios and Rodriguez, 2001. <sup>7</sup>Zunino and Rumiz, 1986; Bicca-Marques and Calegario-Marques, 1994a; Bravo and Sallenave, 2003; Ludwig et al., 2008; Prates and Bicca-Marques, 2008. <sup>8</sup>Mendes, 1989; Chiarello, 1994; Martins, 2008.

**Table 3.8.** Means for plant parts and number of plant species in the diets of seven species of howler monkey (pooled data). An \* indicates significant differences between populations/species at  $p < 0.05$  in a Kruskal-Wallis nonparametric H test.



Species included in the analysis and the sample size (N). A. *A. pigra* in this study (N=1). B. *A. pigra* in other sites (N=5). C. *A. palliata mexicana* (N=25). D. *A. palliata* (N=9). E. *A. belzebul* (N=2). F. *A. seniculus* (N=4). G. *A. caraya* (N=6). I. *A. guariba* (N=3).

**Figure 3.13.** Comparison of plant parts in the average diet of the mangrove howlers compared with pooled feeding data from seven howler species (See Table 3.8 for references). \* $p < 0.025$ .

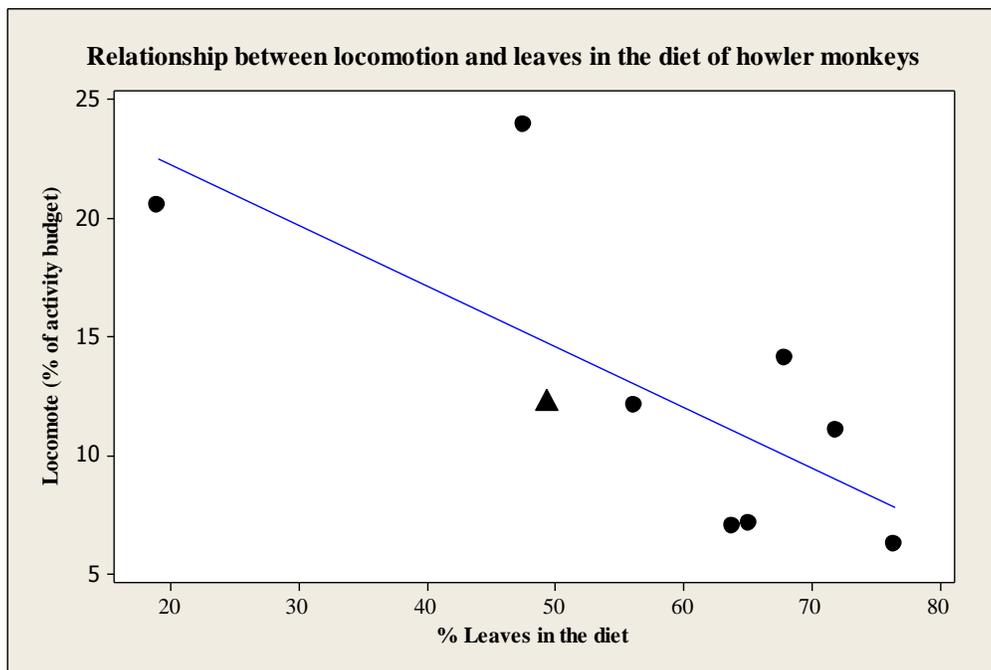
In terms of the number of species in the diet and selectivity indices, the mangrove howlers were similar to other howler populations in altered low-diversity habitats, such as agro-forest communities like cacao and coffee plantations.

#### *Comparative feeding behavior with activity patterns*

Using the comparative data I mined from the literature on various howler monkey species and populations, I conducted regressions of behaviors on the percentage of plant parts in the diet.

After determining whether there was a significant trend, I inserted data from my study, and reran the regressions to see where the mangrove population fell in relation to other howler populations.

In the first regressions, I examined trends with the percentage of leaves in the diet. For locomotion on leaves, there was a significant negative correlation ( $R^2=55.7$ ,  $F=7.55$ ,  $p=0.033$ ). When I added the mangrove population data (Figure 3.11), the result was still significant but the percentage of leaves in the diet explained less of the variation in locomotive behavior ( $R^2=53.2$ ,  $F=7.95$ ,  $p=0.026$ ).



**Figure 3.14.** Regression of locomotion on percentage of leaves in the diet for various howler monkey species (see Table 3.8 for references). The triangle represents the mangrove howler population.

I regressed the percentage of resting and social behaviors on the percentage of leaves in the diets of the comparative howler populations. There was a positive trend showing that as the percentage of leaves increased in the diet, so too did the percentage of resting behavior. However, this trend was not significant ( $R^2=43.1$ ,  $F=4.54$ ,  $p=0.08$ ). There was a negative trend of decreasing social behavior with an increase of leaves in the diet, but this was also not significant ( $R^2=42.2$ ,  $F=4.38$ ,  $p=0.08$ ).

I regressed the same behaviors on the amount of fruit in the diets of several howler species to look at the trend and added the mangrove howler data to see if they had any effect. When I regressed locomotion on percentage of fruit, there was a significant positive trend, so that as the percentage of fruit in the diet increased, the percentage of locomotory behaviors also increased ( $R^2=52.3$ ,  $F=6.57$ ,  $p=0.043$ ). However, when I added the mangrove population, the result was not significant ( $p=0.103$ ) and the trend decreased.

The amount of fruit in the diet of howlers has a negative trend in relation to resting behavior, although this trend was not significant for the comparative population ( $R^2=40.0$ ,  $F=4.0$ ,  $p=0.092$ ). This trend approached significance when I added the mangrove howlers ( $R^2=42.8$ ,  $F=5.23$ ,  $p=0.056$ ) and maintained its negative characteristic. Social behavior had a strong significant relationship with fruit in the diets of the comparative howler populations ( $R^2=65.3$ ,  $F=11.3$ ,  $p=0.015$ ) before I added the mangrove howler data. Adding the mangrove howlers that had 0% fruit in their observed diet and a relatively high percentage of social behavior skewed this trend and made it no longer significant ( $R^2=25.3$ ,  $F=2.37$ ,  $p=0.168$ ).

There were no trends or significant relationships in the amount of time spent feeding and the percentage of leaves or fruit in the diet.

## Discussion

The mangrove howlers exhibit a typical daily activity pattern for howler monkeys. Most time was spent resting and feeding (80% combined), which also follows the pattern for leaf-eating hindgut fermenters (Robbins, 1983). Long resting periods after feeding on abundant yet supposedly low quality foods allows for maximum nutrient absorption and less energy expenditure. Infants tended to have the highest occurrence of movement behaviors and engaged in frequent self- and object play associated with developing gross and fine motor skills (Bateson, 2005). The incidence of travel and social behaviors was highest for juveniles and is likely due to the increased frequency of social play behavior where the game of “chase” is a favorite. For adults, locomotory behaviors were similar to each other and lower in frequency than those seen in younger individuals. Adults also spent approximately the same amount of time resting, which was longer than the resting time observed for juveniles and infants. Studies of animal activity budgets reveal that the adult males of many species spend less time feeding and more time resting than females or younger individuals (Clutton-Brock, 1977a); this is the case in this and other studies of howler monkeys (Smith, 1977; Bicca-Marques and Calegario-Marques, 1994; Muñoz et al., 2001). As expected, lactating females with dependent offspring tend to spend more time eating than other, unencumbered females (Smith, 1977), as was the case in this study. In fact, we observed females with dependent offspring feeding more frequently than any other age/sex class.

Day ranges for howlers average about 700 m and normally stay in the same area over time (Crockett and Eisenberg, 1987; Clarke et al., 2002). We did not calculate day ranges in this study due to the inability to conduct all-day follows; however, howler groups remained faithful to an area throughout the study.

Diversity on the island was limited to an estimated 17 tree/shrub species, 20 primary liana species, several aquatic plant species, and a number of bromeliads (Appendix A). Of these, the howlers used five tree species and seven liana species for food. The most preferred food species was *L. hondurensis*, the swamp dogwood tree, from which the howlers ate leaves, flowers, and seeds, and made up 44.7% of the diet. This tree species ranked fourth in terms of abundance (density) on the island, with an estimated 40 trees per hectare. The second most preferred food resource was the liana *D. brownei*, from which the mangrove howlers ate both leaves and flowers for 23.4% of their annual diets. The estimated above-ground biomass for *Dalbergia* was 483 kg/ha. Dietary composition for the mangrove howlers was most similar to black-and-gold howlers in relatively low-diversity riparian forest and orchard forest in Brazil (Ludwig et al., 2008; Prates and Bicca-Marques, 2008), yet was still lower in diversity than was documented in those studies.

Both tree and liana leaves made up half of the howlers' diet through both the wet and dry seasons. The howlers were observed to eat more liana leaves than tree leaves. The howlers ate leaves from two tree species that are specially adapted to and only grow in mangrove. Young leaves from the white mangrove (*L. racemosa*) were selected in 12.4% of leaf eating observations and red mangrove leaf buds (*R. mangle*) were selected in 5.4%. The most frequently selected leaves for food were from the liana *muco* (*D. brownei*) at 41.9% of leaf-eating and leaves from the *gusano* tree (*L. hondurensis*) at 23.1%. These four plant species were among the most prevalent species in the study area. The howlers were able to obtain most of their nutrients from just a few species, leading me to conclude that the lack of habitat diversity and species richness do not affect howler monkeys in the way that they may affect other, less flexible, animal species, in terms of diet.

We observed that adult females feed on leaves most frequently while adult females with infants fed on leaves least frequently. Adult females with infants spent more time eating overall and fed significantly more often on seeds and flowers when they were available compared to all other groups. These two plant parts made up 57.4% of the dry season diets of females with infants. Factors affecting food choices of lactating females may be the levels of nutrients and/or toxins found in different parts in different species. The phytochemical analysis of food and non-food plant nutrients in this study is found in Chapter 4. Plant samples were not screened for toxins in this study, but this is a direction for future research.

The diet of the howlers in the mangrove during the wet season was 100% foliage for all identifiable observations. There were red mangrove fruits available during this time, but these were not eaten by the howlers. This is more than likely due to the pithy texture of the fruits, which are dispersed by water, not animals. Fruits most often attractive to primates (and many other seed dispersers) tend to have colorful exocarps with fleshy, succulent pulp (Terborgh, 1983; Garber and Lambert, 1998), none of which were seen during this study. The fruits seen most often by the field team in the mangrove belong to the tree species *Pachira aquatica*, a cousin to the Old World durian and baobab trees, and *R. mangle*, the salt-adapted and water-dispersed red mangrove tree. *P. aquatica* fruit can best be described as unattractive in primate terms—bland, texturally woody, with a brown exocarp. These are typical characteristics of the fruits in the mangrove.

The howlers' dry season diet included a significant amount of flowers and seeds. The consumption of these plant parts increased when these items were available, making them important seasonal resources for the howlers. There did not appear to be any unusual food selections during times of flower and seed scarcity as I had predicted—foliage from few species

provided the nutrients required by the howlers for survival during the wet season. This means that the mangrove plants consumed by the howlers are sufficiently nutritious and provide the dietary requirements for the howlers, who are able to successfully extract them through their morphological and behavioral adaptations. For a description of nutrient analysis of plant parts, see Chapter Four.

Compared to howler species in other habitats, the mangrove howlers ate significantly more flowers and seeds and significantly less fruit. The higher percentage of flower consumption may be due to the low-diversity habitat and the need to incorporate as many seasonal foods as possible to supplement their diets. In comparison with other populations of black howlers, the mangrove howlers ate fewer leaves and fruit and more flowers and seeds; this, again, is likely due to the differences in plant diversity between the sites. However, the wet season diet consisting mostly of foliage is similar to the diet of the howlers in Monkey River, Belize after Hurricane Iris decimated their normal food trees and left no fruit or flowers for the monkeys to eat (Behie and Pavelka, 2005; Pavelka and Behie, 2005).

When compared to other howler population trends for activity patterns and diet, the mangrove howlers were not significantly different from conspecifics and congeners in the relationship between the percentage of time spent in locomotory, resting, and social behaviors and the amount of leaves in the annual diet. Because there were no significant differences, I again propose that this low-diversity mangrove habitat is a perfectly sufficient habitat for howler monkeys. As the mangrove howlers were never observed to eat fruit and I put them into the regressions for locomotory and social behaviors on fruit, they were significantly different enough to pull the trend line down and make the overall results non-significant. By putting this population into the pool with fruit-eating howlers, I only show what could happen when howlers

do not have fruit available to them in a low-diversity habitat and do not affect this relationship in howler populations that do have mammal-dispersed fruit available to them.

In a study of the diet of *Alouatta palliata mexicana* on a cacao plantation in Tabasco, Mexico, Muñoz et al. (2006) demonstrated that protein to fiber ratios influenced this group's selection of young versus mature leaves. This study area was restricted to just 12 ha, on which there were 32 tree species. The howlers used 66% (13) of these trees for food, plus two species of epiphytes and one species of vine. The two most important plant families used for food (87%) by the howlers were Moraceae (57%) and Fabaceae (32%). Of the five most used species, three were *Ficus*, an important genus in the diets of many populations of howlers (Serio-Silva et al., 2002; Rivera and Calme, 2006). This group of 20+ mantled howlers fed on 60% leaves, 35% fruit, and 5% flowers and other items over an annual cycle. There were no *Ficus* trees in the mangrove, yet the howlers there ate from a similar number of species as Muñoz's (2006) group of mantled howlers on the cacao plantation mentioned previously, and the mangrove howlers also chose food items from three Fabaceae species, suggesting that the mangrove might be similar in the number of preferred food species as in the agro-forest habitat and that plants in the Fabaceae family may also be a significant resource for howler monkeys.

In another study of *A. p. mexicana* in a small study site (57 ha island), Serio-Silva et al. (2002) showed that this population of 10-29 individuals in one group used 36 of the 63 plant species recorded on the island. The most important food resources for these howlers were six species of *Ficus* (64%), with *Ficus pertusa* as the most-used food resource. The number of species available and used in the aforementioned study are higher than I found for the mangrove population, yet following the pattern for howlers, a similar number of species made up a large percentage of the diet. Vines and lianas represented 6.7% of feeding time, which is lower than

the percentage of time the mangrove howlers used climbing plants as food resources. In a comparison of the phytochemistry among plant species, among plant parts, and between seasons, Serio-Silva and co-authors (ibid.) did not find any significant differences. Additionally, no significant phytochemical differences were found between *Ficus* fruits and fruits of other species. In Chapter Four, I investigate these same variables for the mangrove howler diet.

Bilgener (1995) assayed Ken Glander's plant samples from his dietary study of mantled howlers (*A. palliata*) in Guancaste, Costa Rica. The feeding behavior reported by Glander was that the most common trees at the site were used very little and that the howlers' diets consisted of 64.3% leaves, 18.2% flowers, 12.5% fruit, and 5.7% leaf petioles. When he compared the phytochemistry of eaten and uneaten leaves, Bilgener found that selected leaves were higher in protein content and were more digestible than uneaten leaves.

In the next chapter, I evaluate and describe the phytochemistry of plants in the mangrove, and include several analyses based on plant parts chosen and avoided as food resources by the howlers.

## CHAPTER FOUR

### NUTRITIONAL ECOLOGY AND THE PHYTOCHEMISTRY OF MANGROVE PLANTS

#### **Introduction**

Although not completely out of the normal range, the diet of the mangrove howlers was low in diversity and fairly homogeneous when compared with other howler populations. In addition to being low in diversity, mangroves are assumed to be low in nutritional quality and high in salt and secondary compounds. Thus, it is important to examine the intrinsic properties of the plants in the mangrove and to compare these with nutrient recommendations and with howler foods in other habitats. As stated previously, this population of howler monkeys has access to only mangrove forest at this location. Researchers of other nonhuman primates in mangroves have shown those populations to use mangroves as part of their habitat ranges, and do not rely on them solely for food and shelter (Bennett and Sebastian, 1988; Kool, 1989; Supriatna et al., 1989; Bennett and Davies, 1994; Son, 2003; Galat-Luong and Galat, 2005; Agoramoorthy, 2007; Nowak, 2008).

As reported in the previous chapter, the annual diet and preference for seasonal foods by black howlers at this site were similar and within the range documented for other howler populations in forests of varying richness and densities. The mangrove howlers fed on relatively few species and plant parts over the year. There were some seasonal differences in their feeding habits during the dry season, at which time flowers made up nearly half of all foods selected. They also showed some differences in preference for fruits and seed pods from other populations, choosing to ignore fruits altogether and eating the seed pods of only one tree species. Regardless of these dietary differences, the mangrove howlers retain many similarities

with conspecifics in grouping patterns and population densities, and behavioral patterns typical of the genus. Although their diet is not as diverse as most other howlers and contains a large amount of leaves, I propose that the mangrove howlers are getting the nutrients they require, as outlined by the NRC (2003), from their low-diversity and low-quality diet.

The intrinsic properties of the plants chosen and avoided as food by the howlers may tell us more about primate diets than the actual proportion of each food type selected, as has been suggested by various researchers (Dierenfeld and McCann, 1999; Rothman et al., 2007). For example, populations of mantled (*A. palliata*) and red (*A. seniculus*) howlers appear to select foods high in protein and available energy (Glander, 1978, 1981; Milton, 1979, 1980, 1982; Gaulin and Gaulin, 1982; Estrada, 1984). In some of these same populations, a high protein to fiber ratio may drive food selection (Milton, 1979; Glander, 1981; Bilgener, 2005). In order to elucidate the nutritional ecology and food selection of the mangrove howlers, I analyzed the phytochemistry of 22 plant species and made comparisons to describe their overall make-up and to determine whether mangrove plants were significantly different from non-mangrove plants in this respect.

### **Nutritional Ecology**

Nutritional ecology is the study of the interface of an animal's nutritional intake with its environment and the animal's resulting physiological state (Felton et al., 2009). Nutritional ecology spans many different disciplines including ontogeny, growth and development, anatomy and physiology, and ecology. Because there is strong selective pressure on food choice (Stephens and Krebs, 1986), nutritional ecology is relevant to anthropology because studies involving adaptive food choices of nonhuman primates "can provide important insights into

primate evolutionary ecology” (Fashing et al., 2007:674) and ultimately, the evolution of biological mechanisms that facilitate survival.

The most important aspect of nutritional ecology is the procurement of food to meet nutritional goals of organisms, which are to obtain proper nutrients and avoid toxins. Not all animals have the same intrinsic nutritional requirements, which generally vary according to body size, metabolism, lifestyle, and digestive anatomy and physiology (Milton, 1993). These requirements also vary between individuals of a species according to age or reproductive status. In fact, differences in reproductive success have been linked to food intake disparities in some primate species (Altmann, 1991; Whitten, 1983).

Animal food choices are not only influenced by morphology and physiology, but largely, by ecology. Morphology and physiology are related to what foods can be eaten and digested successfully and include such factors as body size, dentition, gut morphology, digestive physiology, and metabolism. Ecological factors include the foods that are available in the environment. Availability is affected by environmental variables that I have already discussed, including food abundance and distribution, and competition for food with other individuals or groups. In this chapter, I describe the content of foods eaten by the howlers and discuss the effect of phytochemical content of food as a selection factor in howler food choice.

The null hypotheses I test in this chapter are 1) there are no differences in nutritional content between plants selected and ignored as food items by the howlers, 2) nutritional content of plants selected as food by the howlers do not differ significantly from food plants in other howler studies, 3) the nutritional content of mangrove plants do not differ seasonally, 4) the nutritional content of leaves, flowers, and seeds do not differ significantly between trees and lianas, and 5) the nutritional content of foods selected by the howlers in the mangrove provide

adequate nutrient levels as recommended by the National Research Council (2003) for nonhuman primates.

If the general quality of foods available are high in terms of protein levels, protein to fiber ratios, and available nutrients, then being more selective on few species would enable the howlers to decrease foraging time and conserve energy. High quality foods would not limit the mangrove howlers' population in terms of reproduction or activity patterns in terms of energy expenditure or time spent locating food. If the foods are of generally low quality, then I expect to see a significant rise in howler feeding time which would enable them to increase intake and meet nutritional requirements.

I predict that foods chosen will have higher protein to fiber ratios, less overall fiber, and be more easily digestible than foods ignored by the howlers. Of the plants eaten that are high in fiber yet low in protein, I predict that these resources will have high levels of essential nutrients that may be rarer and more limiting than other plants in the mangrove. I predict that the mangrove plants selected as food by the howlers will be nutritionally different from food plants selected by howlers in other studies, but that overall diets will contain adequate nutrients as recommended by the NRC's Committee on Animal Nutrition (2003). I predict that seasonal foods will be of higher quality than leaves available year-round and that the nutritional quality of liana leaves will be higher than tree leaves because liana leaves were selected more often as food resources.

## Methods

### *Field collection and analysis of plants*

A detailed description of the methods used to collect and prepare plants for analysis is located in Chapter Two.

A total of 58 plant samples were analyzed and represent 15 families, 21 genera, and 22 known species. Twelve of these species were selected as food by the howlers and 10 were ignored. Species identifications were confirmed by Professor Ángeles Guadarrama Olivera from the herbarium at Juarez University in Tabasco, Mexico (UJAT). Samples were dried and transported back to the United States. The samples were analyzed by the Forage Laboratory at Dairy One, Inc., Ithaca, NY. Basic wet chemistry profiles were conducted and included percentages of water (H<sub>2</sub>O), crude protein (CP), available protein (AP), fermentable fiber in the forms of acid detergent fiber (ADF) and neutral detergent fiber (NDF), indigestible fiber as lignin (LIG), hemicellulose (HC), cellulose (CS), non-fiber carbohydrates (NFC), starch (ST), soluble sugars (ESC), crude protein to acid detergent fiber ratios (P:F), and finally, ash (ASH). Nitrogen (NIT) was calculated by dividing CP by 6.25. Minerals reported on a percentage basis are calcium (Ca), phosphorus (P), magnesium (Mg), potassium (K), sodium (Na) and sulfur (S). Minerals reported on a milligram per kilogram (mg/kg) basis are iron (Fe), zinc (Zn), copper (Cu), manganese (Mn), and molybdenum (Mb). Because Ca and P are linked through their absorption and elimination, calcium to phosphorus ratios (Ca:P) were calculated. All analyses were on a 100% dry matter basis. I performed statistical analysis using Minitab<sup>®</sup> Statistical Software Version 16 (Minitab Inc., 2012).

Crude protein in a sample is the total protein and is expressed as true protein and non-protein nitrogen. NDF represents total plant cell wall carbohydrates, in which a lower number

means higher quality (less hard-to-digest fiber). ADF is included in the NDF figure and represents the less digestible cell wall components, so a higher ADF means the material is less digestible. Ethanol soluble carbohydrates are sugars solubilized and extracted in 80% ethanol and include primarily monosaccharides and disaccharides that are readily absorbed in the small intestine. Non-fiber carbohydrates are made up of starch, simple sugar, and soluble fiber. A high NFC means the material is more easily digestible. Starches (ST) are polysaccharides (a chain of sugars) that act as storage units for saccharides. Total digestible nutrients (TDN) is a measure that includes the sum of digestible protein, crude fiber, nitrogen-free extract, and fat. Ash (ASH) is a measure of the total mineral content in a sample.

#### *Data analysis*

Data on species and plant parts were analyzed using descriptive statistics in Microsoft Excel to give a general overview of the types and amounts of nutrients in mangrove plants. Phytochemical comparisons were made using Kruskal-Wallis H-tests, and in some cases, Mann-Whitney U-tests for nonparametric data using the statistical software Minitab®. Significance for these tests was set at less than 5% ( $p < 0.05$ ). In cases where the null hypothesis could not be rejected in Kruskal-Wallis tests, and there were significant differences detected, *post hoc* pairwise analysis for nonparametric data was conducted using Mann-Whitney U-tests. Significance for *post hoc* pairwise analysis was set at less than 2.5% ( $p < 0.025$ ).

Phytochemical comparisons were made among plant part nutrients in general, plants used as foods and plants ignored, botanical type, and season (Table 4.1.). Additional comparisons of phytochemistry among the mangrove island at Arroyo Polo and 1) other howler monkey sites, and 2) other primate studies at mangrove sites, were conducted to detect nutritional differences

of foods in various habitats. I compared the nutritional content of food items selected by the howlers with nutrient recommendations published by the NRC's Committee on Animal Nutrition (2003) to evaluate if foods met the nutritional requirements of the howlers in the mangrove.

Comparison	Category	Part	N
All parts and species			59
		Leaves	30
		Flowers	14
		Seeds	4
		Fruits	7
		Stem/bark	2
		Roots	1
Food and non-food			58
Top 5 species		Food	28
		Leaves	17
		Flowers	9
		Seeds	2
	Non-food		30
		Leaves	13
		Flowers	5
		Seeds	2
		Fruits	7
		Stem/bark	2
		Roots	1
Trees and lianas			58
	Trees		26
		Leaves	11
		Flowers	8
		Seeds	3
		Fruits	4
	Lianas		32
		Leaves	19
		Flowers	6
		Seeds	1
		Fruits	3
		Stem/bark	1
Wet and dry seasons			45
	Wet		16
		Leaves	11
		Fruits	4
		Roots	1
	Dry		27
		Leaves	14
		Flowers	9
		Seeds	3
		Stem/bark	1

**Table 4.1.** Plant parts, sample sizes, and comparisons made in this chapter.

## Results

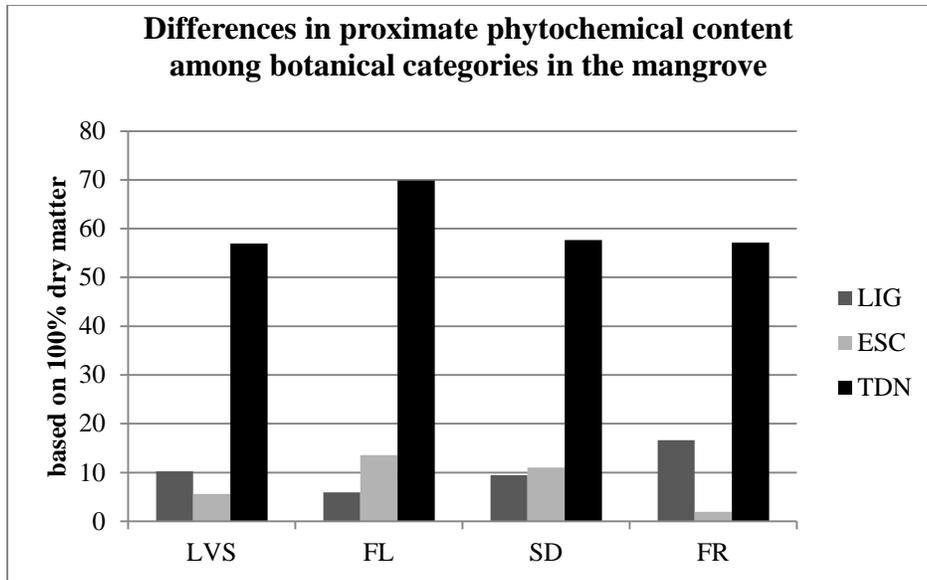
Raw data for all plant samples are in Appendices B (macroelements) and C (minerals).

### *Plant parts - general*

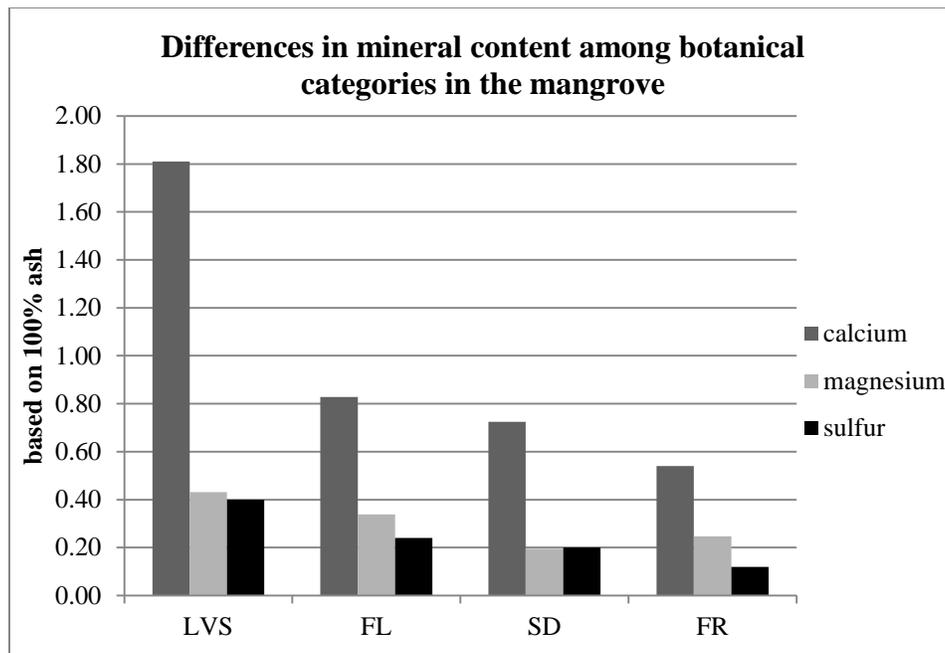
Kruskal-Wallis H tests revealed significant differences between plant parts in general in the macroelements ADF, NDF, HC, LIG, NFC, P:F, STCH, ESC, and TDN (Figure 4.1).

Differences were also detected in the mineral levels of Ca, Ca:P, Mg, Fe, Zn, Mn, and S (Figure 4.2). Pairwise analysis of each plant part in these categories resulted in significant differences in P:F, LIG, ESC, TDN, Ca, Ca:P, Mg, Fe, Mn, and S.

Significant variances were detected in NDF between all botanical categories; however, the null hypothesis could not be rejected in *post hoc* Mann-Whitney pairwise comparisons. Leaves were significantly higher in percentages of LIG (W=474.5,  $p<0.01$ ), Ca (W=459.5,  $p<0.01$ ), and Mn (W=468,  $p<0.01$ ) and were higher in Ca:P ratio (W=457,  $p<0.01$ ) than flowers. Leaves contained higher levels of Mg (W=384,  $p<0.01$ ) and Mn (W=386,  $p<0.025$ ) than seeds. The percentages of Ca (W=382,  $p<0.025$ ) and S (W=381,  $p<0.01$ ) were higher in leaves than in fruits. Flowers consisted of significantly higher TDN (W=295,  $p<0.001$ ), Fe (W=68,  $p<0.025$ ), and ESC (W=294.0,  $p<0.01$ ) than leaves. Flowers displayed significantly higher percentages of Fe when compared with seeds (W=68,  $p<0.01$ ) and fruits (W=66,  $p<0.025$ ), and had higher levels of S (W=68,  $p<0.01$ ) and ESC (W=70,  $p<0.01$ ) than fruits. Protein to fiber ratios were significantly lower in leaves than in flowers (W=66,  $p<0.025$ ) but in all other comparisons of protein to fiber ratios among botanical categories, the null hypothesis could not be rejected.



**Figure 4.1.** Differences among botanical categories in lignin (LIG), simple sugars (ESC), and total digestible nutrients (TDN), all significant in *post hoc* analysis when  $p < 0.025$ .



**Figure 4.2.** Differences among botanical categories in Ca, Mg, and S in the mangrove; all significant in *post hoc* analysis when  $p < 0.025$ .

Kruskal-Wallis H tests were used to test whether or not there were significant differences in the phytochemistry of plant parts under different conditions. These conditions included 1) plants that were chosen for food and those that were not, 2) differences between liana and tree food items, and 3) differences among plant parts during the wet and dry seasons. Significance was set at  $p < 0.05$ . In cases where the null hypothesis was rejected, Mann Whitney U tests or one tailed t-tests were performed to compare categories in pairs. Significance in *post hoc* tests was set at  $p < 0.025$ .

### *Dietary components*

I observed the mangrove howlers to select only 12 plant species as food resources throughout the study period. Of these, the top five species consisted of three trees (*L. hondurensis*, *L. racemosa*, *R. mangle*) and two lianas (*Dalbergia brownei*, *Rhabdadenia biflora*). The most important of these were was *L. hondurensis* (the *gusano* tree), which is not strictly a mangrove species. The mangrove howlers selected leaves, flowers, and seeds from the *gusano* in nearly 45% of all feeding observations. The leaves and flowers of the liana *D. brownei* (known locally as *muco*) were selected in just over 23% of all feeding observations. The leaves and leaf buds of white and red mangrove trees (*L. racemosa* and *R. mangle*) and the liana *R. biflora* together accounted for almost 8% of feeding observations. The species making up the remainder of feeding observations were the trees *T. rosea* and *B. buceras* (*Bucida* was not included in the phytochemical analyses, as the sample was insufficient for most assays), and the lianas *Paullinia pinnata*, *Hippocratea volubilis*, *Clytostoma binatum*, *Passiflora foetida*, and *Malvaviscus arboreus*. I have separated the phytochemical analyses into each of the plant parts eaten by the

mangrove howlers, and then summarize them below. Comparisons between food and non-food items are in the following section.

### Leaves

The leaves of the liana *D. brownei* and the tree *L. hondurensis* were the most important food resources for the mangrove howlers. Together, the leaves of these two plants were eaten in 46% of leaf-eating observations. When combined with the other three of the top five species (*R. biflora*, *L. racemosa*, and *R. mangle*), they were chosen in 62% of leaf-eating observations.

There were no significant differences between leaves eaten the most and leaves eaten least often, however, levels of zinc were lower in leaves eaten most often (approaching significance when  $p < 0.05$ ). Means for macroelements and minerals in the leaves of the five top and four bottom species are depicted in Table 4.2.

LEAVES	WATER %	CP %	AP %	ADF %	NDF %	LIG %	ESC %	NFC %	TDN %
top five sp.	64.0	15.2	5.3	26.5	39.1	10.8	4.4	36.8	56.9
bot. four sp.	53.9	18.8	9.3	27.0	40.2	10.2	7.7	31.2	58.3
ALL	60.2	16.3	6.7	26.7	39.4	10.6	5.6	34.8	57.3
	P:F	CF %	ASH %	Ca %	P %	Ca:P	Mg %	K %	Na %
top five sp.	0.75	2.1	10.4	1.6	0.18	11.9	0.44	1.9	0.67
bot. four sp.	0.71	3.7	9.1	1.3	0.20	10.5	0.36	1.9	0.35
ALL	0.73	2.7	9.9	1.5	0.19	11.4	0.41	1.9	0.55
	S %	Fe mg/kg	*Zn mg/kg	Cu mg/kg	Mb mg/kg	Mn mg/kg			
top five sp.	0.32	71.9	21.3	7.7	0.92	79.1			
bot. four sp.	0.43	94.4	38.4	11.8	0.98	32.4			
ALL	0.36	79.9	27.4	9.1	0.94	62.4			

**Table 4.2.** Macroelements and minerals in leaves selected as food by the mangrove howlers.

The \* means that differences in zinc in leaves between the top five and bottom five food species were approaching significance ( $z = -1.93$ ;  $p = 0.053$ ).

When I isolated the top two species eaten by the howlers in the mangrove, no macroelements or minerals in leaves were significantly different from the eight species used less often. I then separated the true mangrove species, *R. mangle* and *L. racemosa*, from the rest of the sample to see if their leaves were different from the other plants' leaves eaten in the mangrove. Young leaves and leaf buds of the red and white mangrove trees were significantly lower in SP ( $z = -2.13$ ,  $p = 0.033$ ), ESC ( $z = -2.10$ ,  $p = 0.036$ ), and Zn ( $z = -2.34$ ,  $p = 0.02$ ). Approaching significance were differences in CP ( $z = -1.86$ ,  $p = 0.063$ ), NFC ( $z = 1.84$ ,  $p = 0.066$ ), and Mb ( $z = -1.71$ ,  $p = 0.08$ ). Levels of CP and Mb were lower in mangrove tree leaves and levels of NFC were higher. There was no difference in sodium level between the true mangrove leaves and mangrove associates.

When averaged together (Table 4.2), macroelement means for leaves in the diets of the mangrove howlers were 60.2% water, 16.3% CP, 6.7% AP, 26.7% ADF, 39.4% NDF, 10.6% LIG, 5.6% ESC, 34.8% NFC, 57.3 TDN, 2.7% CF, 9.9% ASH, and a protein to fiber ratio of 0.73. Mineral amounts means were 1.5% Ca, 0.19% P, a Ca to P ratio of 11.4, 0.41% Mg, 1.9% K, 0.55% Na, 0.36% S, 79.9 mg/kg Fe, 27.1 mg/kg Zn, 9.1 mg/kg Cu, 0.94 mg/kg Mb, and 62.4 mg/kg Mn.

### Flowers

Flowers from five different plant species were eaten by the mangrove howlers. As with the species most preferred for leaves, *L. hondurensis* (69%) and *D. brownei* (25%) were the most preferred resources for flower-eating. The three species accounting for the remaining 6% of flower-eating were from the trees *T. rosea* (3.7%) and *B. buceras* (1.6%) and the liana *C.*

*binatum* (0.7%). Overall, the means for flower macroelements in the howlers' diets were 72% water, 22% CP, 31% AP, 18% ADF, 28% NDF, 6.6% LIG, 46% NFC, 14.3% ESC, 68% TDN and contained a protein to fiber ratio of 1.4.

I separated the flower species into the top two and the bottom three species in terms of observed consumption (Table 4.3). There were no significant differences in nonparametric tests (KW-H test) with any of the variables, however, the amounts of P and S were lower in the top two species selected, and approached significance ( $z = -1.85$ ,  $p = 0.064$  for both).

FLOWERS	WATER %	CP %	AP %	ADF %	NDF %	LIG %	ESC %	NFC %	TDN %
top two sp.	69.9	18.0	8.1	18.1	29.0	5.7	15.1	47.2	67.3
bot. three sp.	73.6	25.0	2.1	17.9	27.1	7.5	13.6	43.4	69.0
ALL	71.5	20.3	6.6	18.0	28.4	6.3	46.4	14.6	67.8
	P:F	CF %	ASH %	Ca %	*P %	Ca:P	Mg %	K %	Na %
top two sp.	1.1	1.5	7.2	0.60	0.23	2.8	0.32	2.5	0.14
bot. three sp.	1.7	2.5	8.1	0.49	0.38	1.4	0.28	3.0	0.22
ALL	1.3	1.7	7.5	0.56	0.28	2.3	0.31	2.7	0.17
	S %	Fe mg/kg	Zn mg/kg	Cu mg/kg	Mb mg/kg	Mn mg/kg			
top two sp.	0.20	197.0	38.3	14.5	1.65	30.5			
bot. three sp.	0.30	122.0	48.0	25.0	1.20	19.5			
ALL	0.23	172.0	41.5	18.0	1.5	26.8			

**Table 4.3.** Macroelements and minerals in flowers selected as food by the mangrove howlers.

An \* means that the difference in flower phosphorus percentages between the top two and bottom three food species *approached* significance in a Kruskal Wallis nonparametric ANOVA ( $z = -1.85$ ,  $p = 0.064$ ).

## Seeds

The mangrove howlers were observed to eat only the seeds of *L. hondurensis*. These seeds made up 6.4% of the howlers' annual diet. Macroelement and mineral components from two separate samples of *Lonchocarpus* seeds were averaged (Table 4.4).

<i>Lonchocarpus</i> Seed Macroelements				<i>Lonchocarpus</i> Seed Minerals			
WATER%	73.5	AP %	6.3	Ca %	0.85	S %	0.23
CP %	15.4	ADF %	23.5	P %	0.19	Fe mg/kg	44.0
NDF %	38.3	LIG %	7.2	Ca:P	4.5	Zn mg/kg	35.5
NFC %	32.2	ESC %	4.8	Mg %	0.17	Cu mg/kg	9.0
TDN %	60.0	P:F	0.48	K %	1.7	Mn mg/kg	27.5
CF%	2.1	ASH %	5.5	Na %	0.04	Mb mg/kg	1.6

**Table 4.4.** Phytochemical components of seeds and their pods eaten by the mangrove howlers.

Of all the plant parts eaten by the mangrove howlers, leaves were generally highest in fiber, CF, ASH, Ca, Ca:P, Mg, Na, S, and Mn. Leaves were lowest in ESC. With all food species considered, flowers were highest in protein (both crude and available), NFC, ESC, P:F, TDN, P, K, Fe, Zn, and Cu. Flowers had the lowest levels of fiber (ADF, NDF, LIG), Ca, Ca:P, S, and Mn. *Lonchocarpus* seeds exhibited the highest mean content of Mb and the lowest mean for AP, NSC, P:F, ASH, Mg, K, Na, and Fe.

### *Food vs. non-food items*

I calculated P:F ratios and compared them generally in food and non-food plant parts (Table 4.2). In the initial H tests, differences in P:F were approaching significance ( $z=1.89$ ,

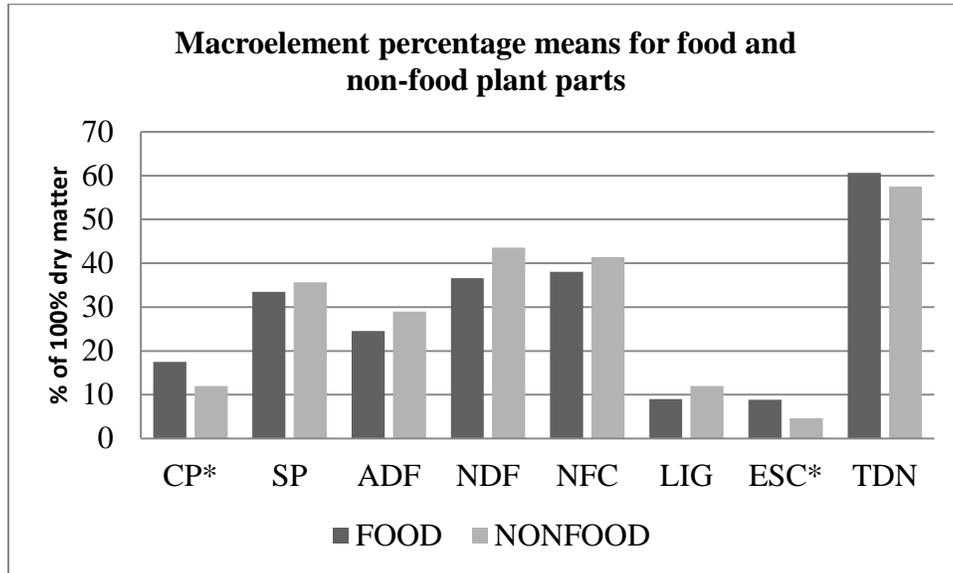
$p=0.059$ ). In subsequent pairwise analysis among plant parts, P:F again approached significance ( $p=0.059$ ), but I could not reject the null hypothesis and foods were not significantly different from nonfoods in this measure. Overall percentages of CP and ESC were significantly different between food and non-food items ( $p<0.025$ ). On closer examination in *post hoc* t-tests, I found significant differences among fruits and the plant parts that were eaten. Fruits were not eaten and were higher in LIG ( $z=1.65$ ,  $p=0.035$ ), lower in CP ( $z= -2.33$ ,  $p<0.025$ ) and ESC ( $z=-2.61$ ,  $p<0.01$ ) than leaves, seed pods, and flowers chosen as food items by the howlers (Figure 4.3). There were no significant differences of mineral components between plant parts eaten and not eaten by the mangrove howlers.

NUTR	PART	FOOD			NON-FOOD		
		MEAN	SD±	RANGE	MEAN	SD±	RANGE
CP*	LV	16.3	8	7.0-30.6	13.4	4.7	7.5-22.6
	FL	20.3	8	11.1-33.5	14.8	10.8	8.2-27.2
	SD	15.4	-	-	15.9	6	11.6-20.1
	FR	-	-	-	9.85	4.8	4.5-17.6
SP	LV	6.7	7.1	0.6-20.9	4.5	3.7	1.1-21.8
	FL	6.6	3.6	2.1-10.8	8.4	11.6	1-6.3
	SD	9.7	-	-	6.3	-	-
	FR	-	-	-	1.1	-	-
ADF	LV	26.7	10.1	10.9-43.8	24.4	5.3	14.4-32.9
	FL	21.0	7.2	12.0-34.3	11.4	3.8	7-14.1
	SD	23.5	12	15.0-32.0	37.2	10.6	29.7-44.7
	FR	-	-	-	30.4	16.8	9.8-54.7
NDF	LV	39.5	14.2	18.4-61.7	38.8	9.7	21.6-56
	FL	31.1	8.4	22.3-49	18.8	7.1	10.7-23.9
	SD	38.3	18.4	25.3-51.3	55.5	16.7	43.7-67.3
	FR	-	-	-	44.9	20.2	17.2-69.4
LIG	LV	10.6	4.9	3.3-18.6	9.8	4.5	4-16.8
	FL	6.6	3.7	2.2-12.7	3.3	2.7	1.4-5.2
	SD	7.2	2.1	5.7-8.7	11.8	1.9	10.4-13.1
	FR	-	-	-	16.6	10.1	4.4-31.2
NFC	LV	34.8	14.2	11.6-59.1	40.1	6.6	28.4-48.1
	FL	46.4	5.3	42.1-55.6	59.9	3.3	56.5-61.2
	SD	32.2	-	-	-	-	-
	FR	-	-	-	40.3	1.7	38.6-42
ESC*	LV	5.6	3.6	1.5-13.3	5.7	5	0.9-18
	FL	14.6	4.1	9.0-19.9	10.5	5.9	6.3-14.7
	SD	14.8	0.3	14.6-15.0	3.4	-	3.4-3.4
	FR	-	-	-	1.9	1.2	1.1-3.9
TDN	LVS	57.3	9.3	44-77	56.5	5.0	50-67
	FL	67.8	6.7	59-79	74	7.6	67-82
	SD	60	-	-	56.5	6.4	52-61
	FR	-	-	-	57.2	17.8	34-80
P:F*	LV	8.4	6.7	2.09-21.3	3.6	1.2	1.7-4.8
	FL	11.1	4.3	6.56-16.8	4.4	1	3.8-5.1
	SD	7.3	-	-	-	-	-
	FR	-	-	-	3.9	2.1	2.4-5.4

**Table 4.5.** Macroelement data for food and non-food plant parts. NUTR=nutrient

(macroelement), the definitions for each are in the methods section of this chapter. PART=plant

part (LV=leaves, FL=flowers, SD=seeds, FR=fruits). SD±=standard deviation. An \* denotes significance when  $p < 0.025$ .



**Figure 4.3.** Macroelement components of plants used for food and plants not selected for food. \* $p < 0.025$ .

#### *Life forms: trees vs. lianas*

Lianas made up a large portion of the howlers' annual diet (44%). To test the hypothesis that there were no differences between liana and tree products, I compared phytochemical content among them. I performed initial H tests on data for all plant parts for both trees and lianas. Overall, I found that tree products were lower in CP, CF, Mg, Fe, Zn, Cu, S, and NIT than lianas. I then performed H tests for closer examination of differences between the leaves and flowers of both life forms. The leaves of lianas were higher in CP ( $z = -2.12$ ,  $p = 0.034$ ), AP ( $z = -2.28$ ,  $p = 0.022$ ), and unavailable protein in the form of NIT ( $z = -2.12$ ,  $p = 0.034$ ) than the

leaves of trees. There were no significant differences in phytochemistry between tree flowers and liana flowers.

### *Seasonal differences*

Nonparametric H tests on overall phytochemical levels between the wet and dry seasons revealed significant differences in crude protein, zinc, and manganese. *Post hoc* pairwise comparisons showed that during the dry season, CP and Zn levels in plant parts were significantly higher than in the wet season when  $p < 0.025$ . This is due to the absence of flowers and seeds in the mangrove during the wet season and their abundance during the dry season.

### *Nutrient concentrations: seasonal and compared with standard recommendations*

I compared concentrations of macroelements and minerals of the annual and seasonal mangrove howler diets with concentrations recommended by the Animal Nutrition Committee of the National Research Council (2003) in Table 4.3. The dry season mean for CP was below range, while the wet season was in the lower range of 15-22% set by the NRC. Fiber levels exceeded NRC values for both wet and dry seasons in ADF and NDF. Also exceeding recommended concentrations were the minerals Ca, Mg, K, Na, and Mn. Mineral concentrations below recommended levels were P, Zn, Cu, and Fe. Iron concentrations were low during the wet season, which can be attributed to lower Fe concentrations in the surrounding soil, possibly diluted by rainfall (Leihner and Cock, 1977) and flooding.

Nutrient	Wet Season Diet	Dry Season Diet				NRC Rec.
	LVS	LVS	FL	SD	Wt Mean	
CP %	15.2	16.3	2.3	15.4	<b>9.8</b>	15-22
ADF %	26.5	26.7	18.0	23.5	17.8	5-15
NDF %	39.1	39.4	28.4	38.3	34.2	10-30
Ca %	1.6	1.5	0.56	0.85	1.0	0.8
P %	<b>0.18</b>	0.19	0.28	0.19	<b>0.22</b>	0.6
Mg %	0.44	0.41	0.31	0.17	0.35	0.08
K %	1.9	1.9	2.7	1.7	2.3	0.4
Na %	0.67	0.55	0.17	0.04	0.34	0.2
Fe mg/kg	<b>71.9</b>	79.9	172.0	44.0	119.9	100
Zn mg/kg	<b>21.3</b>	27.4	41.5	35.5	<b>34.5</b>	100
Cu mg/kg	<b>7.7</b>	9.1	18.0	9.0	<b>13.2</b>	20
Mn mg/kg	79.1	62.4	26.8	27.5	43.3	20

**Table 4.6.** Wet and dry season means for macroelement and mineral composition of dietary items compared with recommended concentrations in the diets of nonhuman primates from the National Research Council (2003). The dry season diet concentrations are averaged for each plant part eaten and a weighted mean was calculated based on percentage of time spent feeding on each part. Values in bold do not meet requirements.

*Comparisons with other howler diets and phytochemistry*

I compared phytochemical properties of plant parts between the mangrove site and two sites in Belize for which black howler diet and nutritional data are published (Silver et al., 2000). Silver's sites included the Community Baboon Sanctuary (CBS) and the Cockscomb Basin Wildlife Sanctuary (CBWS). The CBS was composed of gallery forest and fragments of

secondary growth. The CBWS habitat consisted primarily of evergreen and semi-deciduous broadleaf forest. For comparative data, see Appendix E.

I compared proximate properties of leaves, flowers, and fruits among the different sites. For each of the botanical categories, I compared the proximate values for water, CP, AP, NIT, ADF, NDF, LIG, ASH, P:F, and ESC. Mature and young leaves were combined and because no significant differences existed, both food and non-food foliage were included in the analyses. In all values except water, ASH, P:F, and ESC, leaves in this study were significantly lower in proximate content than lowland forest/riparian leaves (see Table 4.7 for values) Mangrove leaves contained significantly more ash. There were no differences in water, P:F or ESC among leaves in the different habitats. Mangrove flowers were lower in water and fiber (ADF, NDF, LIG) content, yet higher in P:F ratios and ESC than flowers from the other habitats (Table 4.7). There were no differences in protein (CP, AP), NIT, or ASH among flowers from the different habitats. Fruits in the mangrove were not significantly different in any proximate content from other habitat fruits except in one important category: mangrove fruits were significantly lower in ESC (Table 4.7).

PROXIMATE CONTENT: LEAVES

Site	Component	N	Median	Point Est	CI (95%)	W	P value
A	WATER	30	67.5	-5.84	-11.3, -0.4	1286.5	0.0312
B	WATER	75	71.2				
A	CP	23	12.3	-6.12	-9.4, -2.1	854.5	0.002*
B	CP	86	21.1				
A	AP	19	3.4	-9.82	-13.6, -5.9	446.5	0.000*
B	AP	86	16.0				
A	NIT	23	1.9	-0.98	-1.5, -0.3	854.5	0.002*
B	NIT	86	3.3				
A	ADF	25	25.0	-9.82	-14.3, -5.3	798.0	0.000*
B	ADF	86	34.8				
A	NDF	25	40.4	-13.25	-19.3, -7.9	774	0.000*
B	NDF	86	53.0				
A	LIG	24	10.3	-6.9	-10.1, -3.9	752	0.000*
B	LIG	86	16.4				
A	ASH	25	10.2	2.86	1.2, 4.8	1870.5	0.000*
B	ASH	86	7.5				
A	P:F	23	0.44	-0.044	-0.16, 0.09	1191.0	0.585
B	P:F	86	0.56				
A	ESC	23	4.5	1.0	-0.29, 2.38	937.0	0.133
B	ESC	47	3.4				

PROXIMATE CONTENT: FLOWERS

Site	Component	N	Median	Point Est	CI (95%)	W	P value
A	WATER	12	71.0	-9.96	-16.8, -2.3	110.0	0.008*
B	WATER	14	80.5				
A	CP	9	16.8	-0.49	-4.5, -6.9	133.0	0.944
B	CP	20	17.7				
A	AP	7	6.6	-5.16	-9.6, -0.4	61.0	0.434
B	AP	20	11.2				
A	NIT	9	2.7	-0.08	-0.71, 1.11	133.0	0.944
B	NIT	20	2.8				
A	ADF	10	15.9	-18.1	-27.4, -10.7	64.5	0.000*
B	ADF	19	35.6				
A	NDF	10	24.9	-21.13	-29.6, -14.9	62.0	0.000*
B	NDF	20	47.4				
A	LIG	9	5.1	-13.1	-23.0, -8.0	51.0	0.000*
B	LIG	19	18.1				
A	ASH	9	8.4	1.36	-0.7, 3.3	162.5	0.203
B	ASH	20	6.5				
A	P:F	9	0.79	0.33	0.2, 1.5	198.0	0.001*
B	P:F	19	0.47				
A	ESC	8	14.9	8.19	3.0, 12.7	120.0	0.006*
B	ESC	12	4.0				

PROXIMATE CONTENT: FRUIT							
Site	Component	N	Median	Point Est	CI (95%)	W	p value
A	WATER	7	70.4	-3.93	-14.3, 10.9	95	0.628
B	WATER	22	71.6				
A	CP	6	8.2	0.59	-4.2, 5.2	136.0	0.636
B	CP	34	8.2				
A	NIT	6	1.3	0.09	-0.67, 0.84	136.0	0.636
B	NIT	34	1.3				
A	ADF	6	30.7	-3.63	-20.0, 11.8	67.0	0.617
B	ADF	18	35.6				
A	NDF	6	51.4	1.81	-15.3, 23.8	80.0	0.924
B	NDF	19	45.5				
A	LIG	5	13.5	-2.18	-13.3, 9.3	47.0	0.663
B	LIG	15	17.7				
A	ASH	4	6.1	0.45	-2.5, 2.7	85.0	0.835
B	ASH	35	5.6				
A	P:F	6	0.34	0.06	-0.07, 0.35	93.0	0.243
B	P:F	18	0.22				
A	ESC	5	1.4	-3.59	-23.8, 0.7	21.5	0.012*
B	ESC	13	5.2				

**Table 4.7.** Mann-Whitney U test results of the comparison of proximate content of leaves, flowers and fruit from the mangrove with two lowland sites in Belize for black howlers (Silver et al., 2000). A=this study; B=CBS and CBWS pooled data. Point Est=the point estimate is the difference between population medians. CI=confidence interval set at 95%. W=Mann-Whitney statistic, p value significance set at <0.025. \*p<0.025.

Mineral comparisons using one-sample z tests of Ca, P, Ca:P, Mg, Na, Fe, Zn, Cu, and Mn were made among the plant parts of mangrove and Silver's two sites in Belize. There were no significant differences in leaf mineral content among sites, despite the significantly higher percentage of ash in the mangrove leaf samples. There were also no significant differences in

the mineral composition of flowers among sites. However, fruits from Silver's sites were significantly higher in calcium than fruits from the mangrove ( $H=10.1$ ,  $z=1.53$ ,  $p=0.039$ ).

The primary differences among the mangrove site and the Belizean sites in terms of plant phytochemistry are in leaf and fruit composition.

#### *Comparisons with other studies of mangrove phytochemistry*

I compared phytochemical values for the two true mangrove species in Arroyo Polo with the two other primate-mangrove studies in the literature (Supriatna et al., 1989 and Son, 2003) (Appendix F). Unfortunately, differences in species and analyses prevented a full comparison. The only direct comparisons I was able to make were between *R. mangle* leaves and fruit (propagules) in my study site with Son's (2003) data from Vietnam. The red mangrove leaves and fruit in this study contained double the amounts reported by Son (ibid.) for both CP and CF.

## **Discussion**

### *Dietary components*

During the study period, the diet of the mangrove howlers included 47% leaves, 41% flowers, and 6.4% seeds from a total of 12 species. Leaves were eaten from 12 species including five tree and seven liana species. Leaves from the top five species accounted for nearly 62% of the annual leaf consumption, with the leaves of the tree *L. hondurensis* and the liana *D. brownei* being the most important staple foods for the monkeys. Both of these species are part of the leguminous Fabaceae family, a significant food resource family for howler monkeys (Silver et al., 1998; Arroyo-Rodríguez and Mandujano, 2006). More species of liana were chosen for their leaves than species of tree, and the wet season diet of the mangrove howlers was observed to be

100% leaves. Flowers and seeds from the same two species for leaf preference dominated the diet of the mangrove howlers for two months during the dry season. In the following sections, I discuss the dietary components and their phytochemical properties in relation to each other, to recommendations for nonhuman primates by the National Research Council, and to other studies of primate diet and nutrition.

### Leaves

Researchers propose that many primates attempt to maximize protein intake and minimize indigestible fiber (Milton, 1979; McKey et al., 1981; Waterman et al., 1988; Oates et al., 1990; Ganzhorn, 1992; Barton and Whiten, 1994; Yeager et al. 1997; Chapman et al., 2004; Rothman et al., 2007). Less fiber allows longer digestion time and increases effective absorption of nutrients. Researchers of howler monkeys have shown this to be true repeatedly (Milton 1979, 1980; Yeager et al., 1997; Bilgener, 2005). Although not significant, means for fiber were higher and means for total digestible nutrients were lower in leaves than in other plant parts in the analysis. In general, the leaves in this study were significantly higher in Ca, Mg, and S than other plants parts. There were no significant differences between leaves eaten and leaves not eaten in general, components varied significantly between leaves selected most often and those selected rarely, which fell into different life forms: trees and lianas.

Both tree and liana leaves made up half of the howlers' diet through both the wet and dry seasons. The howlers were observed to eat more liana leaves than tree leaves. Two of the tree species from which leaves were eaten included those that are specially adapted to and only grow in mangrove - the white mangrove (*L. racemosa*) and red mangrove leaf buds (*R. mangle*). The most frequently selected leaves for food were from the liana *muco* (*D. brownei*) and leaves from the *gusano* tree (*L. hondurensis*). These four plant species were the most prevalent species in the

study area. The leaves of lianas were found to be higher in CP and AP than the leaves of trees, which may be the reason the howlers selected liana leaves more often. On average, tree and liana leaves in the diet of the mangrove howlers contained 12.4% CP. The average CP percentage for liana leaves in the diet of the mangrove howlers was 19, similar to 20% for herbaceous leaves in the staple diet of mountain gorillas (*Gorilla berengei*) at Virunga in Rwanda (Rothman et al., 2007).

The diet of the howlers in the mangrove during the wet season for all identifiable observations was 100% foliage from only four species. The mangrove howlers ate leaves from six species of liana and four species of tree during the dry season. There did not appear to be any unusual foods selected during times of flower and seed scarcity and foliage provided adequate nutrients for the howlers during the wet season. Foliage from two leguminous species, *D. brownei* and *L. hondurensis*, were most important in the diet of the howlers throughout both the wet and dry seasons. Zinc and crude proteins were more available in plant parts during the dry season, possibly for two reasons: the dilution effect of ground water during the wet season for zinc and the availability of high protein/low fiber flowers during the dry season.

The young leaves and leaf buds of the two true mangrove species present at the site were selected by the howlers as food resources in both the wet and dry seasons. White mangrove (*L. racemosa*) young leaves were eaten in 26% of wet season feeding observations and red mangrove leaf buds in 3%. In the dry season, instances of feeding observations on these two species dropped to 3.8% and 1.6%, respectively, when more leaf species, flowers, and seeds were incorporated into the diet. Young leaves and leaf buds of the white and red mangrove trees were significantly lower in proteins, carbohydrates, and the minerals zinc and molybdenum than the leaves of mangrove associates. It is possible that these leaves were selected because they

were so prevalent or for some other phytochemical factor, such as zinc or tannin content. In addition to being feeding deterrents, tannins can also be beneficial to consumers as they have anti-parasitic and anti-oxidant properties (Rothman et al., 2009).

### Flowers and seeds

The howlers' dry season diet included a significant amount of flowers and seeds, which were abundant during that time. Flowers and seeds were lower than leaves and fruits in indigestible fiber and are higher in ESC and TDN, making them more desirable and likely important seasonal resources for howler nutrition. Flowers and seeds were especially important in the diets of lactating females and their dependent offspring. Flowering and the appearance of seeds occur in abundance during the months of April and May in this area and may influence life history parameters, such as mating and birth seasonality, to synchronize the weaning of infants with the availability of such nutritious and easy to digest foods in this population. Kowaleski and Zunino (2004) found that both conception and weaning of young black-and-gold howlers (*A. caraya*) coincided with peaks in food abundance, which is the pattern I documented here during the annual availability of flowers.

Seeds eaten by the howlers are leguminous and are best described as small, thin pods (10 cm in length) containing one or two very small seeds. We observed the howlers to chew the pods vigorously and did not find any seeds intact during several instances of fecal inspections. These qualitative observations lead me to believe that the mangrove howlers are not acting as dispersal agents in this location at this time for this species. The increased percentages of flowers and fruits in the diets of the mangrove howlers compared with other howler populations could be an indicator of compensation for the lack of fruits in the diet.

## Fruits

The phytochemical content of the mangrove fruits reveals that they are higher in indigestible fiber in the form of LIG and lower in CP, ESC, and Ca than other plant parts, rendering them a somewhat undesirable food source for animals. There were red mangrove fruits available practically year-round, but we never observed the howlers eating them. As I stated previously, the fruits/seeds of mangroves and mangrove associates are intended for dispersal via water and have characteristics to that end. They need not be attractive to mammal dispersers for propagation.

### *Digestibility and chemical factors*

Plant secondary compounds, such as tannins and alkaloids, are common in plants and act as defense mechanisms against herbivory by inhibiting digestion or producing toxicity (Cork and Foley, 1991; Foley and McArthur, 1994). In mangrove trees, plant secondary compounds are of interest, mainly for biomedical research. In the most extensive review on secondary compounds as deterrents to herbivory in mangroves, Kandil and colleagues (2004), describe tannins and flavonoids in the prolific Rhizophoraceae family that are most common family in mangroves worldwide.

In *R. mangle*, one of the dominant species in the study site and one of the top five food species in the diet of the mangrove howlers, secondary compounds are primarily tannins and flavonoids, which can make up 25% of the dry weight of red mangrove leaves (Kandil et al., 2004). The flavonoid compounds are diverse and are normally found in higher concentrations

than are necessary for their functions, proposed to allow them to adapt to changing environmental conditions and stressors. The compounds protect against UV damage, oxidation, and deter herbivory (ibid.). Tannins specifically act as deterrents by chelating with iron and inhibit digestion by binding to proteins, inhibiting protein kinase, and increasing carbon to nitrogen ratios. The measurement of any of these compounds must be site, and even tree specific, as these compounds vary greatly (ibid.).

The problems surrounding accurate measurement of secondary compounds across sites, especially of tannins, arise from the standards used for comparison (Kool, 1992), which tend to over- or underestimate levels. In order to properly assess the influence of tannins and other flavonoids at my mangrove site, a study involving the development of local standards for comparison and collection of new plant samples need to be undertaken, which a direction for future research.

Lignin, a component of the fiber value of plant material, is a polyphenolic compound, as are tannins, are produced by plants to deter herbivory (Van Soest, 1982). Protein to fiber ratios act as an important indicator of digestion inhibition as well. The higher the ratio, the better quality the food because the fiber level is lower, allowing the food material to stay in the gut longer and increase nutrient absorption time. As was expected, leaves in general at the site averaged higher amounts of LIG than other plant parts analyzed. As was reported by Milton (1979, 1980), Glander (1981), and Estrada (1984), mantled howlers prefer leaves with high protein to fiber ratios and high digestibility, even if the resource was considered rare.

### *Age/sex differences*

Leaf consumption was significantly lower and seed consumption was significantly higher for adult females with dependent offspring. Juveniles ate significantly more leaves, fewer flowers, and fewer seeds than other age groups. Adult females were observed to feed on leaves the most at 52.9% while adult females with infants fed on leaves the least. Adult females with infants spent more time eating and fed significantly more on seeds and flowers when they were available than any other group. These two plant parts made up 57.4% of the dry season diets of females with infants. Flowers and seeds provided lower amounts of LIG and higher levels of sugars and total digestible nutrients than did leaves. Combined, flowers and seeds provide as much calcium and more magnesium than do leaves. Therefore, females with infants may be choosing more easily digestible foods while still getting the same amounts of minerals. Secondary compounds may also influence food choice for pregnant and lactating females. Factors driving juvenile plant choice may also be influenced by these same factors. These are directions for future research.

### *Comparison with recommended nutrient concentrations by the National Research Council*

The National Research Council's (2003) adequate nutrient concentrations for macroelements and minerals in the diets of nonhuman primates were compared with nutrient concentrations in the foods of the mangrove howlers. Based on weighted means for specific foods on a seasonal basis, most nutrient concentrations of plant items met and/or exceeded daily recommendations for monkeys. Plants selected for food by the howlers were of higher quality in terms of protein and fiber content and digestible nutrient content than plants ignored in Arroyo Polo. Zinc seems to be a limiting factor in the consumption of leaves, because of all the leaves

eaten, zinc levels were significantly lower in the leaves eaten most often by the howlers. This is contrary to findings by Chapman et al. (2004) and Fashing et al. (2007), in which zinc appeared to be a selection factor in leaf choice by black-and-white colobus monkeys (*Colobus guereza*). Zinc deficiencies in individuals and in a population would result in changes in morphology and social behavior. Because zinc is a fundamental component of gene expression through the metabolism of nucleic acids, low levels affect normal reproduction and growth and development, including socialization of immature individuals (NRC, 2003). Morphological indicators of prolonged zinc deficiency include alopecia and dermatitis. I did not observe any of these characteristics during routine data collection. It is common for soils to be zinc deficient, especially in agricultural areas that require a lot of water, such as rice (Alloway, 2008), however, I found that in mangroves, zinc levels may actually be higher than average in sediments due to pollution from anthropogenic activities (MacFarlane and Burchett, 1999). Copper levels were negatively correlated with zinc levels in my samples (Pearson correlation coefficient 0.583,  $p < 0.01$ ), so it may be the case that the monkeys are moderating copper levels by taking in lower zinc levels. The NRC (2003) reports that too much zinc can cause copper deficiencies in mammals, which presents itself in similar ways as zinc deficiencies. Both copper and zinc affect the cellular uptake of iron (ibid.) and this may also contribute to nutritional selection factors in this population. Phosphorus levels were also low in foods during both seasons, which affected important calcium to phosphorus ratios. In the wet season this ratio was 8:1 and in the dry season it was 4:1, which is much higher than the recommended range of 1:1-2:1. Excess Ca lowers absorption of P (NRC, 2003) and P is a common limiting nutrient in tropical forages (Dierenfeld, pers. comm.). Closer inspection for these specific characteristics in sediments and plant foods in addition to actual levels in the monkey population through blood analysis of

individuals is needed to accurately assess the relationships of these mineral components in the selection of mangrove plant foods.

The results of my general estimation of the mangrove monkeys' dietary nutrition lead me to believe that the mangrove habitat, though low in plant diversity and food choices for howler monkeys, is a perfectly adequate habitat for these primates and should be considered as a viable resource for the conservation of howlers, and other folivorous primates, in the future.

#### *Comparison with diets of other howlers and primates in mangroves*

It is proposed that the same species living in different habitats may have different diets, but have similar nutritional content in the plants they are eating (Dierenfeld and McCann, 1999; Rothman et al., 2007). When I compared leaf-eating between the mangrove population and other black howlers, the mangrove howlers ate fewer leaves, more flowers, more seeds, and less fruit, and ate from significantly fewer plant species on an annual basis. This may be due to the low-diversity habitat, the need to incorporate high quality flowers and seeds to supplement their diets, and the avoidance of mangrove fruit due to high fiber and low protein and sugar content . Nutritionally, mangrove leaves were significantly lower in macroelement content except P:F ratios, ESC, and ASH. Protein to fiber ratios and sugars were similar among sites, indicating that these two factors may influence selection of leaves by the mangrove howlers – however, this was not a conclusion made by the authors (Silver et al., 2000) for the black howlers in Belize. Yet this similarity is reflected in other dietary studies of howlers that show them to choose leaves with a high P:F (Milton, 1979, 1980; Bilgener, 2005).

I proposed several null hypotheses regarding phytochemical content of mangrove plants. The first hypothesis that there was no difference in nutritional content between plants selected

and ignored as food items by the howlers was not supported. Fruits encountered in the mangrove were not selected as food resources by the howlers and were high in indigestible fiber and low in protein, calcium, and sugars compared with selected foods. However, mineral content did not vary significantly between foods and non-foods and I could not reject the null hypothesis in this regard. The second hypothesis was that nutritional content of mangrove plants selected for food would not vary significantly in phytochemical content from food plants in other primate studies. I rejected the null hypothesis on the basis that mangrove plants were significantly different in many nutrients. Leaves in the mangrove were lower in protein and fiber and higher in ash than non-mangrove leaves. Flowers in the mangrove were lower in water, available protein, and fiber than their non-mangrove counterparts yet were higher in sugars and protein to fiber ratios. Habitat quality, in terms of nutrition, of the mangrove is not as poor as I had believed it to be before my study. The major nutritional shortcomings in leaf, flower, and fruits in the mangrove were successfully compensated for by the howlers. Leaves were generally lower in protein and fiber, but the howlers spent more time eating leaves than their conspecifics in other habitats. Mangrove flowers may have been lower in protein and fiber but made up for it by having more readily available, easily digestible energy for the howlers. Mangrove fruits do not have much to offer the howlers in terms of nutrition and so were simply not chosen as food resources.

Comparisons with food plants selected by other black howler populations revealed that leaves in the mangrove selected by the howlers as food were similar in quality than plants in non-mangrove forest. Flowers eaten in the mangrove were of higher quality and provided easy access to more energy from sugars than non-mangrove flowers eaten by other black howlers. Mangrove plants were not higher in sodium than non-mangrove plants.

Species-specific dietary patterns (Sussman, 1978) for howlers are altered in the mangrove habitat due to the limitations imposed by the availability and quality of food resources. The combination of food items eaten on an annual basis and their nutrient concentrations show that the mangrove howlers select foods to balance nutrient intake, even with possible seasonal differences in plant part intake. This allows the population to theoretically maintain a healthy status and remain reproductively viable. From these data, I show that this population of howlers is taking advantage of high quality foods and maximizing net energy intake when it can, as is expected when phytochemistry, in addition to broad food categories, is taken into account in food selection by animals. This information is important when assessing habitats for conservation and for the maintenance of primate populations in captivity. Dietary comparisons with conspecifics and congeners must consider nutritional content in addition to dietary components in order to gain a more complete understanding of food selection and habitat.

## CHAPTER FIVE

### SUMMARY AND CONCLUSIONS

The mangrove forest in Arroyo Polo has a medium-height canopy averaging nearly 9 m with a fairly dense canopy (50-60% closed). Tree species diversity estimated using the Shannon-Weiner Index in the mangrove study site was significantly lower than this measure of diversity reported for other howler study sites, except for one site reported for *A. caraya* on an island in Paraná, Brazil (Ludwig et al., 2008), which was nearly identical in this index, and another mangrove site reported by Snarr (2006) to have a slightly lower diversity index. Species richness for the mangrove site was low and included trees, lianas, epiphytes, and aquatic plants; it was two to nine times lower compared with other primate-inhabited forest types in Gabon, Panama, and Mexico (Table 2.9). Evenness, or the relative abundance of each species in the site (density), of the top two species in the mangrove was two to eight times higher (and thus, uneven) than the other forest sites in the comparative sample, indicating the dominance of two tree species in particular on the landscape. This homogeneous habitat does not provide a diverse selection for food resources for primates that rely on plant products for subsistence, and contributes to the distribution and quality of potential foods, two of the three main factors known to affect feeding strategies and reproductive success in primates (Strier, 2011).

White mangrove (*L. racemosa*) trees formed the majority of the forest inland and red mangrove (*R. mangle*) trees dominated the forest ringing the island on the waterline. These are both true mangrove species that thrive in the perpetually flooded brackish water estuarine conditions. In Arroyo Polo, these two species were of similar heights and produced similar crown areas to each other, which were the largest on the island, second only to the pockte trees

(*B. buceras*), which were typically inland and were 2-3 meters taller and produced a canopy three times the size of the red and white mangrove trees.

Biomass estimates for the red and white mangrove were equivalent to mangrove forests of similar make up (Soares and Schaeffer-Novelli, 2005; Snarr, 2006), producing over 50 million kilograms of leaves, flowers, fruit, wood, bark and roots on the island. Cumulative diameter at breast height (CDBH), a measure of tree productivity, was highest for the most abundant species, the white mangrove. This species was also highest in basal area (BA), another measure of food productivity. Red mangrove trees were second in abundance, CDBH, but were third in terms of BA productivity. Ranked second in terms of BA productivity because of their mass, pockte trees had one of the lowest densities and the third highest CDBH of all the trees in the sample. Leaf biomass for the liana *Dalbergia brownnei* (Indian rosewood) was 525 kg/ha, and produced almost as much biomass as some of the tree species in the sample.

My hypothesis and prediction that the mangrove study site in Arroyo Polo would be lower in species diversity and richness was not rejected. The mangrove study site in Arroyo Polo was lower in diversity to most other howler habitats included in the comparative sample. However, diversity was comparable to two other sites in which mantled howlers were studied (Snarr, 2006; Ludwig et al., 2008). Species richness was lower in this study and the distribution of species was uneven, indicating fewer numbers of species and domination of the landscape by fewer than five tree and liana species.

The primary difference between this study population of howlers and any other study of howlers to-date is that these howlers do not have access to any other habitat and are dependent solely on the mangrove for food and shelter.

The black howlers in the mangrove retain the species-specific behaviors reported for other black howler populations for group size and social structure, despite differences in habitat diversity and richness. Population densities of black howlers are typically lower than densities in other howler species populations, and the mangrove population is no exception. Grouping patterns of the mangrove howlers are also consistent for species patterns across many locations and habitats throughout their distribution, often consisting of one to three adult males, two to three adult females, and one to three immatures. The adult sex ratio favored females and the adult female to immature ratio was relatively even in the mangrove population. These two factors indicate that the population is doing well at this time, and when combined with historical data, I propose that the population has remained stable since my first surveys in 2005.

The low diversity and richness of the mangrove in Arroyo Polo did not alter the behavior/activity patterns of the black howlers on the island when compared to activity patterns of other howler populations. They rested and fed for 80% of the day, with long feeding peaks in the morning and evening just before dark with long resting periods in between. A shorter feeding peak is seen at midday. This behavior pattern is typical of this genus, regardless of habitat type or size.

Seasonal changes in the frequencies of behavior were seen during the dry season, especially in April, when flowers and seeds were available and consumed for nearly half of the time spent feeding. Social behavior (affiliative), feeding, and locomotion within trees increased during this time of seasonal abundance. Resting behavior increased during the wet season when I observed only leaves to be eaten by the howlers.

The howlers selected foods from 12 species in the mangrove. Two plant species, the gusano tree (*L. hondurensis*) and the Indian rosewood liana (*D. browni*) made up 68% of the

diet through the wet and dry seasons. The diet of the mangrove howlers was composed primarily of leaves throughout the wet season, yet was composed of nearly 50% flowers and 6% seedpods during the dry season. The howlers in this study did not consume any fleshy fruits. This is because the fruits in the mangrove are not dependent upon mammals for dispersal and so fruits are structured for water dispersal. Although leaves provided the necessary nutrients during the year when flowers and seeds were not available, food leaves in the mangrove contained the highest levels of fiber, lower protein to fiber ratios, lower levels of sugars, iron, and total digestible nutrients than flowers. Leaves were significantly higher in lignin and calcium than were flowers. Leaves were also significantly higher in magnesium than seedpods. Although the percentages of items in the mangrove howler diet were significantly different from the diets of conspecifics and congeners, they follow species-specific feeding behavior for howlers, feeding on seasonal resources when they are available and subsisting on leaves when they are not.

The leaves of lianas in the mangrove were selected more often as food resources than the leaves of trees. The biomass of the most prevalent liana, and the one eaten most often by the howlers, making up the largest percentage of leaf-eating observations (41.9%), was nearly the biomass of medium-sized trees per hectare in the forest (~500 kg/ha). Liana leaves were higher in protein than tree leaves and perhaps this is why they were chosen more often as food.

The top five species of leaves eaten had significantly lower zinc levels than the four species eaten less often. The young leaves and leaf buds of the two true mangrove species eaten were significantly lower in available protein, sugars, and zinc than the leaves of mangrove associates that were chosen for food. Levels of sodium were not significantly different in mangrove vs. mangrove associate leaves.

Of the different plant parts analyzed, flowers in general were highest in protein, carbohydrates, sugars, digestible nutrients, and the minerals P, K, Fe, and Zn. Flowers were lowest in fiber, Ca, S, and Mn. The mangrove howlers ate flowers from five different species – two lianas and three trees. The most preferred were flowers from the most preferred sources of leaves – the gusano tree (*L. hondurensis*) and the liana Indian rosewood (*D. brownei*), though the flowers of gusano trees were selected most often. There were no differences in nutritional content between tree and liana flowers.

When compared with nutrient requirements for nonhuman primates, the diet of the mangrove howlers met and at times exceeded them on an annual basis. During the dry season, based on weighted means for proportions of plant parts in the diet, crude protein, zinc, and copper were lower than recommended amounts. In the wet season, mineral amounts for iron and zinc were lower and phosphorus was higher than recommended. These are only estimations, however, and a study incorporating daily intake rates would provide better estimates.

My prediction that food items would be higher in nutrients and be of better quality was partially true. There were no differences among food and non-food leaves, flowers, or seedpods; only fruits accounted for significant differences (fruits in this study did not include seedpods). Fruits were significantly lower in sugar and protein content and higher in fiber than food items (leaves, flowers, and seeds pods eaten). Mangrove fruits were not eaten by the howlers.

I found that the differences in proximate nutritional composition of plants among the mangrove and other black howler habitats to be significantly different in many aspects and thus, rejected the null hypothesis.

Overall, the population of black howlers in the mangrove are showing the flexibility that this genus is known for by surviving in yet another habitat that is not necessarily the most

desirable one in terms of diversity and richness. This study adds support to the idea that howlers are highly adaptable to many environments, including those that are anthropogenically disturbed or low in diversity. Although they are not as general in their dietary and morphological regimes as macaques (*Macaca* sp.), a highly adaptable genus of primates in Africa and Asia, howlers are able to exploit a food resource not as nutritionally available to most other primate species in the New World: leaves. This ability to meet nutritional requirements on a diet consisting of mostly leaves for part or all of an annual cycle gives them an advantage over many primates who lack this capability.

The distribution, availability, and quality of foods are the key variables affecting morphological and behavioral adaptations, population health, social organization, and feeding and reproductive strategies in primate populations (Strier, 2011). In the case of the mangrove howlers, the distribution, availability, and quality of foods are measured by the diversity, richness, seasonality, and nutritional components of mangrove trees and lianas. I conclude that despite low diversity and high abundance of tree species resulting in a homogenous landscape, the quality of foods available for the howlers here are high enough throughout both the wet and dry seasons to sustain the present population and is likely to allow it to grow over time to some degree. The howlers rely on high quality seasonal resources and are able to sustain themselves on the foliage of key species during the wet season. The most important food item for the mangrove howlers in the dry season is flowers of just a few species of trees and lianas. The behavior of the howlers in the mangrove falls within the general pattern expected for howlers in all types of habitat with varying quality, but is similar to those populations in other low diversity environments. The most important aspect of a habitat for howlers, and possibly other folivorous primates, is the nutrition available in potential and actual food items. The mangrove seems to be

a perfectly suitable, though not a highly desirable, location for howlers and should be considered as a viable habitat for relocation programs and as part of biological corridors to connect fragmentary forests.

## **Conclusions**

- 1) The mangrove study site is low in plant diversity and species richness and follows a typical pattern for mangrove forest communities.
  
- 2) The mangrove howler population in Arroyo Polo is stable, despite their low-diversity habitat and limited diet. Group sizes, group demographics, and population density are all within the normal range reported for black howlers.
  
- 3) The mangrove howler population in Arroyo Polo adjusts its behavior in response to food availability in general, feeding more frequently and engaging in more affiliative social behavior when seasonal resources are available, and generally resting more during some months when only leaves are available. The low aggression rate in this population, both within and between groups, is indicative of low competition for resources when it comes to either food or mating opportunities.
  
- 4) The mangrove howlers rely heavily on flowers and seeds during the dry season, much more so than is reported for other black howler populations and other howler species. Consumption of leaves was within the range for howlers in general, but was slightly lower than is reported for black howlers at several sites. The consumption of fleshy or propagule fruits in the mangrove

was non-existent and thus was significantly lower than fruit consumption for other howlers. The howlers did not incorporate any novel foods into their diets.

5) The mangrove howlers favored seasonal items when they were available and may have been influenced by protein to fiber ratios. In the case of leaves, lower zinc and higher protein and mineral (Ca, Mg, S) levels seem to influence their selection by the howlers. Selection of foods with lower zinc and higher sulfate concentrations may be acting to keep copper levels in balance and preventing gastrointestinal distress, as is documented in Merck's Veterinary Manual (2010). Flowers consumed by the howlers were high in protein and digestible nutrients. Fleshy and propagule fruits were not selected as food in the mangrove and were higher in lignin (a digestion deterrent), lower in sugars, protein, and Ca than other food items, in addition to being pithy in texture.

6) Within the mangrove site at Arroyo Polo, the howlers did consume young leaves and leaf buds from two true mangrove species. These leaves and leaf buds were significantly lower in available protein, sugars, and zinc than other leaves in the diet. Non-fiber carbohydrates were found in higher levels in these leaves. It is probable that low zinc and high carbohydrate concentrations in these food items were the reason they were selected by the howlers.

7) The diet of the mangrove howlers falls within the range of nutrient recommendations for non-human primates on an annual basis. There do seem to be seasonal deficiencies in some proximate and mineral elements, but these are only broad estimates and more detailed dietary data are needed to make a more accurate description. Despite this possible under or over-

estimation, it is apparent that howlers select high quality foods and are able to balance their nutrient intake, possibly selecting plants low in zinc and high in molybdenum to keep copper levels in check.

8) When compared with the plant foods of howlers in other habitats, the plant foods in the mangrove were different in many respects. Leaves in the mangrove were similar in P:F and sugars, yet higher in ash content than non-mangrove leaves. Although the percentage of ash in a sample contains the mineral concentrations, no differences were detected in leaf minerals among sites. Mangrove flowers were higher in P:F ratios and sugars than non-mangrove flowers, and were lower in water, available protein, and fiber. There were no significant mineral differences. Mangrove fruits were significantly lower in sugar and calcium than non-mangrove fruits.

9) Red mangrove (*R. mangle*) leaves and fruits in Arroyo Polo were double the amounts for crude protein and crude fat than this species in a Vietnam mangrove forest. This fact is a reflection of the differences that exist in similar habitats in different locations and confirms the necessity of site-specific studies and local environmental conditions.

10) Although there were significant differences in dietary components among conspecific populations and the nutritional quality of plants eaten, overall nutritional intake was not significantly different between the populations compared. This is an important part of dietary and conservation research that is often overlooked. In order to evaluate the suitability of potential habitats for monkeys (and other animals), it is most useful to take into consideration the

plants that are available along with their nutritional content. In addition, toxins are important constituents in the selection of foods and should be included in such a study.

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## Appendix A

Flora recorded on the island in Arroyo Polo, Pantanos de Centla Biosphere Reserve and their uses by the howlers and local people.

FAMILY	GENUS	SPECIES	LIFE FORM <sup>3</sup>	CN <sup>4</sup>	RESOURCE USE					
					MONKEYS		HUMANS			
					FOOD	ACTIVITY	FOOD	MEDICINE	CONSTR.	FUELWOOD
Alismataceae	<i>Sagittaria</i>	<i>lancifolia</i>	H	cola de pato						
Amaryllidaceae	<i>Hymenocallis</i>	sp	A	lirio						
Annonaceae	<i>Annona</i>	<i>glabra</i>	T	guayabillo						
Apocynaceae	<i>Echites</i>	<i>yucantanensis</i>	L	-						
	<i>Rhabdadenia</i>	<i>biflora</i>	L	-						
	<i>Urechites</i>	<i>andrieuxii</i>	L	-						
Arecaceae	<i>Acoelorrhaphe</i>	<i>wrightii</i>	P	tasiste					Y	
	<i>Anthurium</i>	<i>schlechtendalii</i>	E	hoja de viento				Y		
Bignoniaceae	<i>Sabal</i>	<i>mexicana</i>	T	guano		Y				Y
	<i>Clytostoma</i>	<i>binatum</i>	L	-	Y					Y
	<i>Tabebuia</i>	<i>rosea</i>	T	maculi	Y					
Bromeliaceae	<i>Aechmea</i>	<i>bracteata</i>	B	pita cimarrona						
Cactaceae	<i>Selenicereus</i>	sp	EC	-						
Caesalpinaceae	<i>Haematoxylum</i>	<i>campechianum</i>	T	tinto				Y		
Celastraceae	<i>Hippocratea</i>	<i>volubilis</i>	L	-	Y					
Combretaceae	<i>Bucida</i>	<i>buceras</i>	T	puckte	Y	Y			Y	
	<i>Laguncularia</i>	<i>racemosa</i>	T	mangle blanco	Y	Y			Y	Y
Fabaceae	<i>Dalbergia</i>	<i>brownei</i>	L	muco	Y	Y				
	<i>Gliricidia</i>	<i>sepium</i>	T	-						
	<i>Lonchocarpus</i>	<i>hondurensis</i>	T	gusano	Y	Y			Y	
	<i>Mimosa</i>	<i>pigra</i>	T	sarsa				Y		

<sup>3</sup>Plant types. H=herbaceous. A=aquatic. T=tree. L=liana. P=palm. E=epiphyte. B=bromeliad. EC=epiphytic cactus. T/S=tree/shrub.

<sup>4</sup> Common name.

FAMILY	GENUS	SPECIES	LIFE FORM <sup>5</sup>	CN <sup>6</sup>	RESOURCE USE					
					MONKEYS		HUMANS			
					FOOD	ACTIVITY	FOOD	MEDICINE	CONSTR.	FUELWOOD
Fabaceae	<i>Pithecellobium</i>	<i>lanceolatum</i>	T	-						
Loranthaceae	<i>Psittacanthus</i>	<i>ramiflorus</i>	T	-						
Malvaceae	<i>Hampea</i>	sp	L	-						
	<i>Malvaviscus</i>	<i>arboreus</i>	L	manzanilla cimarrona	Y					
	<i>Pachira</i>	<i>aquatica</i>	T	zapote de agua		Y	Y		Y	
Marantaceae	<i>Thalia</i>	<i>geniculate</i> L.		popal				Y		
Passifloraceae	<i>Passiflora</i>	<i>foetida</i>	L	-	Y					
Pontederiaceae	<i>Eichhornia</i>	<i>crassipes</i>	A	jacinto						
Polypodiaceae	<i>Polypodium</i>	<i>calaguala</i>	E	calaguala						
Rhizophoraceae	<i>Rhizophora</i>	<i>mangle</i>	T	mangle rojo	Y			Y	Y	Y
Rubiaceae	<i>Randia</i>	<i>aculeata</i>	T/S	-						
		sp	T/S	-						
Sapindaceae	<i>Paullinia</i>	<i>pinnata</i>	L	jujos	Y					
Verbenaceae	<i>Avicennia</i>	<i>germinans</i>	T	mangle negro						

<sup>5</sup>Plant types. H=herbaceous. A=aquatic. T=tree. L=liana. P=palm. E=epiphyte. B=bromeliad. EC=epiphytic cactus. T/S=tree/shrub.

<sup>6</sup> Common name.

APPENDIX B. Mangrove Plant Samples Used in Phytochemical Analysis

ID	FAMILY	GENUS	SPECIES	LIFE FORM	PART	SEASON	FOOD
23	APOCYNACEAE	<i>Echites</i>	<i>yucatanensis</i> Millsp. ex Standl.	L	LV	W	N
168		<i>Rhabdadenia</i>	<i>biflora</i> (Jacq.) Müll. Arg.	L	LV	D	Y
246				L	FL	D	N <sup>7</sup>
145		<i>Urechites</i>	<i>andrieuxii</i> Müll. Arg.	L	ST/BK	D	N
145				L	ST/BK	D	N
184				L	LV	D	N
256	BIGNONIACEAE	<i>Clytostoma</i>	<i>binatum</i> (Thunb.) Sandwith.	L	FL	D	Y
258				L	LV	D	Y
158		<i>Tabebuia</i>	<i>rosea</i> (Bertol.) A. DC.	T	FL	D	Y
198				T	FL	D	Y
162	CACTACEAE	<i>Selenicereus</i>	(A. Berger) Britton & Rose SP	S	LV	D	N
116	CAESALPINIACEAE	<i>Haematoxylum</i>	<i>campechianum</i> L.	T	LV	W	N
174				T	FL	D	N

<sup>7</sup> There are *ad lib* sightings of howlers eating these flowers, but no observations during data collection.

Taxonomy follows that published by the Missouri Botanical Garden's Tropicos plant identification website: <http://www.tropicos.org>  
 LIFE FORM: L=liana, T=tree, S=succulent, E=epiphyte. PART: FL = flowers, FR = fruits, LV = leaves, ML = mature leaves, YL = young leaves, ST/BK = stem/bark. SEASON = collection during W = wet season or D = dry season, FOOD = eaten by the mangrove howlers, Yes or No.

ID	FAMILY	GENUS	SPECIES	LIFE FORM	PART	SEASON	FOOD
207	CELASTRACEAE	<i>Hippocratea</i>	<i>volubilis</i> L.	L	FL	D	Y
224	CELASTRACEAE	<i>Hippocratea</i>	<i>volubilis</i> L.	L	LV	D	Y
175	COMBRETACEAE	<i>Bucida</i>	<i>buceras</i> L.	T	FL	D	Y
239				T	LV	D	Y
244				T	FR	D	N
1		<i>Laguncularia</i>	<i>racemosa</i> (L.) C.F. Gaertn.	T	YL	W	Y
133				T	LV	D	Y
259				T	FL	D	N
57	FABACEAE	<i>Dalbergia</i>	<i>brownei</i> (Jacq.) Schinz	L	LV	W	Y
227				L	LV	D	Y
228				L	FL	D	Y
253				L	YL	D	Y
255				L	FL	D	Y
261				L	SD	D	N
164		<i>Gliricidia</i>	<i>sepium</i> (Jacq.) Kunth ex Walp.	T	FL	D	N
248		<i>Haematoxylum</i>	<i>campechianum</i> L.	T	SD	D	N

ID	FAMILY	GENUS	SPECIES	LIFE FORM	PART	SEASON	FOOD
118	FABACEAE	<i>Lonchocarpus</i>	<i>hondurensis</i> Benth.	T	ML	W	Y
173				T	FL	D	Y
181				T	FL	D	Y
225				T	LV	D	Y
241				T	SD	D	Y
249				T	SD	D	Y
51		<i>Pithecellobium</i>	<i>lanceolatum</i> (Humb. & Bonpl. Willd.) Benth.	T	LV	W	N
122	LORANTHACEAE	<i>Psittacanthus</i>	<i>ramiflorus</i> (Moc & Sessé D.C.) G. Don	T	LV	W	N
124				T	FR	W	N
232	MALVACEAE	<i>Hampea</i> Schltldl.	sp	L	LV	D	N
247		<i>Malvaviscus</i>	<i>arboreus</i> Cav.	L	LV	D	Y
27	PASSIFLORACEAE	<i>Passiflora</i>	<i>foetida</i> L.	L	FR	D	N
200				L	LV	D	Y
260				L	FL	D	N
100	POLYPODIACEAE	<i>Polypodium</i>	<i>calaguala</i> Ruiz	E	LV	W	N
102				E	RT	W	N

ID	FAMILY	GENUS	SPECIES	LIFE FORM	PART	SEASON	FOOD
5	RHIZOPHORACEAE	<i>Rhizophora</i>	<i>mangle</i> L.	T	FR	W	N
7				T	ML	W	N
52				T	LB	D	Y
56				T	FR	D	N
197				T	LB	D	Y
48	RUBIACEAE	<i>Randia</i>	<i>aculeata</i> L.	S	LV	W	N
85		<i>Randia</i> L.	sp	S	LV	W	N
86				S	FR	W	N
31	SAPINDACEAE	<i>Paullinia</i>	<i>pinnata</i> L.	L	FR	W	N
38				L	LV	D	Y
169				L	LV	D	Y
178				L	YL	D	Y
140	VERBENACEAE	<i>Avicennia</i>	<i>germinans</i> (L.) L.	T	LV	D	N

### Appendix C. Macronutrients in Mangrove Plant Samples

ID	GENUS	SPECIES	PT <sup>8</sup>	H <sub>2</sub> O <sup>9</sup>	CP <sub>10</sub>	SP <sup>11</sup>	NIT <sub>12</sub>	ADF <sub>13</sub>	NDF <sub>14</sub>	LIG <sub>15</sub>	HC <sub>16</sub>	CS <sub>17</sub>	NFC <sub>18</sub>	ST <sub>19</sub>	ESC <sub>20</sub>	CF <sub>21</sub>	P:F <sub>22</sub>	TDN <sub>23</sub>
140	<i>Avicennia</i>	<i>germinans</i>	LV	68.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
175	<i>Buceda</i>	<i>buceras</i>	FL	75.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
239			LV	55.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
244			FR	73.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
256	<i>Clytostoma</i>	<i>binatum</i>	FL	62.8	33.5	-	5.36	12.0	22.3	2.2	10.3	9.8	-	-	16.5	-	2.8	79
258			LV	58.3	25.5	20.9	4.08	38.5	61.7	15.0	23.2	23.5	11.6	0.7	3.5	1.2	0.7	46
57	<i>Dalbergia</i>	<i>brownei</i>	LV	60.0	9.1	-	1.46	24.1	41.1	9.1	17.0	15.0	-	-	1.5	-	0.4	55
227			LV	73.2	24.5	12.3	3.92	22.6	41.4	11.4	18.8	11.2	29.2	0.3	4.3	1.4	1.1	56

<sup>8</sup>, FL=flowers, FR=fruit, LV= leaves (ML=mature, YL=young, LB=leaf buds), SD=seeds, RT=roots, ST/BK=stem/bark

<sup>9</sup> % water

<sup>10</sup> % crude protein

<sup>11</sup> % available protein

<sup>12</sup> % nitrogen

<sup>13</sup> % acid detergent fiber

<sup>14</sup> % neutral detergent fiber

<sup>15</sup> % lignin

<sup>16</sup> % hemicellulose

<sup>17</sup> % cellulose

<sup>18</sup> % non-fiber carbohydrates

<sup>19</sup> % starch

<sup>20</sup> % ethanol soluble carbohydrates (sugars)

<sup>21</sup> % crude fat

<sup>22</sup> protein to fiber ratio

<sup>23</sup> % total digestible nutrients

ID	GENUS	SPECIES	PT	H <sub>2</sub> O	CP	SP	NIT	ADF	NDF	LIG	HC	CS	NFC	ST	ESC	CF	P:F	TDN
228	<i>Dalbergia</i>	<i>brownei</i>	FL	78.6	25.8	10.8	4.13	13.3	24.1	5.1	10.8	8.2	42.1	0.7	9.0	2.0	1.9	69
253			YL	73.9	30.6	18.3 6	4.90	10.9	21.4	3.3	10.5	7.6	-	-	7.6	-	2.8	77
255			FL	79.8	11.1	-	1.78	17.7	25.6	3.3	7.9	14.4	55.6	0.7	19.9	1.6	0.6	70
261			SD	57.1	20.1	-	-	29.7	43.7	10.4	14.0	19.3	-	-	-	-	0.7	61
23	<i>Echites</i>	<i>yucatanensis</i>	LV	66.7	10.6	1.70	1.70	27.5	35.9	13.8	8.4	13.7	43.8	1.3	5.2	2.2	0.4	53
116	<i>Haematoxylum</i>	<i>campechianum</i>	LV	16.7	11.2	-	1.79	26.8	40.4	6.4	13.6	20.4	-	-	5.2	-	0.4	67
174			FL	78.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
248			SD	62.5	11.6	6.26	1.86	44.7	67.3	13.1	22.6	31.6	-	-	3.4	-	0.3	52
232	<i>Hampea</i>	sp	LV	72.7	18.0	6.30	2.88	25.0	37.5	8.4	12.5	16.6	28.4	0.5	4.3	4.4	0.7	57
207	<i>Hippocratea</i>	<i>volubilis</i>	FL	69.7	9.0	0.99	1.44	14.1	23.9	5.2	9.8	8.9	56.5	0.9	14.7	2.4	0.6	67
224			LV	61.5	8.5	1.44	1.36	19.4	32.3	6.9	12.9	12.5	47	0.7	9.4	3.5	0.4	62
1	<i>Laguncularia</i>	<i>racemosa</i>	YL	81.6	7.0	0.63	1.12	19.6	25.5	10.2	5.9	9.4	59.1	1.4	2.6	1.6	0.4	62
133			LV	65.8	10.1	1.41	1.62	16.2	21.4	7.1	5.2	9.1	55.6	3.0	2.0	1.6	0.6	62
259			FL	65.7	8.2	2.46	1.31	13.0	21.9	1.4	8.9	11.6	61.2	0.2	6.3	1.6	0.6	73
118	<i>Lonchocarpus</i>	<i>hondurensis</i>	ML	50.0	16.0	4.00	2.56	43.8	60.8	5.1	17.0	38.7	22.5	0.5	4.8	1.0	0.4	59
173			FL	54.1	16.8	6.55	2.69	21.4	34.6	6.0	13.2	15.4	45.1	1.5	16.5	1.0	0.8	65
181			FL	67.3	18.3	6.77	2.93	19.8	31.8	8.3	12.0	11.5	46	0.3	15.1	1.5	0.9	65
225			LV	44.2	16.3	3.10	2.61	34.6	49.5	16.0	14.9	18.6	28	0.5	9.5	2.6	0.5	49
241			SD	71.4	-	-	-	15.0	25.3	5.7	10.3	9.3	-	-	14.6	-	-	-
249			SD	75.6	15.4	9.70	2.46	32.0	51.3	8.7	19.3	23.3	32.2	0.2	15.0	2.1	0.5	60
247	<i>Malvaviscus</i>	<i>arboreus</i>	LV	72.7	16.8	11.8 0	2.69	23.3	39.7	4.7	16.4	18.6	-	-	3.6	-	0.7	54

ID	GENUS	SPECIES	PT	H <sub>2</sub> O	CP	SP	NIT	ADF	NDF	LIG	HC	CS	NFC	ST	ESC	CF	P:F	TDN
27	<i>Passiflora</i>	<i>foetida</i>	FR	75.0	17.6	-	2.82	41.3	56.3	21.3	15.0	20.0	-	-	1.3	-	0.4	48
200			LV	68.4	27.4	10.4 1	4.38	13.5	18.4	4.7	4.9	8.8	37.9	0.7	3.1	3.5	2.0	68
260			FL	72.2	27.2	21.7 6	4.35	7.0	10.7	-	3.7	7.0	-	-	-	-	3.9	82
31	<i>Paullinia</i>	<i>pinnata</i>	FR	56.0	13.6	-	2.18	54.7	69.4	31.2	14.7	23.5	-	-	2.0	-	0.2	34
38			LV	45.2	13.8	4.42	2.21	34.4	48.7	14.3	14.3	20.1	28.4	1.8	9.4	6.6	0.4	57
169			LV	53.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
178			YL	36.4	-	-	0.00	29.4	39.8	10.3	10.4	19.1	-	0.3	13.3	3.6	-	-
51	<i>Pithecellobium</i>	<i>lanceolatum</i>	LV	38.2	15.2	5.02	2.43	24.8	36.1	10.6	11.3	14.2	40.5	1.2	5.7	3.9	0.6	62
100	<i>Polypodium</i>	<i>calaguata</i>	LV	74.2	22.6	-	3.62	27.0	56.0	-	29.0	27.0	-	-	-	-	0.8	58
102			RT	67.9	10.3	-	1.65	53.1	69.4	-	16.3	53.1	-	-	3.8	-	0.2	66
122	<i>Psittacanthus</i>	<i>ramiflorus</i>	LV	78.2	8.6	3.44	1.38	14.4	21.6	6.0	7.2	8.4	-	-	0.9	-	0.6	52
124			FR	70.4	7.6	-	1.22	9.8	17.2	4.4	7.4	5.4	-	-	3.9	-	0.8	80
85	<i>Randia</i>	sp	LV	69.6	12.3	-	1.97	32.9	48.1	16.8	15.2	16.1	48.1	-	1.2	-	0.4	50
86			FR	75.0	8.8	-	1.41	15.0	23.9	-	8.9	15.0	-	-	-	-	0.6	77
48		<i>aculeata</i>	LV	35.3	11.5	2.19	1.84	26.9	45.5	13.6	18.6	13.3	38.4	2.7	18.0	3.4	0.4	56
168	<i>Rhabdadenia</i>	<i>biflora</i>	LV	75.4	12.2	1.46	1.95	32.0	40.5	16.6	8.5	15.4	32	0.9	4.5	4.2	0.4	48
246			FL	60.0	-	-	-	25.7	29.2	4.4	3.5	21.3	-	-	-	-	-	-
5	<i>Rhizophora</i>	<i>mangle</i>	FR	63.3	4.5	-	0.72	26.7	48.6	12.6	21.9	14.1	42	3.8	1.4	1.9	0.2	52
7			ML	76.4	7.5	1.05	1.20	23.8	40.7	13.4	16.9	10.4	41.3	1.2	7.1	4.5	0.3	56
52			LB	71.2	11.1	1.89	1.78	35.1	50.4	18.6	15.3	16.5	31.3	0.5	2.4	2.1	0.3	44
56			FR	53.6	7.0	1.05	1.12	34.7	54.1	13.5	19.4	21.2	38.6	7.3	1.1	1.3	0.2	52

ID	GENUS	SPECIES	PT	H <sub>2</sub> O	CP	SP	NIT	ADF	NDF	LIG	HC	CS	NFC	ST	ESC	CF	P:F	TDN
162	<i>Selenicereus</i>	sp	LV	98.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
158	<i>Tabebuia</i>	<i>rosea</i>	FL	50.0	-	-	-	34.3	49.0	10.7	14.7	23.6	-	-	-	-	-	-
198			FL	83.1	16.4	2.13	2.62	23.7	31.8	12.7	8.1	11.0	43.4	1.9	10.6	2.5	0.7	59
145	<i>Urechites</i>	<i>andrieuxii</i>	ST/ BK	-	5.2	2.76	0.83	51.9	71.7	22.9	19.8	29.0	-	1.2	2.4	1.4	0.1	35
145			ST/ BK	-	3.0	0.87	0.48	60.9	85.0	18.2	24.1	42.7	16.4	0.5	1.3	0.7		36
184			LV	71.4	-	-	0.00	15.7	25.2	4.0	9.5	11.7	-	-	-	-	-	-

Appendix D. Mineral Content of Mangrove Plants

ID	GENUS	SPECIES	PART	ASH	Ca <sup>24</sup>	P <sup>25</sup>	Ca:P <sup>26</sup>	Mg <sup>27</sup>	K <sup>28</sup>	Na <sup>29</sup>	Fe <sup>30</sup>	Zn <sup>31</sup>	Cu <sup>32</sup>	Mn <sup>33</sup>	Mb <sup>34</sup>	S <sup>35</sup>
256	<i>Clytostoma</i>	<i>binatum</i>	FL	7.05	0.21	0.4	0.53	0.25	3.2	0.078	116	67	32	25	1.9	0.35
258			LV	6.18	0.43	0.31	1.39	0.26	2.49	0.105	63	64	21	31	1.2	0.3
57	<i>Dalbergia</i>	<i>brownei</i>	LV	-	3.33	0.12	27.75	0.59	1.42	1.197	109	13	9	42	0.3	0.48
227			LV	9.38	0.89	0.24	3.71	0.56	2.12	0.237	92	43	16	38	1	0.25
228			FL	13.43	0.51	0.32	1.59	0.44	2.74	0.209	102	43	21	30	1.1	0.22
253			YL	9.29	0.38	0.41	0.93	0.42	3.24	0.387	93	56	16	41	1.6	0.29
255			FL	15.11	0.62	0.21	2.95	0.46	3.12	0.267	507	32	21	25	1.6	0.18
261			SD	7.65	0.57	0.21	2.71	0.31	2.03	0.346	62	38	17	22	2.7	0.2
23	<i>Echites</i>	<i>yucatanensis</i>	LV	11.15	1.39	1.39	1.00	0.12	3.58	0.35	95	18	10	59	1.1	0.35
116	<i>Haematoxylum</i>	<i>campechianum</i>	LV	-	1.64	0.11	14.91	0.2	1.29	0.089	116	22	6	30	0.4	0.18
174			FL	7.03	-	-	-	-	-	-	-	-	-	-	-	-
248			SD	-	0.64	0.16	4.00	0.13	1.52	0.205	53	30	11	13	0.9	0.14
232	<i>Hampea</i>	sp	LV	6.89	2.61	0.22	11.86	0.59	2.75	0.36	130	25	15	38	0.6	0.59
207	<i>Hippocratea</i>	<i>volubilis</i>	FL	4.87	1.45	0.17	8.53	0.48	1.93	0.533	93	22	9	23	0.4	0.31

<sup>24</sup> Calcium %

<sup>25</sup> Phosphorus %

<sup>26</sup> Calcium to phosphorus ratio

<sup>27</sup> Magnesium %

<sup>28</sup> Potassium %

<sup>29</sup> Sodium %

<sup>30</sup> Iron %

<sup>31</sup> Zinc kg/mg

<sup>32</sup> Copper kg/mg

<sup>33</sup> Manganese kg/mg

<sup>34</sup> Molybdenum kg/mg

<sup>35</sup> Sulfur kg/mg

ID	GENUS	SPECIES	PART	ASH	Ca	P	Ca:P	Mg	K	Na	Fe	Zn	Cu	Mn	Mb	S
224	<i>Hippocratea</i>	<i>volubilis</i>	LV	10.54	2.39	0.08	29.88	0.52	0.89	0.855	105	14	3	25	0.7	0.38
1	<i>Laguncularia</i>	<i>racemosa</i>	YL	11.85	1.45	0.12	12.08	0.37	1.8	0.77	76	10	4	21	0.4	0.2
133			LV	-	2.62	0.18	14.56	0.44	2.2	0.787	68	12	4	38	0.6	0.59
259			FL	-	1.24	0.18	6.89	0.34	1.89	0.787	74	12	2	28	0.9	0.23
118	<i>Lonchocarpus</i>	<i>hondurensis</i>	ML	8.41	1.08	0.12	9.00	0.24	1.54	0.088	44	20	7	34	1.9	0.22
173			FL	8.07	0.75	0.19	3.95	0.21	2.04	0.055	102	41	7	37	2.5	0.19
181			FL	8.73	0.51	0.2	2.55	0.18	2.08	0.031	77	37	9	30	1.4	0.21
225			LV	7.33	1.98	0.11	18.00	0.32	0.85	0.085	52	20	4	43	0.7	0.24
241			SD	5.86	1.12	0.21	5.33	0.2	1.86	0.055	51	41	9	36	1.9	0.27
249			SD	5.99	0.57	0.16	3.56	0.14	1.51	0.015	37	30	9	19	1.2	0.19
247	<i>Malvaviscus</i>	<i>arboreus</i>	LV	4.10	5.15	0.17	30.29	0.68	2.1	0.912	104	22	12	58	1.1	1.08
200	<i>Passiflora</i>	<i>foetida</i>	LV	-	1.86	0.22	8.45	0.54	2.59	0.701	111	66	8	31	1.4	1.14
31	<i>Paullinia</i>	<i>pinnata</i>	FR	10.07	0.46	0.25	1.84	0.23	2.24	0.025	52	29	19	26	1	0.16
38			LV	10.23	1.49	0.13	11.46	0.27	1.35	0.032	125	21	10	59	0.6	0.18
169			LV	4.43	-	-	-	-	-	-	-	-	-	-	-	-
178			YL	5.81	0.39	0.28	1.39	0.19	2.18	0.038	68	27	17	16	1	0.15
51	<i>Pithecellobium</i>	<i>lanceolatum</i>	LV	29.11	1.38	0.09	15.33	0.27	0.96	0.175	342	14	6	70	1.3	0.41
100	<i>Polypodium</i>	<i>calaguala</i>	LV	15.43	1.33	0.44	3.02	0.44	6.36	0.084	185	39	8	286	0.6	0.3
102			RT	22.48	0.51	0.22	2.32	0.4	4.01	0.096	290	21	5	47	1	0.26
122	<i>Psittacanthus</i>	<i>ramiflorus</i>	LV	5.65	3.66	0.25	14.64	0.54	6.66	2.346	132	15	7	69	0.9	0.62
124			FR	8.63	0.35	0.22	1.59	0.32	3.26	0.074	79	16	6	19	1.1	0.13
48	<i>Randia</i>	<i>aculeata</i>	LV	17.54	1.13	0.1	11.30	0.46	0.75	0.389	65	16	5	223	0.5	0.34
85	<i>Randia</i>	sp	LV	-	2.48	0.09	27.56	0.89	0.57	0.684	96	58	7	706	1.2	0.38
86			FR	7.92	-	-	-	-	-	-	-	-	-	-	-	-
168	<i>Rhabdadenia</i>	<i>biflora</i>	LV	15.16	1.37	0.13	10.54	0.57	3.19	1.205	77	10	4	337	1.1	0.44
5	<i>Rhizophora</i>	<i>mangle</i>	FR	7.91	1.18	0.08	14.75	0.32	0.89	1.226	27	4	<1	105	1	0.12

ID	GENUS	SPECIES	PART	ASH	Ca	P	Ca:P	Mg	K	Na	Fe	Zn	Cu	Mn	Mb	S
7	<i>Rhizophora</i>	<i>mangle</i>	ML	-	1.28	0.09	14.22	0.41	1.71	1.164	67	3	<1	226	0.6	0.27
52			LB	14.65	1.62	0.16	10.13	0.47	1.08	1.249	36	8	5	118	0.7	0.21
56			FR	5.85	0.17	0.16	1.06	0.12	1.06	0.908	60	4	5	20	0.5	0.08
158	<i>Tabebuia</i>	<i>rosea</i>	FL	-	1.4	0.12	11.67	0.37	1.27	0.79	144	14	13	33	1.1	0.67
198			FL	9.21	0.76	0.35	2.17	0.31	2.75	0.354	128	29	18	14	0.5	0.25
145	<i>Urechites</i>	<i>andrieuxii</i>	ST/BK	-	1.35	0.03	45.00	0.16	1.22	0.532	188	79	10	238	1	0.29
145			ST/BK	3.06	0.25	0.03	8.33	0.06	0.87	0.217	73	27	5	105	0.4	0.18
184			LV	16.71	-	-	-	-	-	-	-	-	-	-	-	-

Appendix E  
Means and standard deviations for proximate content of leaves from (A) the mangrove plants eaten by the howlers and foods eaten by black howlers in (B) Silver (2000).

	N	H <sub>2</sub> O <sup>36</sup>	ASH <sup>37</sup>	CP <sup>38</sup>	AP <sup>39</sup>	NDF <sup>40</sup>	ADF <sup>41</sup>	LIG <sup>42</sup>	ESC <sup>43</sup>
Leaves A	30	61.9 ±17.2	11. ±5.7	15.1* ±6.8	5.8* ±6.0	39.2* ±12.2	25.7* ±8.3	10.3* ±4.6	5.6 ±4.1
		*	7						
Leaves B	74	69.2 ±12.0	8.5 ±5.8	20.4 ±7.3	15.3 ±7.5	52.5 ±12.9	36.5 ±11.0	18.2 ±8.8	4.0 ±2.2
			*						
Flowers A	12	70.6 ±8.9	7.9 ±1.8	18.5 ±8.8	7.4* ±7.2	25.6* ±6.9	16.8* ±5.9	5.4* ±3.4	13.6 ±4.5
		*							
Flowers B	20	80.7 ±7.5	6.8 ±2.8	17.1 ±5.3	11.6 ±4.8	47.9 ±10.0	35.4 ±10.4	20.5 ±9.5	6.2* ±5.4
Fruit A <sup>44</sup>	6	66.7 ±9.1	6.1 ±1.5	9.9 ±4.8	1.1 -	45.0 ±20.2	30.8 ±16.8	16.6 ±10.1	1.9* ±1.2
Fruit B	35	63.6 ±26.5	6.0 ±2.4	10.9 ±9.7	6.4 ±1.2	42.8 ±18.0	33.9 ±15.0	19.0 ±8.7	11.3 ±12.1

A=this study. B=Silver et al., 2000. N=sample size.

<sup>36</sup> % water content.

<sup>37</sup> % ash.

<sup>38</sup> % crude protein.

<sup>39</sup> % available protein.

<sup>40</sup> % neutral detergent fiber.

<sup>41</sup> % acid detergent fiber.

<sup>42</sup> % lignin.

<sup>43</sup> % ethanol soluble carbohydrates.

<sup>44</sup> The howlers in this study did not eat any of the fruits included here; they ate only seed pods from one species.

Appendix F  
Mean Percentages of Macroelement Components of Mangrove Trees  
Based on 100% Dry Matter

MANGROVE GENERA	PT <sup>45</sup>	N	H <sub>2</sub> O <sub>46</sub>	CP <sub>47</sub>	SP <sub>48</sub>	ADF <sub>49</sub>	NDF <sub>50</sub>	LIG <sub>51</sub>	NFC <sub>52</sub>	ESC <sub>53</sub>	CF <sub>54</sub>	P:F <sub>55</sub>	TDN <sub>56</sub>	REFERENCE
<i>Aegericas</i>	LVS	1	40.8	5.3	-	-	-	-	-	-	5.8	-	-	Supriatna et al., 1989
<i>Avicennia</i>	FR	1	60.0	3.6	-	-	-	-	-	-	0.3	-	-	Supriatna et al., 1989
<i>Avicennia</i>	LVS	1	69.7	5.2	-	-	-	-	-	-	1.4	-	-	Supriatna et al., 1989
<i>Avicennia</i>	LVS	1	-	3.9	-	-	-	-	-	-	1.2	-	-	Son, 2003
<i>Avicennia</i>	RT	1	64.9	3.7	-	-	-	-	-	-	1.6	-	-	Supriatna et al., 1989
<i>Bruguiera</i>	FR	1	57.4	2.9	-	-	-	-	-	-	0.8	-	-	Supriatna et al., 1989

<sup>45</sup> FL=flowers, FR=fruit, LV= leaves (ML=mature, YL=young, LB=leaf buds), SD=seeds, RT=roots, ST/BK=stem/bark

<sup>46</sup> % water

<sup>47</sup> % crude protein

<sup>48</sup> % available protein

<sup>49</sup> % acid detergent fiber

<sup>50</sup> % neutral detergent fiber

<sup>51</sup> % lignin

<sup>52</sup> % non-fiber carbohydrates

<sup>53</sup> % ethanol soluble carbohydrates

<sup>54</sup> % crude fat

<sup>55</sup> Protein (CP) to fiber (ADF) ratio

<sup>56</sup> % total digestible nutrients

<i>Bruguiera</i>	LVS	1	68.9	4.8	-	-	-	-	-	-	1.3	-	-	Supriatna et al., 1989
<i>Laguncularia</i>	FL	1	65.7	8.2	2.5	13.0	22.0	1.4	61.2	6.3	1.6	5.1	73	This Study
<i>Laguncularia</i>	LVS	2	73.7	8.6	1.0	17.9	23.5	8.7	57.4	2.3	1.6	5.3	62	This Study
<i>Rhizophora</i>	FR	2	58.5	5.8	1.1	30.7	51.4	13.1	40.3	1.3	1.6	3.9	52	This Study
<i>Rhizophora</i>	FR	1	-	2.1	-	-	-	-	-	-	0.7	-	-	Son, 2003
<i>Rhizophora</i>	LVS	2	64.0	9.3	1.5	29.5	45.6	16.0	36.3	4.8	3.3	3.5	50	This Study
<i>Rhizophora</i>	LVS	1	-	3.3	-	-	-	-	-	-	2.1	-	-	Son, 2003
<i>Sonneratia</i>	FR	1	74.1	2.2	-	-	-	-	-	-	0.7	-	-	Supriatna et al., 1989
<i>Sonneratia</i>	LVS	1	74.8	3.1	-	-	-	-	-	-	0.8	-	-	Supriatna et al., 1989
<i>Sonneratia</i>	RT	1	68.1	1.7	-	-	-	-	-	-	0.4	-	-	Supriatna et al., 1989

### Means of Mineral Components of Mangrove Trees

MANGROVE GENERA	PT	N	ASH <sup>57</sup>	Ca <sup>58</sup>	P <sup>59</sup>	Ca:P <sub>60</sub>	Mg <sup>61</sup>	K <sub>62</sub>	Na <sub>63</sub>	Fe <sup>64</sup>	Zn <sub>65</sub>	Cu <sub>66</sub>	Mn <sup>67</sup>	Mb <sub>68</sub>	S <sup>69</sup>	REFERENCE
<i>Aegericas</i>	LVS	1	5.0	-	-	-	-	-	-	-	-	-	-	-	-	Supriatna et al., 1989
<i>Avicennia</i>	FR	1	0.7	-	-	-	-	-	-	-	-	-	-	-	-	Supriatna et al., 1989
<i>Avicennia</i>	LVS	1	3.1	-	-	-	-	-	-	-	-	-	-	-	-	Supriatna et al., 1989
<i>Avicennia</i>	LVS	1	-	0.2	0.1	2.0	-	-	-	-	-	-	-	-	-	Son, 2003
<i>Avicennia</i>	RT	1	3.5	-	-	-	-	-	-	-	-	-	-	-	-	Supriatna et al., 1989
<i>Bruguiera</i>	FR	1	1.4	-	-	-	-	-	-	-	-	-	-	-	-	Supriatna et al., 1989

<sup>57</sup> % ash

<sup>58</sup> % calcium

<sup>59</sup> % phosphorus

<sup>60</sup> Calcium to phosphorus ratio

<sup>61</sup> % magnesium

<sup>62</sup> % potassium

<sup>63</sup> % sodium

<sup>64</sup> Iron kg/mg

<sup>65</sup> Zinc kg/mg

<sup>66</sup> Copper kg/mg

<sup>67</sup> Manganese kg/mg

<sup>68</sup> Molybdenum kg/mg

<sup>69</sup> Sulfur kg/mg

MANGROVE GENERA	PT	N	ASH <sup>70</sup>	Ca <sup>71</sup>	P <sup>72</sup>	Ca:P <sub>73</sub>	Mg <sup>74</sup>	K <sub>75</sub>	Na <sub>76</sub>	Fe <sup>77</sup>	Zn <sub>78</sub>	Cu <sub>79</sub>	Mn <sup>80</sup>	Mb <sub>81</sub>	S <sup>82</sup>	REFERENCE
<i>Bruguiera</i>	LVS	1	4.3	-	-	-	-	-	-	-	-	-	-	-	-	Supriatna et al., 1989
<i>Laguncularia</i>	FL	1	9.3	1.2	0.2	6.0	0.3	1.9	0.8	74.0	12.0	2.0	28.0	0.9	0.2	This Study
<i>Laguncularia</i>	LVS	2	11.4	2.1	0.1	14.7	0.4	2.0	0.8	72.0	11.0	4.0	29.5	0.5	0.4	This Study
<i>Rhizophora</i>	FR	2	6.2	0.7	0.1	5.3	0.2	1.0	1.1	43.5	4.0	2.9	62.5	0.8	0.1	This Study
<i>Rhizophora</i>	FR	1	-	0.1	0.3	0.3	-	-	-	-	-	-	-	-	-	Son, 2003
<i>Rhizophora</i>	ML	1	10.1	1.3	0.1	13.0	0.4	1.7	1.2	67.0	3.0	<1	226.0	0.6	0.3	This Study
<i>Rhizophora</i>	LB	1	10.2	1.6	0.2	8.0	0.1	1.1	1.3	36.0	8.0	5.0	118.0	0.7	0.2	This Study
<i>Rhizophora</i>	ML	1	-	0.4	0.1	4.0	-	-	-	-	-	-	-	-	-	Son, 2003
<i>Sonneratia</i>	FR	1	0.7	-	-	-	-	-	-	-	-	-	-	-	-	Supriatna et al., 1989

<sup>70</sup> % ash

<sup>71</sup> % calcium

<sup>72</sup> % phosphorus

<sup>73</sup> Calcium to phosphorus ratio

<sup>74</sup> % magnesium

<sup>75</sup> % potassium

<sup>76</sup> % sodium

<sup>77</sup> Iron kg/mg

<sup>78</sup> Zinc kg/mg

<sup>79</sup> Copper kg/mg

<sup>80</sup> Manganese kg/mg

<sup>81</sup> Molybdenum kg/mg

<sup>82</sup> Sulfur kg/mg

*Sonneratia* LVS 1 1.0 - - - - - - - - - - - - - - -

Supriatna et al., 1989