Investigating How Ecology and Demography Influence Folivorous Primate Biomass in the Western Amazon

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Abigail Marie Derby

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Abstract of the Dissertation

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The aim of this study is to examine the relationships between ecology, demography and behavior in order to address the question of which factors are influencing density in two populations of red howler monkeys (*Alouatta seniculus*) occurring at different densities and in different forest types in Yasuní National Park, Eastern Ecuador. Attempting to narrow down and distinguish between the many closely related biological factors thought to affect primate density is important not only because it may further our understanding of the process of behavioral adaptations, but also because it is a critical component in aiding conservation endeavors. This project employs a multivariate approach which tests eight ecological factors, particularly those suggested by previous research to be important influences on folivore density, that are distinguished by how they would affect the behavior of folivorous primates. Specifically, each factor is accompanied by a set of mutually exclusive *a priori* predictions regarding how each should, all other aspects remaining equal, affect the behavior of folivorous primates in areas of **high versus low population density**. This enables a comparison to determine which ecological variable(s) best predict the observed patterns of *Alouatta* behavior at the high density site, and thus identify those aspects of forest ecology which are influencing population density. This study has three main goals. The first goal is to evaluate whether the predicted differences in the ecological variables occur at the site with high howler monkey population density. The second is to identify whether the predicted trends in demography with increasing population density proposed for other primates are present at the high density site, and the third is to test which ecological variables best predicted the observed patterns of *Alouatta* behavior in order to determine which variables are playing the largest roles influencing *Alouatta* densities.

Out of eight variables examined, six aspects of forest ecology are supported to possibly contribute to higher howler monkey population density: (1) hunting, (2) higher soil fertility, (3) higher phenological productivity, (4) higher resource quality in the form of leaves with higher protein levels, (5) higher density of leaves with higher protein levels and (6) higher resource density of leaves lower in total phenolic content. There is a pronounced difference in the number of groups present at each site (ten at the higher density site versus three at the low density site); however no significant differences are found in the demographic patterns at either the population or the group level between sites, and birth rates appears to be similar. These results suggest that density per se may not be affecting population or group composition because both populations appear to be at equilibrium and thus equally constrained reproductively. Lastly, when predicted behavioral patterns for each of the supported ecological variables are compared to the observed patterns of *Alouatta* behavior, it is found that both higher plant quality (higher protein and lower phenolic levels) and higher density of these resources are influencing differences in *Alouatta* density. While low levels of hunting is likely affecting population density at the low density site, it is suggested that resource quality in addition to abundance are the primary factors contributing to the differences in densities, supporting previous findings in folivorous Old World primates.

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CHAPTER 1

Investigating How Ecology and Demography Influence Folivore Primate Biomass: Project Introduction and Background

1.1 Introduction

Non-human primates are an integral component in many fields of academic inquiry, ranging from anatomical science and biomedicine to anthropology and psychology, to name just a few. There is a long history of scholars using primates as comparative study subjects to further our knowledge and understanding of issues related to the processes of behavioral adaptation, the development and study of clinical research on human health, and the evolution of language and cognition. A common denominator to all of these fields of inquiry is the underlying recognition of the similarities — morphological, physiological, behavioral, and cognitive — that exist between non-human primates and our own species.

Yet the current rate of destruction to primate habitats may vanquish future opportunities to study our closest living relatives in their natural environments. For example, reports estimate that in the past 40 years, 20 percent of the Amazon forests have been cut down (Wallace, 2007). Furthermore, the current rate of worldwide tropical forest destruction is estimated to be as high as 81 hectares per minute, driven mainly by the demand for commercial logging and expansion of agricultural farming for an increasing human population (Lahsen and Nobre, 2007). Climate change is also playing a role in the current and projected global crisis of low crop yields in the tropics (IRRI, 2006; Tubiello et al., 2007). As a result, the rising global commodity prices, now at an all time high for items such as rice, will likely fuel even more clearing of land for farms. The synergistic effects of this situation will no doubt be profound for the faunal and floral assemblages occurring within tropical forests, including about 90 percent of all primate species (Park, 1992). In particular, primates play an integral role in the ecology of their habitat (e.g., seed dispersal: Schupp et al., 2001; Wenny, 2001; Corlett, 2002), which has lead primatologists and ecologists alike to focus their attention on questions related to how ecology influences primate distribution and abundance in order to clarify processes of behavioral adaptation as well as to aid in conservation efforts.

Ecological Influences on Primate Density

There have been numerous ecological factors proposed to explain the variation that exists in the distribution and biomass of primate species. Many of these factors are closely related biological functions such as soil fertility (Janzen, 1975; Peres, 1997; Peres and Haugaasen, 2005), food availability (Terborgh and van Schaik, 1987; Davies, 1994) and food quality (Waterman et al., 1988; Oates et al., 1990, Ganzhorn, 1992), as well as anthropogenic influences including hunting (Redford, 1992; Alvard, 1997, Peres, 2000) and forest fragmentation (DeGama-Blanchet and Fedigan, 2006). Food availability in particular has been proposed as one of the main determinants of primate abundance in general because it directly influences female fertility (Gilmore and Cook, 1981; Davies, 1994; Chapman and Chapman, 1999). Even though female fertility can be affected by other factors like social organization (i.e., group composition and size), age, and stress, the quality of the foraging environment is the single most important factor in determining fertility amongst nonhuman primates (e.g. Borries et al., 2001; Altmann and Alberts, 2003).

There has been a specific focus regarding ecological influences on folivorous primate population density because these species account for most of the biomass variation exhibited in primate communities due to their large size (Terborgh and van Schaik, 1987). The diet of folivores is predominately leaves, which are difficult to digest due to their high cellulose and secondary compound content and thus investigations on these taxa have centered on examining food quality as a major influence on population abundance. For example, it has been shown that folivorous primate density is positively correlated with the average leaf quality in a habitat, reflected as the amount of protein, or ratio of protein-to-fiber in leaves, or in the amount of secondary compounds in the leaves, known as phenolics, that can affect digestibility. This idea has been well supported in an array of folivorous taxa, including strepsirrhines, colobines, and platyrrhines (Strepsirrhini: Ganzhorn, 1992; Colobinae: Oates and Davies, 1990; Chapman et al., 2002, 2004; Wasserman and Chapman, 2003; Platyrrhini: Milton, 1980; Peres, 1997). While much of this research has focused on African and Asian taxa, there is mounting evidence that similar patterns exist for Neotropical folivores, which are characterized by a different digestive morphology.

The most folivorous New World primate is the howler monkey (genus *Alouatta*) and although certain species and populations are known to include a high percentage of fruit in their diet, many consume leaves as the primary component most of the year (e.g., Milton, 1979; Julliot, 1996; Lopez et al., 2005). Howler monkeys are the most widely distributed Neotropical primate genus in both their geographic range and habitat type

(Peres, 1997). The population density of howler monkeys, however, varies widely throughout their distribution, which has prompted primatologists and ecologists alike to investigate the factor(s) influencing this variation in order to 1) better understand how habitat ecology affects the density of New World folivorous primates and 2) compare whether New World folivores are limited by the same factors as Old World taxa (Peres, 1997).

It is well documented that the degree of hunting pressure profoundly affects mammalian biomass in a given habitat (e.g., Peres, 1997, 2000), and howler monkeys are no exception to this. Peres (1997) showed that howler monkey populations subjected to varying degrees of harvest intensity occurred at significantly lower densities and biomass than those which had never been subject to hunting, or no longer hunted for more than fifteen years. While hunting pressure was found to be a good indicator of howler monkey population density, this was most evident in presumably high quality habitats such as deciduous, late-successional, floodplain and gallery forests, and had far less predictive power for evergreen forests which housed "intrinsically low howler monkey densities even in the complete absence of hunting" (Peres, 1997). Furthermore, Peres (1997) showed that hunting pressure alone only accounted for one-quarter of the variation exhibited in howler monkey densities and biomass across twenty-three Amazonian sites.

In light of these results, Peres (1997) pointed to the necessity of considering the effects of site-specific indicators of habitat quality, in addition to hunting pressure, to explain the variation in howler monkey population density throughout the Amazonian region. A large-scale geographic comparison examining both the effects of hunting pressure and several indirect indicators of habitat quality on the abundance of howler monkeys showed that, once differences in hunting pressure were controlled for, most of the variation in howler monkey densities was explained by indirect measures of habitat quality, specifically forest structure, seasonality, and geomorphic correlates of soil fertility (Peres, 1997). Additionally, the single best predictor of *Alouatta* densities in evergreen forests of central lowland Amazonia was found to be the distance to major white-water rivers, which co-varies with forest heterogeneity and soil fertility (Peres, 1997; Haugaasen and Peres, 2005). Amazonian white-water rivers originate in the young alluvial soils of the Andes Mountains and are laden with nutrient-rich sediments. Soils in the forests adjacent to white-water sources are annually flooded and thus consistently replenished with nutrients (Peres, 1997). Higher soil fertility, in the form of higher levels of primary and secondary macronutrients, can in turn influence the abundance, quality, heterogeneity and associated phenological patterns of the resources that grow upon them (Janzen, 1975; Peres, 1997; Haugaasen and Peres, 2005).

However, the association of howler monkey density with flooded forest ecosystems may not hold true in all parts of the Amazon. Surveys conducted by Iwanaga and Ferrari (2002) in flooded and unflooded regions throughout the Brazilian state of Rondônia in southwestern Amazonia, for example, found that howlers were only present at one-third of the thirty-six sites surveyed and were absent from most of the floodplains adjacent to white-water rivers. Furthermore, in areas where howler monkeys were present, they were reported to be relatively rare, especially in comparison with sympatric atelids (*Ateles* and *Lagothrix*) (Iwanaga and Ferrari, 2002).

Thus, while it is clear that habitat ecology greatly influences the density of *Alouatta* in the Neotropics, the exact factors affecting differences in their abundance in different regions of Amazonia still remain somewhat unresolved. Additionally, most of the comparative ecology studies on howler monkeys have correlated population density with indirect measures of habitat quality instead of directly sampling and comparing the ecological variables between sites. What is now needed is an effort to tease apart the following closely related variables, and directly compare them between sites, in order to determine what exerts the greatest influence on a given folivorous primate population.

A brief summary of the six major aspects of ecology potentially influencing folivore density, and the effects of each, is given below:

(1) **Hunting:** The amount of hunting which occurs in an area can affect primate populations. For instance, it is known that hunters target large-bodied primate species preferentially and this has been proposed as a major determinant for the variation in *Alouatta* density (Peres, 1997, 1999).

(2) **Soil fertility:** Soil fertility refers to the level of macronutrients (including Nitrogen, Phosphorus, Potassium, Sodium, Calcium, and Magnesium), as well as the pH, and clay and sand content found in soil. The composition of soil has been suggested to influence folivorous primates whereby habitats higher in soil fertility also support a higher biomass of folivorous taxa (McKey, 1978). This is based on the idea that nutrients contained within the soil can be transferred to the plants that grow on them, providing a more productive substrate. Therefore soils higher in fertility may be able to produce both greater quality and quantity of food, enabling a habitat to support a higher biomass of folivorous primates.

(3) **Habitat heterogeneity:** Habitat heterogeneity describes the mosaic structure of a mature rainforest produced by the floristic and physical properties of its vegetation and the various stages of regeneration (Bourliere, 1985). Basically, the more heterogeneous a habitat, the more niches may be available (Fleagle, 1999). Two components of habitat heterogeneity have been suggested to affect primate population densities - plant species diversity and forest structure. Plant species diversity refers to the number of plant species in a habitat. A high diversity is likely to increase the variety of food types available at any one time and may increase primate folivore density (Oates et al., 1990). Forest structure describes the physical structure of the forest and how this can influence the size, nature, and orientation of positional supports (Bourliere, 1985). The structure of a forest also determines the degree of exposure to direct sunlight of subcanopy trees and vines, and thus the potential of rapid growth of tender foliage (Ganzhorn, 1995). A high structural diversity can therefore increase the amount of travel pathways and sleeping sites in a habitat, as well as potentially increase new leaf production, which could increase the carrying capacity and primate biomass in a given habitat (Ganzhorn, 1993).

(4) **Phenology:** Phenology may be divided into productivity and seasonality. Productivity is simply the overall abundance of food resources in a habitat, and an absolute higher abundance of food may support a higher carrying capacity. On the other hand, seasonality refers to variation in resource availability over an annual cycle. Less seasonal habitats can be described as having less variation in food resources over an annual cycle and possibly lead to a higher primate biomass (Ripley, 1979; Gupta and Chivers, 1999). Habitats with asynchronous food production may have high quality fallback foods, such as young leaves, being produced during these lean periods and possibly resulting in higher primate biomass. While recent evidence suggests that synchronization of fruiting and leafing is not present at most Neotropical sites (Heymann, 2001), individual areas may still be affected by this factor. In contrast, the biomass of folivorous lemurs (Ganzhorn, 1992; Ganzhorn et al., 1999), as well as *Alouatta* (Peres, 1997), has been reported to increase with increasing seasonality. One explanation for this is that because greater seasonality directly relates to the production of young foliage, and thus a more deciduous and shorter leaf life span, it can in turn influence resource quality because plants will be investing less in chemical defenses (Coley & Baronet 1996; Janson & Chapman 1999; Brockman and van Schaik, 2005). However, in regions that do not have a pronounced or prolonged dry period, such as the lowland Amazonian region in Eastern Ecuador where annual rainfall is ~3,200 mm and no month receives less than 100 mm of rain (Pitman, 2000; Di Fiore and Rodman, 2001), less seasonal habitats should be more beneficial to primate populations.

(5) **Density of food resources:** The number of food trees in a given area can affect primate populations whereby an increase in the overall density of food resources, and in turn the overall abundance of food, can increase the carrying capacity of a habitat and possibly increase primate biomass (Sadleir, 1969; Rodman, 1978).

(6) **Leaf quality:** Folivorous primates can be influenced by the nutrient, mineral, or digestibility of foliage (for a review see Janson and Chapman, 1999). Leaf quality may also be divided into three components, which independently or together may affect density - digestibility, mineral levels, and protein-to-fiber ratio. Digestibility of leaves can refer either to the level of secondary compounds (Coley and Barone, 1996) or to fiber content (Milton, 1980). More than 12,000 plant secondary metabolites are known to be involved with plant-animal interactions (Lambert, 1998) and they are typically divided into two broad categories: 1) digestion inhibitors which interfere with the efficiency with which an animal obtains nutrients and 2) toxins which are harmful to the animal because they interfere with normal physiology (Waterman and Kool, 1994). One of the most well-studied group of digestion inhibitors are the polyphenolic compounds known as tannins. Tannins bind to the protein in plants and thus inhibit the digestion and uptake of protein from plant material (Waterman and Kool, 1994). Several studies have shown the presence of condensed tannins in plant material is negatively related to primate feeding (e.g., Wrangham and Waterman, 1981). While all foods contain some phenolic compounds, some foods have a much higher content than others. When an organism cannot process out the phenolic compounds as fast as they consume them, phenols can start backing up in the system and a cumulative effect of increasing levels can cause a myriad of negative reactions, in essence acting as a toxin to the body (Bryant et al. 1992).

Digestibility can also be affected by bulk foods, such as leaves that are high in fiber, because they require a longer amount of time to ferment and digest in order to maximize the absorption of nutritional content (Waterman and Kool, 1994). It has been suggested that habitats that have a higher digestibility of leaves can allow for a higher amount of food per unit time to be consumed (Gilmore and Cook, 1981). In addition protein has been considered a major limiting factor in the evolution of primate, and animal, evolution and life history traits (e.g., White, 1993). Foods with the combined characteristics of higher protein and lower fiber represent items that are both higher quality and more efficiently digested. The ability to consume and digest more food with higher protein may shorten inter-birth intervals (hence, increase birth rates) and possibly lead to higher primate biomass.

The second component, mineral level, describes the amount of Phosphorus, Potassium, Sodium, Calcium, and Magnesium in leaves. Individuals who are not limited by mineral deficiencies may have improved overall health, leading to higher survivability and shorter inter-birth intervals which could result in a higher primate biomass (Gilmore and Cook, 1981; Oates et al., 1990). Finally, a high protein-to-fiber ratio (i.e., a high amount of protein relative to fiber) may increase overall health, leading to higher survivability and an increase in female birth rate due to shorter inter-birth intervals (Gilmore and Cook, 1981; Milton, 1980).

Ecological Influences on Demographic Patterns

Habitat ecology not only affects population density, but also the demographic patterns of the populations. For example, increasing both food availability and food quality can provide a diet higher in protein, and better nutrition may influence such aspects as shorter inter-birth intervals and higher overall reproductive output (Sadlier, 1969; Jorde and Spuhler, 1974). Thus demography may be viewed as a proxy for fertility and survivorship, the two main components that contribute to population density (Gotelli, 1998). In order to understand how changes in density arise as a result of this variation in demography and which factors affect density, it is necessary to examine both the mechanisms that influence changes in population density and the ecology of a habitat. Some of the trends in demography at high versus low population density observed for other primate populations are: 1) The average number of males per group is **higher** (Crockett, 1996), 2) The average number of adult female howler monkey per group is

higher (Crockett, 1996), but does **not exceed four** (Crockett, 1996; Crockett and Janson, 2000; Horwich et al., 2001), 3) The average group size is **larger** (Crockett, 1996) and 4) The ratio of infants and juveniles to adult females is **higher**, (Sadlier, 1969; Jorde and Spuhler, 1974). It is possible that factors such as sex biased dispersal may influence these patterns. For example, male biased dispersal, which is the most common pattern within Cercopithecidae (Lawson Handley and Perrin, 2007), may increase the number of females but not males per group. Furthermore, if dispersal distance is relatively great in this scenario and/or the males become solitary they may experience higher mortality (e.g., due to predation) which could potentially decrease the percentage of males in the population as well.

It is possible, however, that different ecological variables could produce the same observable demographic patterns in a population. Therefore focusing on ecology and demography alone may not provide enough information to fully distinguish between which factor(s) play the largest role in affecting differences in folivore density. One way to address these issues is to look at the behavior of primates, which is affected by both the ecology of a habitat as well as the density and demography of a population.

Interrelationships of Ecology, Demography and Behavior

Behavioral predictions about how primates should respond to differences in resource availability can be derived from either a theoretical perspective, such as Optimal Foraging Theory (MacArthur and Pianka, 1966; Charnov, 1979; Hume, 1989), or from empirical data in the literature indicating that differences in the activity budgets of folivorous primates in response to variation in food availability (e.g., da Silva, 1992; Fashing et al., 2007; Korstjens and Dunbar, 2007). By integrating the ecological, demographic and behavioral information, a new perspective on how to tease apart which closely related biological factors are influencing density may be gained. One way to do this is to employ a multivariate approach which tests multiple ecological factors that can be distinguished by how they would affect the behavior of folivorous primates. Specifically, each factor would be accompanied by a set of mutually exclusive *a priori* predictions regarding how each should, all other aspects remaining equal, affect the behavior of folivorous primates in areas of **high versus low population density**. This enables a comparison of which ecological variable(s) best predict the observed patterns of *Alouatta* behavior at the high density site, and thus identify those aspects of forest ecology which are influencing population density. This study will examine the relationships between ecology, demography and behavior in order to address the question of which factors affect Neotropical folivore density in two populations of howler monkeys (*Alouatta seniculus*) that are geographically close, but occur in different forest types and at different densities.

1.2 Specific Aims

This study has three main goals. The first is to evaluate whether predicted differences in ecology occur at the site with high howler monkey density. Based on the ecological variables previous research has suggested affect folivore primate density, eight ecological factors were identified (i.e., the six variables presented in section 1.1 and two additional factors that combine the effects of plant quality and plant density) and will be evaluated and compared between the two study sites (Table 1). The second goal is to identify whether high population density was linked to the following changes in demography that have been observed in other primate populations: 1) The average number of males per group is higher, 2) The average number of adult female howler monkey per group is higher, but does not exceed four, 3) The average group size is higher and 4) The ratio of infants and juveniles to adult females is higher. The third goal is to examine which ecological variable(s) have best predicted the observed patterns of *Alouatta* behavior at the high density site in order to identify which aspects of forest ecology are influencing howler monkey densities in Yasuní National Park, Ecuador. The behavioral predictions for each of the ecological hypotheses are summarized in Table 1 and the specific rationales behind each of them are given below:

Behavioral Predictions for the categories of (1) percentage of time spent resting, (2) percentage of time spent feeding, (3) percentage of time spent moving, (4) between patch movement and (5) the number of trees fed upon per day are given for the eight ecological variables based on how each should, all aspects remaining equal, affect howler monkeys in a high versus a low density area:

(H1) Lower Hunting: The behavior of howler monkeys at a high versus a low density population is expected to be the same, except for the category of percentage of time spent moving. Howler monkeys are predicted to spend a higher percentage of time moving if they are exposed to a lower level of hunting. This is because primates are known to adopt a cryptic movement pattern in areas where they are (or have recently been) hunted in order to avoid detection by hunters (Janson, 1992; Derby, personal observation). Thus individuals should spend more time moving if they do not have to contend with hunting avoidance.

(H2) High Soil Fertility/Habitat Heterogeneity: Higher soil fertility and a more heterogeneous habitat are indistinguishable in their predictions for these particular behavioral categories and are therefore considered together here. Both variables, with all other aspects of ecology remaining equal, are predicted to have a similar effect on the behavior of howler monkeys in a high versus a low density population. It is predicted that the percentage of time spent resting, feeding, moving, and the between patch distance will be the same between sites.

(H3) Less Phenological Seasonality: Although both a lower as well as a higher degree of seasonality have been suggested to increase primate population density, less seasonality is expected to be of greater importance in regions where precipitation is relatively higher throughout the year and as such there are no pronounced dry seasons. The study sites in Eastern Ecuador are characterized by such a pattern (Pitman, 2000; Di Fiore and Rodman, 2001). Less seasonal habitats should have a more asynchronous pattern of food production, and thus a higher availability of food throughout the year, which supports a higher *Alouatta* density. Less seasonality is expected to have the same effect on behavior in both a high versus a low density population, with the exception of a lower between patch movement. This is based on the assumption that higher food availability should allow for primates to travel shorter distances between patches in order to locate food at any given time (e.g., Charnov, 1979).The percentage of time spent resting, feeding and moving are predicted to be the same between the sites.

(H4) Higher Phenological Productivity: A higher overall production of food throughout the year is predicted to enable howler monkeys to spend a lower percentage of time moving, or foraging, in order to locate resources throughout their habitat (e.g., MacArthur and Pianka, 1966).

(H5) Resource Quality (lower level of phenolic content): Phenolics, such as tannins, can act as digestion inhibitors and have been shown to reduce feeding time (Wrangham and Waterman, 1981). Leaves containing a lower phenolic content should allow howler monkeys to spend a lower percentage of time resting and a greater percentage of time feeding. The percentage of time spent moving and the between patch distance are not predicted to differ between a high versus a low population density.

(H6) Resource Quality (a higher ratio of protein-to-fiber in leaves): The foraging strategy of howler monkeys should be to select food of a relatively high quality, to minimize the costs of procuring such foods and generally to conserve energy (Milton, 1980). Leaves that have a higher ratio of protein-to-fiber enable howlers to acquire a greater nutritional amount per feeding bout and thus they should spend a greater percentage of time feeding as well as have a longer period of time to rest.

(H7) Resource Density (higher density of resources lower in phenolic content): The combined effect of resources lower in phenolic content and a higher density of these resources available differs from H5 in that higher density decreases the distance between patches, and thus the percentage of time spent moving.

(H8) Resource Density (higher density of resources with a higher ratio of protein-to-fiber in leaves): The combined effect of having resources higher in protein-to-fiber and a higher density of these resources differs from H6 in that higher density decreases the distance between patches thus decreasing the percentage of time spent moving. It is also predicted that howler monkeys will be able to feed on a higher number of trees per day. This prediction is based on the assumption that under these conditions individuals may be less nutritionally limited due to a diet higher in protein, enabling them to travel to more patches per day facilitated by the decreased distance between those patches.

1.3 Dissertation Overview

Chapters two through four are written as a collection of independent manuscripts centered on the themes that have been introduced here. Chapter two focuses on the issue of hunting (variable one) in Yasuní N.P. and examines what effect it may be having on the primate community and howler monkeys in particular. Chapter three describes the comparative ecology of the two study sites and tests the ecological predictions for soil fertility/forest heterogeneity, phenological seasonality, and phenological productivity (variables two through four). Chapter four examines 1) the density and quality of resources (variables five through eight) and 2) the population demographic patterns between the sites and evaluates which ecological variables best predict the observed patterns of *Alouatta* behavior. Finally in chapter five, the predicted behavioral patterns for each of the supported ecological variables presented in the previous chapters are compared to the observed patterns of *Alouatta* behavior. The dissertation concludes by proposing which ecological factors are playing significant roles influencing differences in

Alouatta density in Yasuní N. P. and suggests possible conservation implications for the region.

1.4 Literature Cited

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1.5 Tables

TABLE 1: Ecological variables examined and compared between the two study sites, along with their corresponding predictions of the patterns expected to occur at the high population density site.

Ecological variable	**Predictions for the ecological context expected to occur at the high density howler monkey site**	**References**
(1) Hunting	*Lower* hunting	e.g., Peres, 1997, 1999
(2) Soil fertility/ Forest heterogeneity	*Higher* heterogeneity and *higher* soil fertility	Soil fertility: McKey, 1978; Peres, 1997; Hauggesen and Peres, 2005 Forest heterogeneity: Fleagle, 1999; Bourliere, 1985; Oates et al., 1990; Ganzhorn, 1993
(3) Phenological seasonality	*Less* phenological seasonality	Ripley, 1979; Terborgh, 1986; Gupta and Chivers, 1999
(4) Phenological productivity	*Higher* phenological productivity	Sadleir, 1969; Chapman and Chapman, 1999
(5) Resource quality: Phenolic level	*Lower* level of phenolics in leaves	Coley and Barone, 1996
(6) Resource quality: Ratio of protein-to-fiber	*Higher* ratio of protein-to-fiber in leaves	Milton, 1980; Chapman et al., 2002, 2004
(7) Resource density: Phenolic content	*Higher* density of plants low in phenolics	Chapman et al., 2002, 2004
(8) Resource density: Ratio of protein-to-fiber	*Higher* density of plants with high ratios of protein-to-fiber in leaves	Chapman et al., 2002, 2004

TABLE 2: Summary of ecological variables and their corresponding behavioral predictions. Predictions were made based on how each variable should, all aspects remaining equal, affect howler monkeys in a high versus a low density area.

	Behavioral Predictions				
Ecological Hypotheses	**% Time spent resting**	**% Time spent feeding**	**% Time spent moving**	**Between patch movement**	**# of trees fed upon per day**
H1 **Hunting:** ***lower***	**Predicted:** *same*	**Predicted:** *same*	**Predicted:** *higher*	**Predicted:** *same*	**N/A**
H2 **Soil fertility/habitat heterogeneity:** ***higher***	**Predicted:** *same*	**Predicted:** *same*	**Predicted:** *same*	**Predicted:** *same*	**N/A**
H3 **Phenological seasonality:** ***less***	**Predicted:** *same*	**Predicted:** *same*	**Predicted:** *same*	**Predicted:** *lower*	**N/A**
H4 **Phenological productivity:** ***higher***	**N/A**	**N/A**	**Predicted:** *higher*	**Predicted:** *same*	**N/A**
H5 **Resource quality: phenolic content in leaves** ***lower***	**Predicted:** *lower*	**Predicted:** *higher*	**Predicted:** *same*	**Predicted:** *same*	**N/A**
H6 **Resource quality: protein-to-fiber ratio in leaves** ***higher***	**Predicted:** *higher*	**Predicted:** *higher*	**N/A**	**N/A**	**N/A**
H7 **Resource density: low phenolic content in leaves** ***higher***	**Predicted:** *lower*	**Predicted:** *higher*	**Predicted:** *lower*	**Predicted:** *lower*	**N/A**
H8 **Resource density: high protein-to-fiber ratio in leaves** ***higher***	**Predicted:** *higher*	**Predicted:** *higher*	**Predicted:** *lower*	**Predicted:** *lower*	**Predicted:** *higher*

CHAPTER 2

Primate Population Density at Two Sites in Amazonian Ecuador: Possible Impacts of Subsistence Hunting

2.1 Abstract

This chapter presents the first systematic data on primate population density in two different regions in Yasuní National Park, Western Amazon. The study sites are located close together (~36 km apart) and are characterized by the same primate community; however the level of hunting pressure differs between regions (no hunting versus some hunting). The prediction is tested that larger-bodied species should be relatively less abundant when hunted than smaller-bodied species. Population density data from this study are then combined with existing data on the annual harvest rates for primate species in the region where hunting occurs. When the hunted site is compared to the non-hunted site the results support the prediction by indicating that 1) the majority of species occur at slightly lower densities, 2) the large bodied taxa occur at significantly lower densities compared to that of small and medium size taxa and, 3) the average group size is significantly larger. However, when all taxa are compared, there is not a significant relationship between the comparative density ratio in the hunted versus the non-hunted region and the annual harvest rates. These data are discussed in the context of human population density and indigenous hunting practices in YNP as well as the biological factors influencing primate species' vulnerability for local depletion and the possible conservation implications these issues may have for the region.

2.2 Introduction

Hunting of mammalian communities by humans is widespread throughout the tropics. It varies in intensity and context, ranging from subsistence to game or market hunting (Peres, 2000). It has been shown that while habitat destruction has the greatest negative impact on rainforest wildlife, hunting remains the greatest single threat to tropical biodiversity in the forests that are still standing (Redford, 1992; Alvard, 1997). Recently, both anthropologists and applied ecologists have focused their attention on the influence that hunting is having on tropical mammal populations and how this in turn impacts entire forest ecosystems (Robinson and Bennett, 1999; Peres, 2000; for recent review see Biotropica Special Section, 2007). One example is the influence that preferential hunting of large-bodied primate species (e.g., Peres, 1997, 1999) has on seed dispersal, a key process in forest maintenance (Howe and Smallwood, 1982; Cain et al., 2000; Schupp et al., 2001; Wenny, 2001; Corlett, 2002). Detailed studies of primates and fruiting trees have shown they are involved in very complex interactions and it has been suggested that the removal of primates through hunting may decrease and/or eliminate important seed dispersers, severely limiting the ability of forest regeneration (Corlett, 1998; Bohning-Gaese et al., 1999; Knogge and Heymann, 2003; Lambert and Chapman, 2005; Link and Di Fiore, 2006; Moura and McConkey, 2007).

Today subsistence hunting in particular affects vast tracts of tropical wilderness in South America (Peres, 1997, 2000; Carrillo et al., 2000), and probably has to some extent for at least the last 12,000 years, since indigenous peoples first colonized the neotropics (Roosevelt et al., 1996). Historically, subsistence hunting was thought to occur within the construct of an inherent ecological balance that existed between human hunter-gathers and wildlife, and certainly at one time this might have been true. More recently, however, the concept of sustainable harvests of tropical wildlife by forest-dwelling people has been the focus of much discussion and debate by both conservation and development professionals (Mena et al., 2000).

A central issue is the rapid cultural change forest-dwelling people are undergoing that often occurs within a very short time period. Two well documented examples of this rapid transformation that have occurred in indigenous Amazonian populations during the last several decades are 1) the transition from using traditional weapons to hunting with guns (e.g., shotguns and rifles) and 2) the pronounced shift from a nomadic to a permanently settled lifestyle (Leeuwenberg and Robinson, 2005; Mena et al., 2005; Franzen, 2006). One direct outcome of this shift in settlement pattern has been increased human colonization both nearby and within forests, a pattern shown to lead to prolonged hunting pressure and forest clearing and to result in significant negative effects on the abundance and the diversity of mammalian assemblages (Leeuwenberg and Robinson, 2000; Lopes and Ferrari, 2000; Mena et al., 2000; Franzen, 2006). Indeed there is grave concern that the combination of more centralized and growing subsistence human populations, more efficient hunting technology, and an increasing market for bush meat is driving many neotropical species to local extinction (Mittermeier and Cheney, 1987; Peres, 1990; Avard et al., 1997). Yasuní National Park and Biosphere Reserve (YNP), Eastern Ecuador, provides an example and a test case for this scenario.

YNP is a 900,000 km^2 area in Eastern Ecuador that conserves one of the larger contiguous tracts of western Amazonian rainforest. The region is characterized by extreme faunal and floral biodiversity; examples include the highest documented herptofauna diversity in all of South America (105 amphibian & 83 reptile species), the highest known biodiversity of insects in the world (> 100,000 species of insects/ha), one of the most diverse avian sites in the world (housing 44% of all Amazonian bird species), and over 1,576 plant species (Koester, 2001; Nabe-Nielson, 2001; Scientists Concerned for Yasuní Technical Advisory Report, 2004 unpublished data). YNP is also home to 173 mammals including 10 primate species, two of which appear as Vulnerable on the IUCN Red List (*Ateles belzebuth*: Rylands and Mittermeier, 2003; *Lagothrix poeppigii*: Rylands et al., 2003).

During the last decade in Ecuador, YNP has experienced an increase in human colonization by indigenous ethnic groups (Scientists Concerned for Yasuní, unpublished data; F. Koester, personal communication). The influx of human habitation is largely due to the construction of a road built in the early 1990's by the oil company Maxus Energy Corporation, attracting people from other areas who establish permanent settlements along it because of the ease of mobility it provides (Franzen, 2006). Rural development, and roads in particular, provide greater access to areas of the forest that otherwise would not have been accessible to hunters (Peres and Terborgh, 1995; Wilkie et al., 2000). Recent data suggests this is occurring within YNP and that the Maxus road has led to increased subsistence hunting, threatening the local depletion of large bodied primates in areas of persistent hunting (Franzen, 2006).

Residing within the reserve are two indigenous groups, the Quichua and the Waorani, who occupy mutually exclusive areas. In 1990, the Ecuadorian government granted 6,100 km^2 to the Waorani, designated as the Waorani Ethnic Reserve (Lu, 1999). The last published estimates suggested between 1,500 and 2,000 Waorani lived in this region (Lu, 2001), but the extent to which the population has increased in the last 6 years has not been closely documented.

The Waorani are subsistence hunters who traditionally used weapons such as blowguns for hunting arboreal prey and spears for terrestrial prey (Mena et al., 2000). One recent study, however, revealed that they have also become involved in market hunting on a limited scale, and that nearly all hunters in the communities located in the region this study took place now use guns (Franzen, 2005, 2006). In fact, only 12% of the weapons hunters use today are traditional (e.g., blowgun, spear, barbasco, sticks, nets, and hands) while the remaining 88% consist of rifles, shotguns, dynamite, hook and line, and dogs (Franzen, 2005, 2006). A striking element to this transition is that it occurred in less than three decades (Mena et al., 2000).

Despite these changes, there has not been any published systematic long-term data on primate, or other mammal, densities in YNP. Hence, even though there has been an influx of human colonization, increased subsistence hunting, and a shift in hunting style, the effects on primates have been largely undocumented (but see Franzen, 2006). As a first step in understanding the effects of hunting on the primate community, it seems vital to assess the abundance and diversity of the primate community within this region. This study evaluates the primate community population density in two regions of YNP, one where low levels of hunting occur and one where hunting has not been reported to occur in order to 1) establish base-line population density data for YNP and 2) assess what possible effect hunting may be having on the primate communities. Specifically, based on existing data from regions where hunting occurs (e.g., Peres, 1990, Robinson and

Redford, 1991), the prediction is tested that larger-bodied species should be relatively less abundant when hunted than smaller-bodied species.

2. 3 Methods

Study Area

Research took place from February-December 2005 in the Yasuní National Park and Biosphere Reserve, a primary neotropical rainforest located south of the Rio Napo in the Amazon region of Ecuador (Koester, 2001). This region has been designated as an UNESCO Man and the Biosphere reserve due to its extremely high species diversity (Di Fiore, 1997). At least ten species of non-human primates occur within the region, including three genera of large-bodied atelids (*Ateles belzebuth, Lagothrix poeppigii*, and *Alouatta seniculus*), making it one of the few areas in South America where significant populations of these closely related taxa can be found sympatrically (Di Fiore, 1997). The region is moist tropical forest composed of approximately 80% *terra firme* forest and smaller areas of riparian forest and swamp (Pitman et al., 2001). The elevation ranges from 190-350 m and there is no distinct dry season. Mean annual rainfall is ca. 3,200 mm, and, although rainfall is variable throughout the year, all months typically receive more than 100 mm (Di Fiore and Rodman, 2001). Mean annual temperature is 26˚C and is relatively constant throughout the year (Di Fiore, 1997, 2003; Di Fiore and Rodman, 2001). Until recently, much of the park remained pristine, but human subsistence practices and resource extraction have altered portions of the reserve (Di Fiore, 1997), including a road built by the Maxus Ecuador Corporation, which now stretches over 100 km inside YNP (Franzen, 2006).

Study Sites

The study was conducted at two sites within YNP. The first location is the Proyecto Primates Research Area (PPRA) that was established in the mid-nineties (Di Fiore, 1997, 2001; Dew, 2001; Suarez, 2003; Spehar, 2006). The PPRA site is approximately 650 ha in size and is characterized by primary, non-flooded *terra firme* forest with a road that borders the area on two sides. Due to regular researcher presence and a long-standing agreement with two nearby Waorani communities, this site has experienced low levels of hunting over the last decade compared to that of the surrounding area (A. Di Fiore, personal communication). This low level of hunting has mainly occurred during periods of researcher absence. Therefore, the results for this study site represent a conservative estimate of the effect of hunting on the primate community at YNP.

The second site, bordering the Tiputini River near the Tiputini Biodiversity Station (TBS), is also a roughly 650 ha area and consists of a mix of *terra firme* and seasonally flooded habitat. It is located further from the Waorani communities and thus far hunting has not been reported at TBS. The PPRA and TBS study sites are located approximately 36 km apart from each other (Figure 1) and both are contiguous with large tracts of unfragmented tropical rainforest. It can therefore be assumed that the primate populations at the two sites are potentially part of larger populations.

Density Estimates

Two types of surveys were conducted: 1) distributional surveys to determine the presence or absence of primate species at the two study sites and 2) line transect surveys to quantify densities of primate groups. Only diurnal surveys were conducted. Hence, although at least 10 primate species occur within YNP, the nocturnal owl monkey (*Aotus vericifons*) was not considered in this study. Thus, the following nine primate species were expected to occur during surveys: woolly monkeys (*Lagothrix poeppigii*), spider monkeys (*Ateles belzebuth*), howler monkeys (*Alouatta seniculus*), white-fronted capuchins (*Cebus albifrons*), dusky titi monkeys (*Callicebus discolor)*, saki monkeys (*Pithecia* spp.), squirrel monkeys (*Saimiri sciureus*), golden mantled tamarins (*Saguinus tripartitus*) and pygmy marmosets (*Cebuella pygmaea*).

Distributional surveys were conducted at both sites on a weekly basis throughout the study period. As part of a larger project investigating howler monkey density, surveys were done with the intent to search and conduct a complete count of howler groups in the study sites. During these surveys, however, all primate encounters were recorded to augment information obtained from the line transect surveys in order to gain a more comprehensive knowledge of primate group density and composition. One to three days per week were spent surveying each site, and data on the species, location, time of contact, activity, and group size and composition were recorded each time primates were encountered.

Population density for each species was estimated using standard line transect sampling following methods outlined by the National Resource Council (1981) and Peres (1999). During October 2004, 4 km and 3 km transects were established at the PPRA and

TBS study sites, respectively, and data were collected 2-3 days per month from February until December 2005. Transects were walked at a mean velocity of 1 km per hour, between 0600 and 1400 hours, and for each primate sighting the following data were recorded: contact start/stop time, transect location, observer-to-animal distance, perpendicular distance, angle from the transect to first animal observed, species, group size, group spread, activity and mode of detection. Groups were defined as all adult and immature members visible during a 10 minute contact duration (following Peres, 1999). However, the associated social and ranging patterns of species that live in large groups (e.g., *Saimiri*), have large group spreads (e.g., *Lagothrix*), or have fission-fusion social organizations (e.g., *Ateles*) rarely allowed for a complete group count during a single contact (Peres, 1993, 1997). For example, *Lagothrix* is characterized as a socially cohesive but spatially dispersed species (Di Fiore, 1997), with group spreads ranging more than 100m (Di Fiore, 1997; this study, unpublished data). The average group size for this species more accurately reflects group "pods", or groups of potentially socially interacting individuals (Di Fiore, 1997). In a situation where *Lagothrix* pods are separated by 50-100m from each other (the approximate maximum distance along the transect one could detect large-bodied primates either by site or sound) and by more than 10 minutes of contact duration (the cut-off time for individual contacts), it would technically be considered two contacts and two groups, instead of one contact with one group. Thus, to avoid overestimating the densities of species in large groups, a correction factor was applied based on group spread for every independent sighting that was clearly a continuation of the group from the previous contact (judged by the distance between pods and time duration between contacts: see above) (Peres, 1999; Janson and Terborgh, 1980).

Density estimates were calculated separately for each species by assessing the effective transect width (**w**) based on the maximum reliability sighting distance for that taxon evaluated over the entire set of transect walks (observer-to-animal distance: National Resource Council, 1981, Janson and Terborgh unpublished cited in NRC, 1981). This distance was estimated by examining histograms of total sightings for each species. The transect width was assumed to be the first distance interval at which the number of detected groups or individuals dropped to two-thirds or less than that of the preceding distance interval (i.e., “fall of distance” criterion; see Kelker, 1945). Transect width (**w**) was assumed to be the same for both sides of the transect. The census area was calculated by multiplying the transect length (**l**), by twice the transect width (**w**). On this basis, population densities ($\mathbf{d_{ind}}$) along with the number of groups encountered ($\mathbf{d_{groups}}$) per km^2 were calculated by dividing the mean number of individuals ($\mathbf{n_{ind}}$) or groups ($\mathbf{n_{groups}}$) recorded during censuses by the census area covered (**2lw**).

$$\mathbf{d = n/2lw}$$

Additionally, average group size was calculated from the line transect data and reflects the average number of individuals recorded per contact for each species. Despite a number of potential problems, line transect surveying is considered the best method for the evaluation of diurnal rainforest primate densities (Emmons, 1984; Lopes and Ferrari, 2000) except if species are cryptic or occur in very low densities (McDonald, 2004). There are many methods available for calculating population density from line transect data (Brockelman and Ali, 1987; Buckland et al., 1993), all of which require a rather high number of sightings. Recommendations for the minimum number of sightings to calculate reliable densities range from 40 (Buckland et al., 1993) to 100 sightings (Plumptre, 2000), and, depending on the methods employed, small sample size can result in widely varying estimates of population density at the same site and differentially between both sites and species (Lopes and Ferrari, 1993, 2000). Because these numbers were not reached for any of the species in this study, I evaluated the reliability of my density estimates in three ways. First, data on average group size collected from long-term behavioral and demographic research conducted on two of the primate species at both study sites (*Ateles*: Spehar, 2006; A. Di Fiore and A. Link unpublished data; *Alouatta*: this study, unpublished data) were compared to line transect data for these species. Second, cumulative densities were calculated to look for continuity in the data (e.g., Borries et al., 2002). Even though this method does not estimate the accuracy of the values, it does evaluate its precision. Third, standard deviations were calculated for each of the species' values to estimate the degree of variation present (Krebs, 1998).

Annual Harvest Rate

Hunting data were compiled from a recent study that evaluated and compared the sustainability of subsistence hunting practices across the three Waorani communities that occur in proximity to the PPRA study site (Franzen, 2005). The study employed Robinson and Redford's (1991) model to evaluate the sustainability of hunting rates, measured as the number of individuals taken/km^2/year (or harvest "rate"). The information was gained by giving Polaroid cameras to 20 households in the three communities, and members were asked to photograph harvests from each hunting episode over the study period (N = 413 hunting episodes). Interviews were conducted weekly and the Polaroid photographs were used to facilitate the interviewees' recall and confirm hunters' reports of the species harvested during interviews. Since hunting by indigenous habitants within YNP is permitted, Franzen (2006) felt there was no reason to expect concealed data.

Franzen's (2006) annual harvest rate data for primates were combined with population density estimates from this study in order to 1) examine the relationship between harvest rates and inter-site population density differences and 2) calculate an index of hunting pressure. A comparative density ratio was first calculated to measure between site density differences by dividing species' density in the lightly hunted site by the non-hunted site. Second, in order to look at the relationship between harvest rate and body mass, which is likely confounded by the population density of these species, an index of hunting pressure was calculated separately for each species. This index was defined as the number of individuals harvested per year divided by the raw population density, which was assumed to be the density from the non-hunted site; the index thus can be thought of as the relative ratio of hunted to available individuals. It is expected that if hunting is mainly driving lower population density in the hunted site then species with the lowest comparative density should also have the highest hunting pressure index.

Statistical Testing

In addition to the accuracy and precision assessments of the density data (see above), the following statistical tests were applied. A Wilcoxon Matched Pairs Test was performed on the line transect data to compare species' densities and average group size between the sites (Siegel & Castellan 1988). A one-tailed test was used to compare species' densities following the prediction that primate population densities, overall, should be higher in the non-hunted region, while a two-tailed test was used to compare average group size between the two sites because studies have demonstrated that primates may respond to hunting either by increasing or decreasing group size, depending on their anti-predator strategy (Isbell 1994, Janson & Goldsmith 1995, Hill & Lee 1998, Croes et al 2007). In addition, the following analyses were conducted in order to evaluate the possible effects of hunting. First, I used Spearman's Rank Order Correlation (Siegel & Castellan 1988) to look at the relationship between the comparative density ratio and the annual harvest rate for each species. Second, a Mann-Whitney U Test was used to compare specifically the density ratio of large versus small and medium primate species in the hunted compared to the non-hunted region. Third, Spearman's Rank Order Correlation (Siegel & Castellan 1988) was again used to analyze the relationship between body mass and the annual harvest rate for each species. Body mass was estimated using values taken from Franzen (2005) for all species except *Saguinus*; data for this species were not available and were instead taken from the literature (Smith and Jungers 1997). However, since this relationship is likely confounded by species' population density, I also used Spearman's Rank Order Correlation (Siegel & Castellan 1988) to examine the relationship between the index of hunting pressure and the comparative density ratios for each species.

2.4 Results

Primate Population Density

A total of 128 km of transect were walked at the two sites (PPRA: 80 km, TBS: 48 km) resulting in 93 primate contacts recorded at PPRA and 99 contacts recorded at TBS. Primate communities at both sites were characterized by the same 10 species, however population densities were found to differ (Table 1). Comparative densities for three species could not be calculated from line transect sampling either because they are nocturnal (*Aotus vociferans*), rarely observed (*Cebuella pygmaea*), or not seen at all at one of the sites (*Pithecia* spp.*,* which was not observed on PPRA transect, although direct observations of this species were made during distributional surveys, indicating they do occur at low densities in the PPRA).

At both sites, the same three species (*Lagothrix poeppigii, Saimiri sciureus,* and *Saguinus tripartitus*) were found to occur at the highest population densities. In general, species were found to occur at higher population densities at the TBS as compared to the PPRA site (Table 1), including the three atelids (*Lagothrix poeppigii*, *Ateles belzebuth*, *Alouatta seniculus*), *Callicebus discolor* and *Saguinus tripartitus*. The exceptions to this, albeit slight, are *Cebus albifrons* and *Saimiri sciureus*. While these data indicate a trend toward higher density in the non hunted site, it fails to reach statistical significance (Wilcoxon Matched Pairs Test: N= 7, T= 5.0, Z= 1.52, P (1-tailed) = 0.06).

There was a significant difference found in the average group size between sites. Across all species, the site difference is in the same direction, toward larger average group size in the hunted versus the non-hunted region (Wilcoxon Matched Pairs Test: N= 7, T= 0.0, Z= 2.37, P (2-tailed) = 0.02). As previously mentioned, line transect data can sometimes underestimate actual group size (National Resource Council 1981, Plumptre 2000). Evidence from this study does in fact show that average group size of *Alouatta* and *Ateles* calculated from transect data is an underestimate when compared to the known average group size (Table 1). Additionally, *Ateles* and *Lagothrix* are characterized by a fission-fusion social organization and a large group spread, respectively, and thus average “group size” for these species more accurately reflects average “subgroup” size. However, the issues of what “group size” defines aside, the species’ averages recorded in this study represent the same characteristics of social organization at both sites and are therefore comparable for the same taxon between sites.

The accuracy and precision assessments performed on the density estimates calculated from line transect sampling indicate that overall, despite low contact numbers, the data appear to have a moderate to high reliability for most species. Figure 2 shows the cumulative densities calculated for each species at each site. The results illustrate a general trend for high variation during the onset of the study and then leveling off toward the middle or end of the study, depending on the species, as the distance and number of contacts increased. Two exceptions to this trend are *Samiri* and *Lagothrix*. *Samiri* density at TBS shows the most variation of any species at both sites, coinciding with the lowest number of transect contacts (N = 3). In addition, these two species also have the largest group size and the highest standard deviation in average group size recorded during contacts (Table 1).

Annual Harvest Rates and the Effects of Hunting

The hunting data reported here are taken from Franzen (2006) and represent the combined total of animals harvested per year by three Waorani communities in the vicinity of the PPRA study area. Franzen (2006) estimated that in these three communities, the following number of individuals of each species were harvested per year: *Lagothrix* = 83, *Ateles* = 58, *Alouatta* = 28, *Cebus* = 18, *Saimiri* = 4, *Callicebus* = 10, *Saguinus* = 2. Based on these estimated harvest rates, Franzen (2006) concluded that woolly monkeys, spider monkeys, howler monkeys, and capuchin monkeys are at risk of being over-hunted in at least one community. Franzen (2006) also suggested that evidence from harvest composition comparisons indicate that two primate species, the woolly monkeys and spider monkeys, are already facing local depletion in the areas surrounding the two oldest communities. Her study also reports that it is not the market sale of hunted meat which appears to be a significant force driving hunting rates, but rather subsistence hunting (Franzen, 2005, 2006).

Figure 3 plots, for each species, the annual harvest rate reported by Franzen (2006) and the comparative density ratio (density in hunted site/density in non-hunted site). The relationship between these two variables is not significant (Spearman's $r_s = -0.375$, $P > 0.05$). However, when the comparative density ratios of the three largest-bodied primates (*Lagothrix, Ateles,* and *Alouatta*) are contrasted with those of small and medium sized taxa, the data show large bodied taxa occur at significantly lower densities in the hunted site (Figure 4: Mann Whitney U Test, $P < 0.05$).

Figure 5a illustrates the correlation between annual harvest rates and body size estimates taken from Franzen (2005) and the literature (Smith and Jungers, 1997). In this analysis it appears the largest bodied species are being hunted at the highest rates (Spearman's $r_s = 0.90$, $P < 0.001$). This result, however, becomes non-significant when instead the hunting pressure index is used (Table 2) and correlated with the comparative density ratio (Figure 5b: Spearman's $r_s = -0.107$, $P > 0.05$).

2.5 Discussion

Density Estimates

This paper has two main objectives; the first is to establish baseline population density data for primates in YNP. The reliability estimates performed on the line-transect density data indicate that, while sample sizes are small, the ensemble of the data appears to be reasonably precise for the majority of species. The exceptions to this are the data for *Samiri* at the TBS site and *Lagothrix* at PPRA site; these species exhibited high variability in their cumulative densities and standard deviations of average group size. Reasons for this may be due in part to large group size in these species and small sample size for *Samiri*, which resulted in this study being unable to provide reliable information on species' density for these two taxa. A final reliability assessment performed on the data is comparisons of average group size for *Ateles* and *Alouatta*, calculated from line transect sampling, to the actual group size (or sub-group size in the case of *Ateles*) gathered from long-term behavioral and demographic research at both sites. The average size estimated for both species underestimated actual group or sub-group size (Table 1), a caveat of line transect sampling that previous authors have cautioned about (e.g., National Resource Council, 1981; Plumptre, 2000). It is therefore suggested that the comparative population density estimates for five of the seven primate species reported here can be viewed as reliable base-line data, but the value for average group size should be used with caution as it likely underestimates actual group size for all species at both sites.

However, while the actual values may be underestimates, this does not negate the significantly larger average group sizes seen across taxa at the PPRA site. There are several possible explanations for this. Predation pressure has long been proposed as a determinant of group living in mammals whereby larger groups reduce the rate of predation through increased vigilance and predator detection distances and decrease the probability that any particular individual will be killed during a predation attempt (Hamilton, 1971; Alexander, 1974). Human hunting could have an effect similar to predation and may also lead to larger group size in areas where hunting occurs. This idea is not universally supported in primates though, as other studies have shown that predation risk - including that of human hunting - may increase, decrease, or have no effect on primate group size (Isbell, 1994; Janson and Goldsmith 1995; Hill and Lee, 1998; Croes et al., 2007) depending on the level of predation pressure, anti-predator strategies, as well as ecological and social constraints.

However, not only is average group size larger at the PPRA site but group density, the number of groups contacted per distance surveyed, is lower (Table 1). In addition to the direct effect hunting may be having on group size, lower group density may be due to hunting indirectly affecting demography by reducing individuals in the surrounding area and thereby freeing up space for dispersal. Considering both the lower density of most species at the PPRA site and the possibility of anti-predator grouping strategies, individuals may be coming into the area to avoid higher hunting pressure outside the study site and aggregating within larger groups for protection.

Impact of Hunting on the YNP Primate Community

The second objective of this paper is to assess what effect hunting may be having on the primate community of YNP. This assessment can be done by looking both at how primates are directly as well as indirectly affected by hunting. The data indicate that the majority of species in this study occur at slightly lower densities at PPRA versus TBS (Table 1) and that large bodied taxa occur at significantly lower densities in the hunted site compared to that of small and medium size taxa (Figure 4: Mann Whitney U Test, $P < 0.05$). These data support the prediction that larger-bodied species should decline more rapidly when hunted than smaller-bodied species. Nonetheless when all taxa are compared there is not a significant relationship between the comparative density ratio in the hunted versus the non-hunted region and annual harvest rates as would be expected if larger-bodied primates were differentially harvested to the point where that harvest has a measurable effect on the population. Additionally while the correlation between harvest rate and body size appears to illustrate a significant relationship (Figure 5a: Spearman's $r_s = 1.0$, $P < 0.001$), it becomes non-significant when the hunting pressure index is instead used and compared with the comparative density ratio (Figure 5b: Spearman's $r_s = -0.107$, $P > 0.05$).

Two major differences between the hunting pressure index-to-comparative density ratio correlation versus the harvest rate-to-body size correlation are where *Ateles* and *Alouatta* fall along the slope (Figure 5a and 5b). *Ateles* has a high harvest rate (N=58) but also a high comparative density ratio (close to 1), meaning there is not a large disparity between the densities they occur at within TBS compared to PPRA. There is the possibility that this pattern is real and spider monkeys are not being heavily affected by harvest rates in the region. However, because the harvest rate for this species is so high and indicative of unsustainable hunting practices, the pattern could also be representing an indirect effect of hunting as mentioned above, where individuals may be coming into the study site to avoid hunting pressure from the surrounding area. If this were the case, the comparable density of *Ateles* at the PPRA site relative to that of the TBS site may, in fact, not be reflecting the density of *Ateles* in the larger hunted portion of YNP. Another explanation could be that *Ateles* density is somewhat lower than expected at TBS due to increased resource competition with *Lagothrix*. At the TBS site *Lagothrix* density is 56% higher than it is at PPRA while *Ateles* is only 15.7% higher. Considering both species have a large fruit component to their diet, increased feeding competition could be influencing spider monkey density at TBS.

The second major difference is where *Alouatta* falls along the slope. Howler monkeys are ranked third in harvest rate (N=28) and yet have the lowest comparative density ratio. A likely explanation for this pattern is that while hunting pressure might be affecting their density to some degree, ecology may be playing a much larger role in the inter-site density differences. *Alouatta* is one of the most folivorous New World monkeys (Milton, 1980) and previous research has shown the density of leaf eating primates to be correlated with several ecological factors such as leaf quality and content (e.g., Waterman et al., 1988; Oates et al., 1990, Ganzhorn, 1992).

The current population density estimations and analyses taken at face value could imply that hunting is not having a large impact on the primate community as a whole. However several aspects of these data should be examined more closely and in concert with the current cultural transitions occurring within YNP.

One factor to consider when evaluating the potential effects of hunting pressure on a primate community is body size. Previous studies have shown that large-bodied primates are preferentially hunted and are most often the first taxa to become locally depleted (Peres, 1999). Franzen's data (2006) shows large bodied primates may be experiencing selective hunting by indigenous communities within YNP. Her study suggests that *Lagothrix, Ateles,* and *Alouatta* are at risk of being over-hunted in at least one community, while the woolly and spider monkey are already facing local depletion in the areas surrounding the two oldest communities. This study did not show that larger-bodied species are overall less abundant than smaller-bodied species in an area where some limited hunting occurs. Although *Lagothrix* and *Alouatta* both have high hunting pressure indices and low comparative densities, *Ateles*, which showed the highest hunting pressure index, showed instead a high comparative density (see above). Thus two of the three large bodied primates show a relationship between a high hunting pressure and a low comparative density ratio.

Behavioral differences between the sites may also be indicative of hunting pressure. It is worth noting that personal observations of unhabituated *Alouatta* groups at PPRA during surveys or transect walks indicated they were extremely shy around humans. They were very vigilant of myself and my field assistants (whether I was alone or with assistants), and would hide at the top of large trees for long periods of time (often up to an hour) followed by the group splitting up to flee the area. Typically the male would display an overt behavior, for example more conspicuous movements or, on occasion, even vocalizing, while the females and immature would quietly but quickly move off in another direction. This pattern has also been observed in other species, such as *Simias concolor* in areas where they have been hunted (Tilson and Tenaza, 1976). On some occasions all members would cryptically leave from the tree we were observing them, making almost no noise whatsoever as they slowing bridged across to adjoining tree canopies. This behavior, however, was also observed in groups of unhabituated of howler monkeys at TBS, but to a slightly lesser extent, suggesting it may be a species-specific response to unfamiliar entities. Compared to the other large bodied species (*Ateles* and *Lagothrix*), the locomotion pattern of howler monkeys is generally less conspicuous because they rarely use suspensory behavior or jump across tree gaps, and as such naturally have an relatively quieter mode of travel. That being said, howler monkeys at the PPRA site were not only more deliberate and cautious in their movements than those at TBS, but they rarely vocalized. Several studies have found that rain forest monkeys alter their anti-predatory behavior in response to hunting by becoming more secretive when hunted, commencing alarm calls only when at a certain distance (typically > 50 m) from humans (Croes et al., 2007) or not at all (Watanabe, 1981). Howler monkeys were found to vocalize significantly less at PPRA compared to those at TBS (4.7% of observation days versus 40.6%, see Chapter 4), but it is possible that low density, as opposed to hunting per se, could be influencing this pattern.

Considering there have been researchers working in the study site on and off for the past ten years, it is surprising that the howler monkeys would be so wary of humans if there was no effect of human hunting pressure. This behavior could presumably be attributed to higher non-human predation at PPRA, but there is little evidence to support this. Evaluating predation risk is a difficult endeavor, but a study currently in progress may suggest that TBS has one of the highest reported densities of jaguar and puma populations in the region (J. Blake, personal communication). To my knowledge there are no such published studies from PPRA from which to compare, but considering PPRA is situated in an area of higher disturbance (surrounded on two sides by a road that is traversed by an influx of vehicles from oil development plants and Waorani settlements in close proximity) I would suspect that the non-human predation may be less at PPRA.

While there may be very low human hunting pressure that has occurred in recent years, past exposure to hunting may have lasting behavioral modifications. Although primate species vary in their responses to hunters, for instance *Lagothrix* has been observed to confront and display aggressive behavior against unknown humans or hunters (personal observation), it is possible that the hyper-cryptic behaviors observed in howler monkeys at PPRA reflect their species-specific behavioral adaptations in response to past hunting pressure.

The second aspect to consider when evaluating the current population density estimations and whether hunting is having an impact on the primate community as a whole is how the reproductive biology of the hunted taxa may influence the likelihood of species extinction (Bodmer et al., 1997; Mena et al., 2000). Large bodied platyrrhine primates are long-lived mammals characterized by 1) long inter-birth intervals, with average intervals ranging from 2 years in *Alouatta* (Pope, 1997) to 3 years in the atelins (Peres, 1994, Fedigan and Rose, 1995, Di Fiore and Campbell, 2007), 2) long gestation periods, averaging 6 months in *Alouatta* (Pope, 1997) to 7 months in *Ateles* (Fedigan and Rose, 1995) and 7.5 months in *Lagothrix* (Nishimura et al., 1992) and 3) delayed age at first reproduction, ranging from 4.5 years in *Alouatta* to at least 5 years and as many as 8 years in the atelins (Robinson and Redford, 1986; Nishmura, 2004). These traits greatly influence the parameters limiting population growth and recovery, and in fact a recent study shows that Amazonian species with lower rates of maximum reproduction, longer-lived individuals, and longer generation times are more vulnerable to extinction (Bodmer et al., 1997). This applies directly to the three large bodied primates at YNP and thus increases their vulnerability for local depletion in areas of hunting.

It is also important to view this information together with the current cultural transitions taking place in the indigenous communities. The increase in human colonization in the form of permanent settlements along the Maxus road means that the demand for meat will be higher. This demand will likely be met by acquiring large game with the aid of shotguns and rifles, which have all but replaced traditional hunting weapons (Franzen, 2005), enabling an increased return to hunters, in terms of both mean kilograms recovered per unit effort and number of animals killed per hour (Mena et al., 2000). Therefore an increase in annual harvest rates appears inevitable unless changes in the current hunting practices occur. However, previous research suggests that once a shift from the use of traditional to more technologically advanced weapons takes place there is no reason to believe hunters will revert back (Mena et al., 2000). Furthermore, even if current harvest rates are maintained this situation places *Lagothrix, Ateles*, and *Alouatta* at serious risk for local extinction.

Other Factors Contributing to Lower Primate Density at PPRA

Aside from hunting, another factor that may be contributing to the overall lower primate density at PPRA versus TBS is the difference in habitat ecology. This research is part of a larger project specifically focusing on how ecology influences red howler monkey density, the most folivorous Neotropical primate. While hunting may be responsible for reducing the primate community as whole at PPRA, this is not the only factor that appears to be contributing to the lower density of particular taxa. The data presented here show that the species with the lowest comparative density is *Alouatta*, even though this species ranked only third in annual harvest rates, behind *Lagothix* and *Ateles*. This seems to indicate that ecological factors may be influencing howler monkey population density. Data to address this question are currently being analyzed and results will be forthcoming.

Conservation implications for YNP

This study showed that there is a trend toward lower primate density at the site located near hunted areas. While this trend is not significant, the three largest bodied primates do occur at significantly lower densities in the hunted site compared to small/medium sized taxa. Both group size and group density within the site may reflect behavioral adaptations to increased predation pressure. It is important to note that this study represents a conservative estimate of the impact of hunting, likely a "best-case scenario" due to the much lower level of hunting within the PPRA compared to that outside the study site. Viewed as such, it is possible that if hunting continues at the current rate several of the large bodied species may be at risk for local depletion. Projects attempting to introduce alternative protein resources (e.g., chicken farming) have not yet been approved (F. Koester, personal communication.) and yucca as well as other crop farming has been steadily increasing alongside the communities (A.D., personal observation). The implications of a reduction, or local extinction, of protein resources may mean that the nutritional quality of the Waorani diet could decline, along with their health. Moreover the increased farming will result in increased deforestation and reduction in available animal habitat, exacerbating an already precarious situation.

There is an urgent need to continue primate population monitoring in YNP in order to assess and evaluate the changes in density that are occurring. It is suggested that this work be done in collaboration with Waorani counterparts to allow for local involvement, training opportunities and stewardship in the long-term monitoring and preservation of YNP’s primate community.

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2.7 Tables and Figures

TABLE 1: Primate density and average group size at hunted vs. non-hunted regions in YNP. Species density reported as number of individuals/km^2 in the non-hunted (TBS = NH) versus the hunted (PPRA = H) region and the total number of contacts for each species in parentheses. The symbol * appears when fewer than 3 contacts occurred on a transect and an estimate was not calculated. The symbol ** refers to numbers representing sub-group size instead of total group size. Species Key: LP= *Lagothrix poeppigii,* AB= *Ateles belzebuth,* AS= *Alouatta seniculus*, CA= *Cebus albifrons,* CD= *Callicebus discolor*, Ps= *Pithecia spp.*, SS= *Saimiri sciureus*, ST= *Saguinus tripartitus*.

	Population Density (individuals/km^2)		**Group Density** (groups/km^2)		**Avg. Group Size** (line transect survey data)		**Actual Group Size** (long-term behavioral data)	
Species	**H**	**NH**	**H**	**NH**	**H**	**NH**	**H**	**NH**
LP	20.40 (11)	31.80 (13)	1.96	3.86	9.50 (SD= 6.43)	7.87 (SD= 4.52)		
AB	6.75 (12)	7.81 (9)	1.63	2.60	3.50** (SD= 2.19)	1.79** (SD= 1.25)	4.55** (1)	
AS	5.00 (6)	11.45 (8)	1.25	4.17	4.14 (SD= 2.34)	1.50 (SD= 1.41)	6 (SD= 2.0) (3)	5.1 (SD= 2.2) (9)
CA	7.97 (10)	7.29 (4)	1.60	2.08	5.10 (SD= 2.73)	3.50 (SD= 2.38)		
CD	9.69 (13)	10.80 (11)	3.75	4.60	2.26 (SD= 0.62)	2.10 (SD= 0.41)		
Ps	*	7.29 (4)	*	2.08	*	3.50 (SD= 1.29)		
SS	32.75 (6)	31.25 (3)	1.50	1.50	21.83 (SD= 6.18)	20.00 (SD= 5)		
ST	18.75 (12)	26.60 (7)	5.00	8.10	3.75 (SD= 1.29)	3.50 (SD= 1.51)		

TABLE 2: Harvest rate, hunting pressure, and comparative density at hunted vs. non-hunted regions in YNP. Species harvest rates are reported as individuals harvested/year and density reported as number of individuals/km^2 in the non-hunted (TBS= NH) versus the hunted (PPRA= H) region. Hunting pressure is given as an index of harvest rate/raw population density (NH) and comparative density is the ratio of H/NH density. Species Key: LP= *Lagothrix poeppigii,* AB= *Ateles belzebuth,* AS= *Alouatta seniculus*, CA= *Cebus albifrons,* CD= *Callicebus discolor*, Ps= *Pithecia spp.*, SS= *Saimiri sciureus*, ST= *Saguinus tripartitus*.

Species	**Harvest Rate**	**H Density**	**NH Density**	**Hunting Pressure Index**	**Comparative Density Ratio**
LP	83	20.40	31.8	2.61	0.64
AB	58	6.75	7.81	7.43	0.86
AS	28	5.00	11.45	2.45	0.44
CA	18	7.97	7.29	2.47	1.09
CD	10	9.69	10.80	0.32	0.89
SS	4	32.75	31.25	0.37	0.90
ST	2	18.75	26.60	0.08	0.70

FIGURE 1: Map of the study sites in YNP

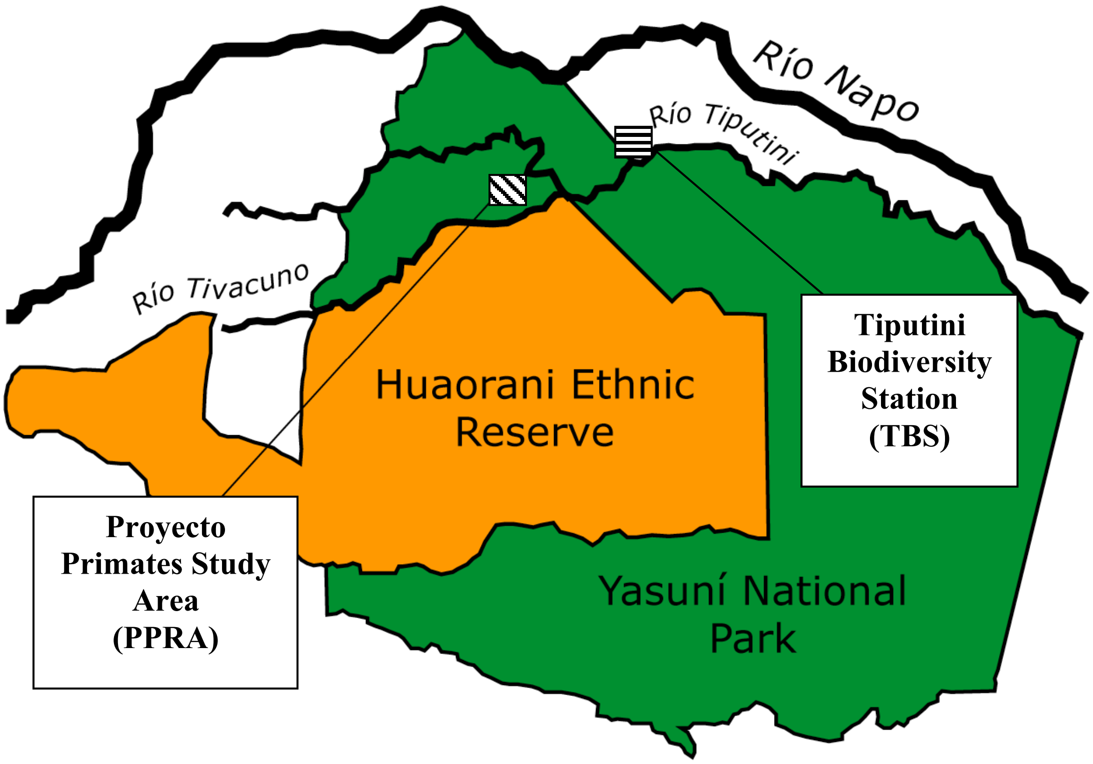


FIGURE 2a: Reliability Test: Cumulative Densities The figures indicate cumulative densities calculated for each species at the PPRA (2a) and TBS (2b). The Y axis shows population density calculated as the number of individuals per km^2. The X axis indicates the transect walk and the total distance in km used for each cumulative calculation shown in parentheses. Species Key: LP= *Lagothrix poeppigii*, AB= *Ateles belzebuth,* AS= *Alouatta seniculus*, CA= *Cebus albifrons*, CD= *Callicebus discolor,* SS= *Saimiri sciureus,* ST= *Saguinus tripartitus*.

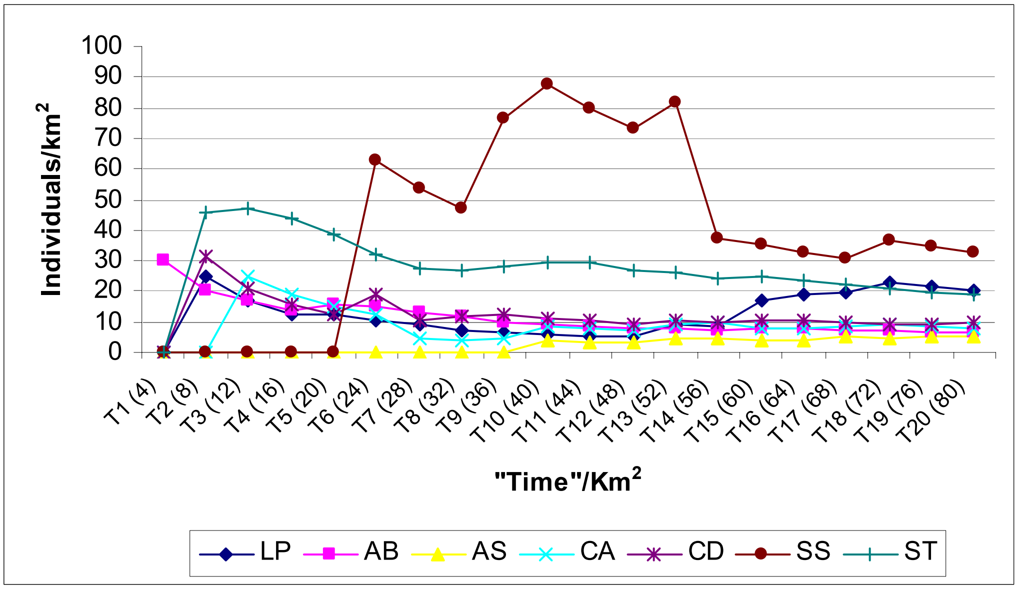
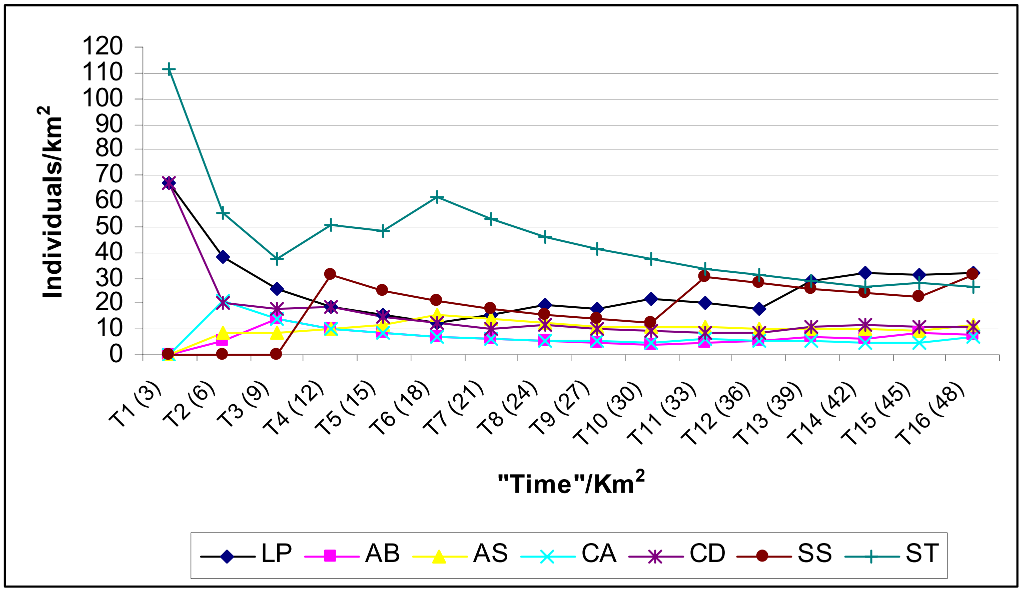


FIGURE 2b



Individuals/km^2
120
110
100
90
80
70
60
50
40
30
20
10
0
T1 (3)
T2 (6)
T3 (9)
T4 (12)
T5 (15)
T6 (18)
T7 (21)
T8 (24)
T9 (27)
T10 (30)
T11 (33)
T12 (36)
T13 (39)
T14 (42)
T15 (45)
T16 (48)
"Time"/Km^2
LP
AB
AS
CA
CD
SS
ST

FIGURE 3: Correlation between comparative density ratio and annual harvest rate. The left Y axis indicates species' comparative density ratio in the hunted as compared to the non-hunted site and the right Y axis shows annual harvest rates (calculated as # of individuals/year). The X axis indicates the primate species [**LP**= *Lagothrix poeppigii*, **AB**= *Ateles belzebuth,* **AS**= *Alouatta seniculus*, **CA**= *Cebus albifrons*, **CD**= *Callicebus discolor,* **SS**= *Saimiri sciureus,* **ST**= *Saguinus tripartitus*].

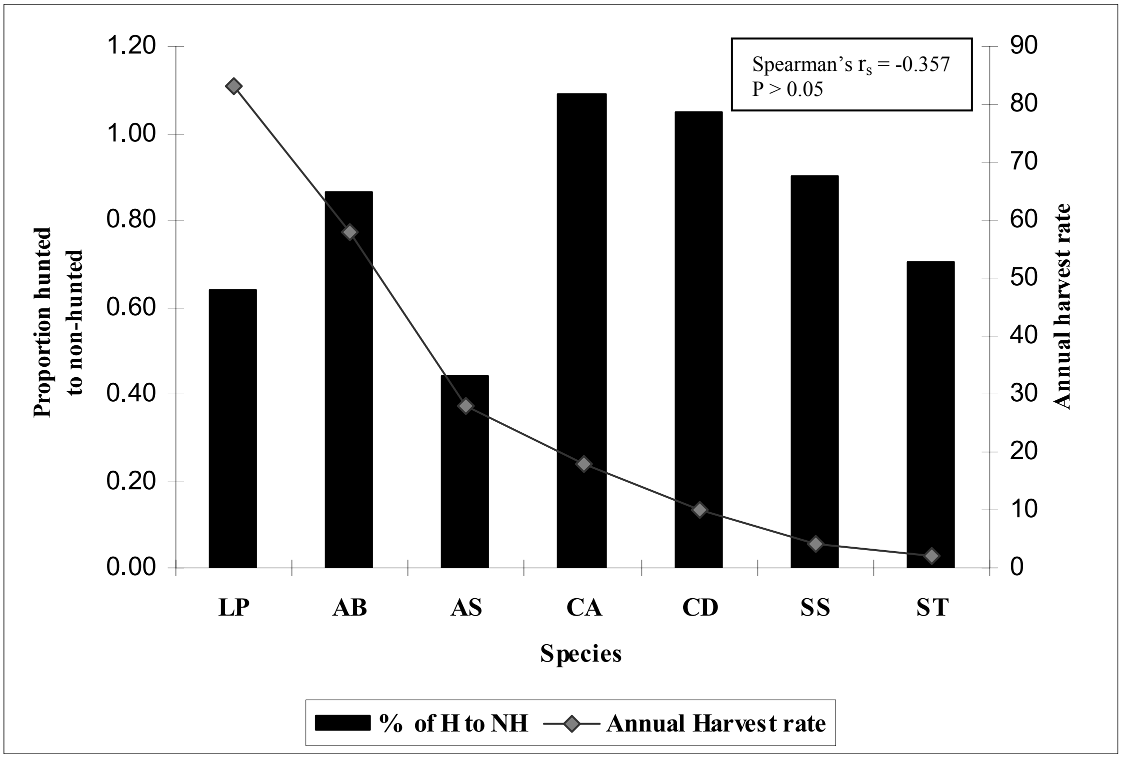


FIGURE 4: Comparative density ratio of large versus small/medium species' density. The left Y axis indicates species' density ratio in the hunted as compared to the non-hunted site. The X axis compares large primate species [**LP**= *Lagothrix poeppigii*, **AB**= *Ateles belzebuth,* **AS**= *Alouatta seniculus*] to small/medium species [**CA**= *Cebus albifrons*, **CD**= *Callicebus discolor,* **SS**= *Saimiri sciureus,* **ST**= *Saguinus tripartitus*].

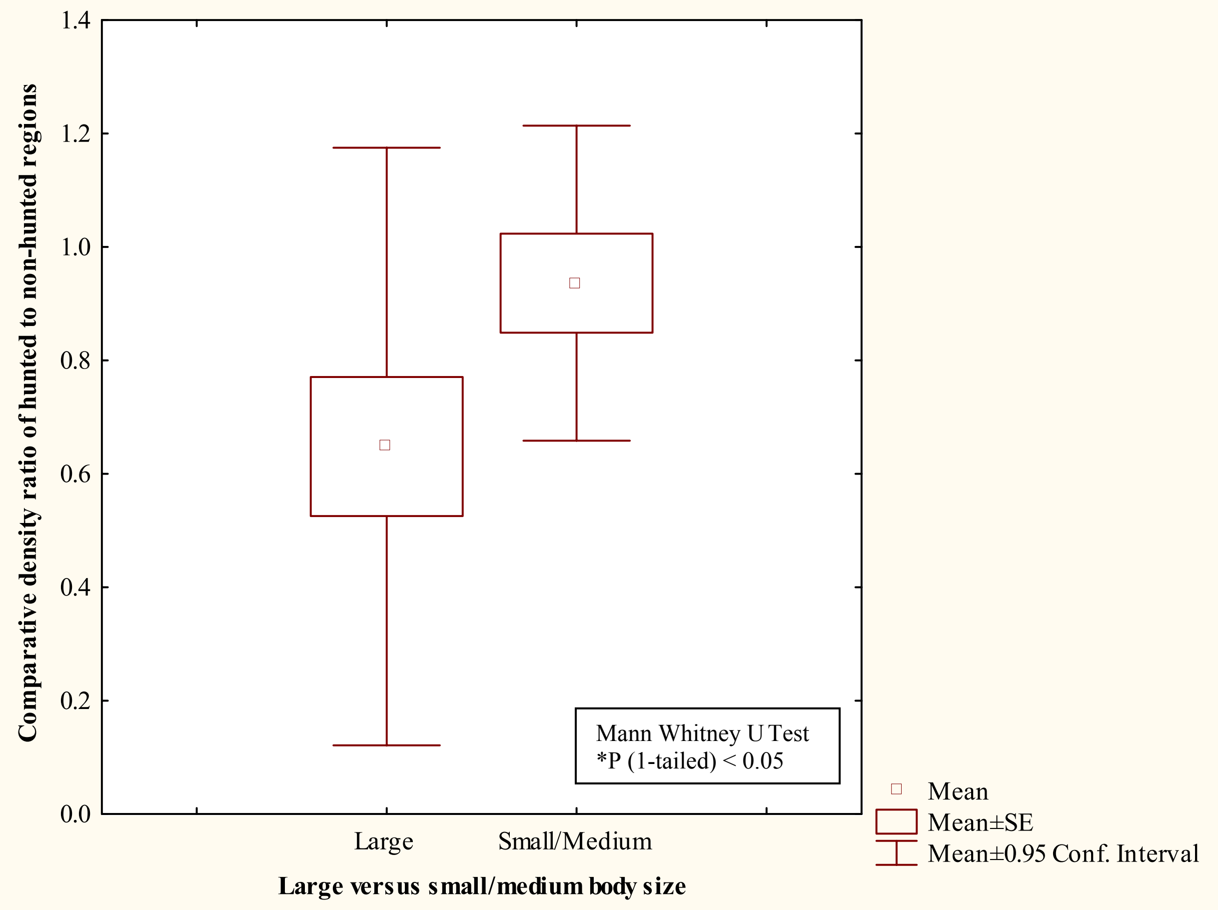


FIGURE 5a: Correlation between body size and annual harvest rate
The Y axis indicates average primate body size (taken Franzen 2005 and Smith & Jungers 1997) and the X axis shows annual harvest rates (calculated as # of individuals/year). Markers indicate the primate species [**LP**= *Lagothrix poeppigii*, **AB**= *Ateles belzebuth,* **AS**= *Alouatta seniculus*, **CA**= *Cebus albifrons*, **Ps**= *Pithecia* species, **CD**= *Callicebus discolor,* **SS**= *Saimiri sciureus,* **ST**= *Saguinus tripartitus*].

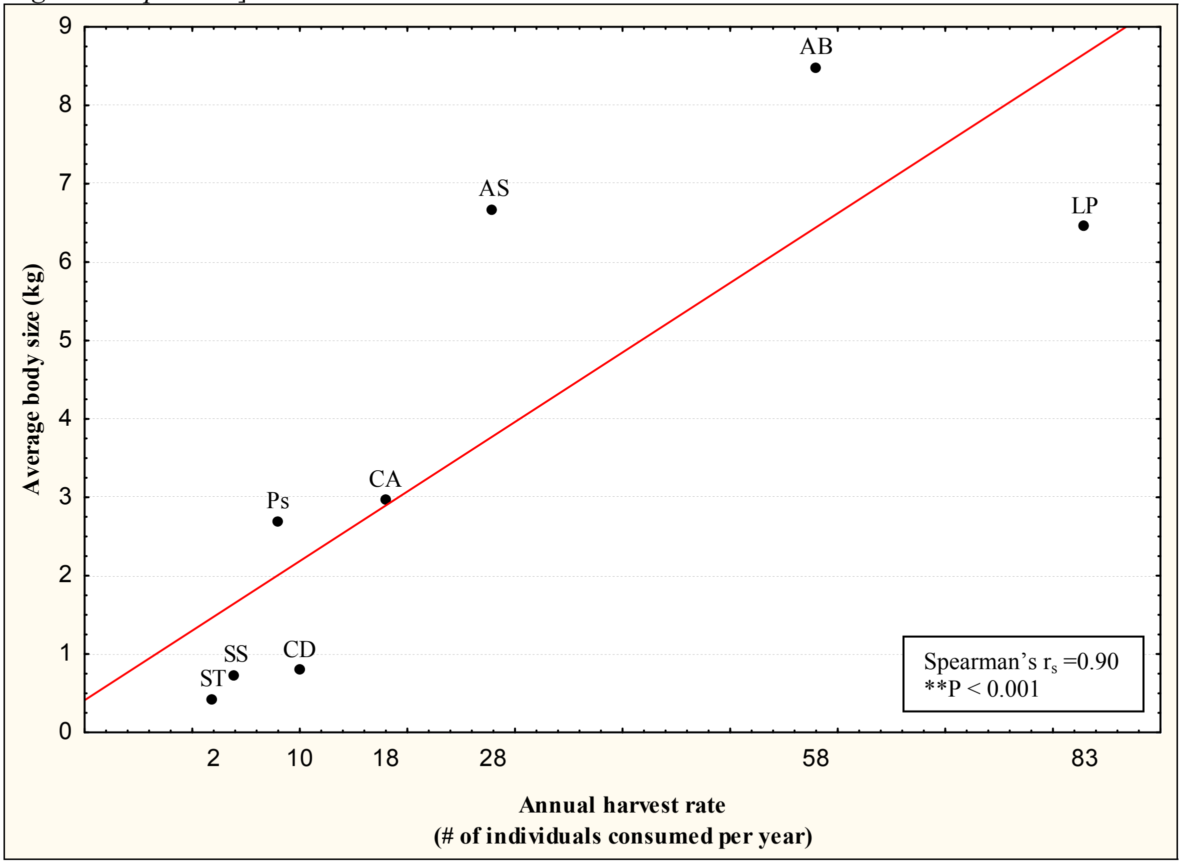
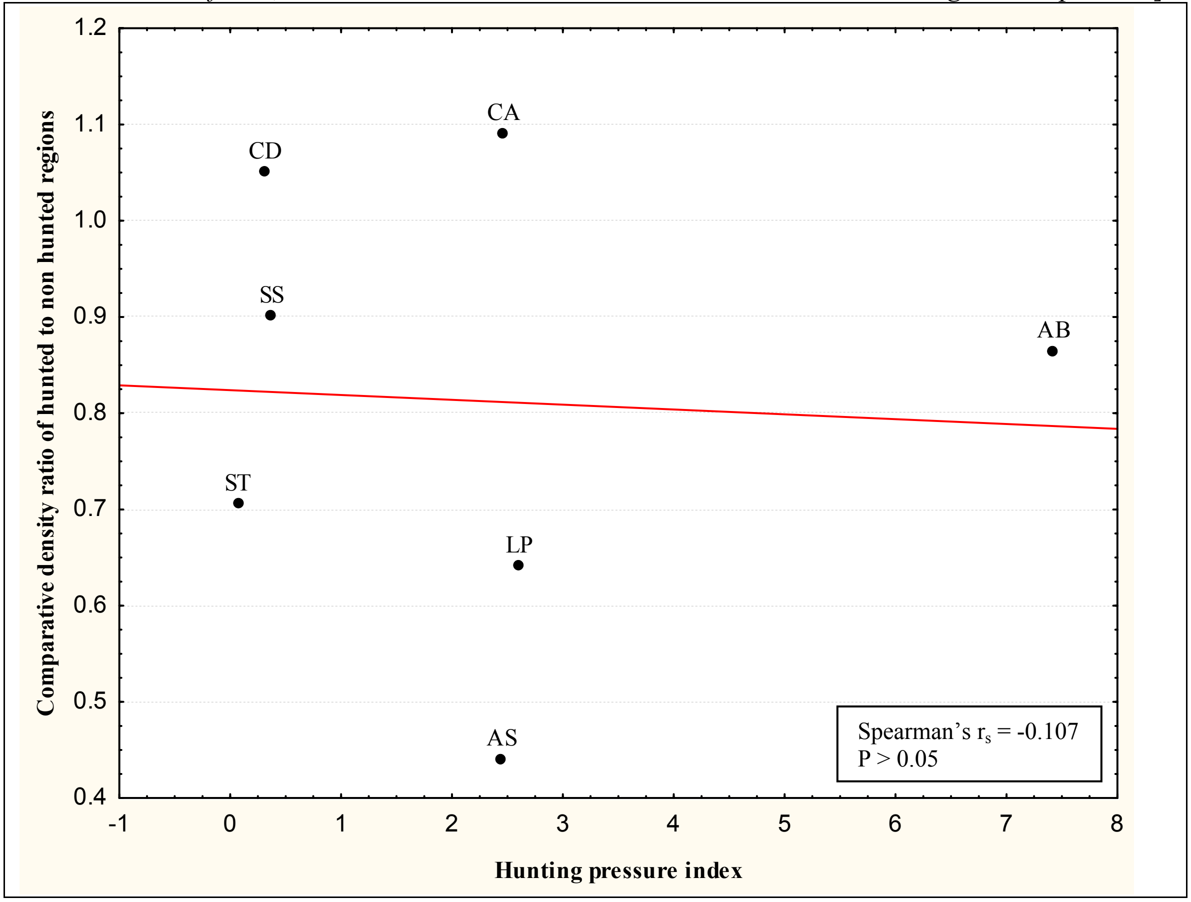


FIGURE 5b: Correlation between comparative density ratio and hunting pressure index The Y axis indicates the comparative density as a ratio of H/NH density and the X axis shows hunting pressure given as an index of harvest rate/raw population density (NH).Markers indicate the primate species [**LP**= *Lagothrix poeppigii*, **AB**= *Ateles belzebuth,* **AS**= *Alouatta seniculus*, **CA**= *Cebus albifrons*, **CD**= *Callicebus discolor,* **SS**= *Saimiri sciureus,* **ST**= *Saguinus tripartitus*].



CHAPTER 3

Ecological Influences On Red Howler Monkey (*Alouatta seniculus*) Density: A Comparison of Two Western Amazonian Sites

3.1 Abstract

This chapter presents data on comparative forest ecology for two study sites in Yasuní National Park. These sites differ in habitat type and howler monkey population density (PPRA: predominately terra firm habitat with lower howler monkey density and TBS: large areas of seasonally flooded habitat with higher howler monkey density). The following four hypotheses regarding ecological influences on howler monkey density are tested in this study: Higher howler monkey population density should be associated with 1) higher overall stem density indicative of higher food abundance and hence a greater carrying capacity of the habitat, 2) higher floristic diversity (as a proxy for a more heterogeneous habitat) indicative of a high diversity of successional habitats and thus a greater availability of alternative resources during times of low food abundance, 3) higher annual phenological productivity reflecting higher food productivity throughout the year and 4) higher soil fertility as evidenced by higher levels of macronutrients and a pH level hospitable for growth and production (i.e., closer to the range of 6- 6.5).

The ecological data showed support for hypothesis three and, to some extent, hypothesis four. Resource abundance, proposed to be the primary determinants of primate, and mammalian, abundance was higher in the form of leaves, flower buds and flowers at TBS. Additionally, a significantly higher DBH (and basal area) was found at

TBS, which may contribute to higher resource productivity. There were no overall differences in soil fertility found between sites, but differences were found between the microhabitats within sites. Soils in riparian areas, or those close to water sources, were found to be significantly higher in secondary macronutrients (Mg and Ca) and have a pH level more favorable for growth and production. When a three-way factorial ANOVA was performed on the phenological data to look more closely at the effects of study site, flooded versus non-flooded transects, and months may be having on phenology, an overall difference between months and between sites was found. Additionally, there was a trend for higher average fruit production on flooded transects at TBS ($p = 0.058$). These data suggest that while a higher production of food may be influencing a higher *Alouatta* population density higher, soil fertility itself was not shown to be directly related to this, except in the case of fruit.

3.2 Introduction

Community ecology focuses on the way groupings of species are distributed in nature, how they are influenced by other species and how they are affected by their environment (Begon et al., 1996). In order to uncover major patterns of plant diversity and productivity throughout wide ranging ecosystems, there have been numerous large scale floristic and phenological studies in tropical forest regions conducted. An example of this is in the Amazon Rainforest, which occupies more than 6 million square kilometers located within nine nations: Brazil (with 60 percent of the rainforest), Colombia, Peru, Venezuela, Ecuador, Bolivia, Guyana, Suriname, and French Guiana (Rylands et al. 2002; da Silva et al., 2005). The Amazon represents over half of the planet's remaining rainforests and comprises the largest and most species-rich tract of tropical rainforest in the world (Rylands et al., 2002). Given the immense area encompassed by this tropical forest wilderness area, it is not surprising that it is quite heterogeneous in both plant and animal communities. Overall, the region is characterized by a mosaic of distinct areas of endemism, each with their own evolutionary histories and biotic assemblages, separated by major rivers (da Silva et al., 2005). However, depending on the scale used to examine certain eco-regions within the Amazon, the ecological, floristic, and animal assemblages can appear to be either homogenous (Larger regional scale, e.g., Western Amazonia: Pitman, 2001) or heterogeneous (Smaller microhabitat/local scale, e.g., Central Amazonia: Haugaasen and Peres, 2005a, b).

Thus it is important that research focus on the scale (regional versus local) most appropriate for the questions, concepts and specimens being examined. Patterns of habitat structure and productivity on larger scales, for example, may not be biologically applicable for questions aimed at understanding the distributions of animals that utilize relatively small home ranges. For instance, while regional scales may be appropriate when investigating migratory birds that demonstrate patterns of long distance seasonal movement (Chesser, 1998), it may not hold true for primates, especially arboreal taxa, which generally occupy smaller, site-specific home ranges. Due to the variation in habitat ecology that can exist on a small scale, it raises the question of whether animal populations, such as primates, are impacted by small scale ecological variation.

Indeed, a great deal of research on primates has focused on investigating which of many potential ecological factors influence distributions and differences in population density. One of the primary determinants of primate, and mammalian, abundance appears to be the availability of food resources (Terborgh and van Schaik, 1987; Davies, 1994). The general concept is that females are primarily governed by the abundance and distribution of resources, whereby a female's reproductive success is limited by the access she has to the resources she needs in order to successfully raise her offspring (Emlen and Oring, 1977; Clutton-Brock, 1991). Thus, a greater abundance of food availability allows for a greater maximum availability of energy, ultimately enabling higher reproductive rates (Chapman and Chapman, 1999). This hypothesis has been well supported from studies on a variety of Old World monkeys (e.g., mangabeys: Olupot et al., 1994; toque macaques: Dittus, 1979; yellow baboons: Hausfater, 1975, Altmann et al., 1985; vervets: Struhsaker, 1973).

Additionally, most of the variation in biomass exhibited in primate communities is accounted for by folivores, or leaf eating taxa, which has lead to a great deal of research directed at species occupying this dietary niche (e.g., Terborgh and van Schaik,1987). Due to the challenges that leaf consumption can pose, such as difficult to digest cellulose and high levels of potentially toxic secondary compounds, data on resource quality as well as density became a focus. For instance, it has been suggested that folivorous primate density is positively correlated with the average leaf quality in a habitat, reflected as the amount of protein, or ratio of protein to fiber in leaves, or in the amount of secondary compounds in the leaves, known as phenolics, that can affect digestibility (e.g., Milton, 1980; Chapman et al., 2002, 2004). This idea has also been well supported in an array of folivorous taxa, including strepshirrines, colobines, and platyrrhines (Strepsirhini: Ganzhorn, 1992; Colobinae: Oates and Davies, 1990; Chapman et al., 2002, 2004; Wasserman and Chapman, 2003; Platyrrhini: Peres, 1997).

However, most of these efforts have been concentrated on African & Asian folivores, while less attention has been paid to New World species characterized by a different digestive morphology (But see Milton, 1980; Peres, 1997).

Nevertheless, there has been mounting evidence to suggest similar patterns may exist in the Neotropics. The most folivorous Neotropical primate is the howler monkey (genus *Alouatta*), and although they are characterized as a folivore-frugivore because they have the behavioral flexibility to include large amounts of fruit in their diet, many species and/or populations consume leaves as the primary component for most of the year (e.g., Milton, 1979; Julliot, 1996; Lopez et al., 2005). As such, howler monkey density can be tied directly to the quality and quantity of available resources in a habitat. Peres and colleagues (Peres, 1997; Haugaasen and Peres, 2005) have found that the single best predictor of *Alouatta* densities in central lowland Amazonia is the distance to major white water rivers, which co-varied with forest heterogeneity and soil fertility.

White water rivers originate in the young and easily erodible landscapes of the Andes Mountains and, because of this, carry with them large amounts of nutrient rich suspended sediments (Peres, 1997) and typically have a higher pH level that is more hospitable for plant growth and production (Mengel and Kirkby, 2001). Forests in close proximity to these rivers, called varzea, are annually flooded up to six months each year and the seasonal influx of nutrients results in these forests being exceptionally productive (Peres, 1997; Haugaasen and Peres, 2005). Due to these seasonal inundations, soils in varzea habitats are more fertile than those in non-flooded, or *terra firme*, forests resulting in lower levels of secondary defenses in the leaves because nutrient uptake is less limited (Janzen, 1974). In this situation, the plant metabolic costs of replacing leaf tissue lost to herbivores are relatively low, and the foliage quality is presumed to be more favorable for arboreal folivores (Janzen, 1974; Haugeaasen and Peres, 2005). Furthermore, the macronutrient renewal and flood disturbance of the soils every year in varzea forests may increase overall resource production and generate a more heterogeneous environment with a greater diversity of successional habitats (Haugaasen and Peres, 2005). Habitats that have a high diversity of successional habitats would tend to produce phenological stages at different times of the year, providing alternative resources during periods of general food scarcity (Haugaasen and Peres, 2005). An overall higher productivity of resources throughout the year, or during periods of relative food scarcity, would allow for a higher carrying capacity and possibly higher primates densities (Terborgh, 1983; Haugaasen and Peres, 2005).

In contrast, flooded forests adjacent to nutrient-poor black water rivers originating in the lowlands, known as igapós, are chemically different from the white waters of upper Amazonia and appear to support lower howler monkey densities (Peres, 1997). However, both varzea and igapó flooded forests have been found to have higher densities of howler monkeys in comparison to *terra firm* forests, which are never inundated and thus have leached soils lower in nutrients (Peres, 1997). It is possible, however, that the association of howler monkeys with flooded forest ecosystems may not hold true in all parts of the Amazon. Iwanaga and Ferrari (2002) surveyed *Alouatta* in flooded and unflooded regions throughout the Brazilian state of Rondônia in southwestern Amazonia, and found that howlers were only present at one-third of the thirty-six sites surveyed, and absent from most of the floodplains adjacent to white water rivers. Furthermore, in areas where howler monkeys were present, they were relatively rare, especially in comparison with sympatric atelids (*Ateles* and *Lagothrix*). It is clear that habitat ecology greatly influences the density of *Alouatta* in the Neotropics, but the exact factors affecting differences in their abundance in different regions of Amazonia still remain somewhat unresolved. In order to gain a better understanding of whether small scale variations in habitat ecology are affecting *Alouatta* density, it is necessary to conduct local comparative studies of populations occurring at different densities in different forest types.

This approach is the focus of the current study, which is investigating small-scale ecological patterns between two Western Amazonian sites in Ecuador, South America that are geographically close in proximity but differ in habitat type and primate density. Specifically, this paper presents comparative ecological data from a small scale micro-habitat perspective on the vegetation structure, diversity and phenology as well as soil nutritional content. In addition, I test the following hypotheses regarding ecological influences on howler monkey density: Higher howler monkey population density should be associated with 1) higher overall stem density indicative of higher food abundance and hence a greater carrying capacity of the habitat, 2) higher floristic diversity (as a proxy for a more heterogeneous habitat) indicative of a high diversity of successional habitats and thus a greater availability of alternative resources during times of low food abundance, 3) higher annual phenological productivity reflecting higher food productivity throughout the year and 4) higher soil fertility as evidenced by higher levels of macronutrients and a pH level hospitable for growth and production (i.e., closer to the range of 6- 6.5).

3.3 Background

Yasuní National Park (YNP) is a 900,000 km^2 area in Eastern Ecuador that conserves one of the larger contiguous tracts of western Amazonian rainforest. The region is characterized by extreme faunal and floral biodiversity including the highest known biodiversity of insects in the world (> 100,000 species of insects/ha) and over 1,576 plant species (Koester, 2001; Nabe-Nielson, 2001; Scientists Concerned for Yasuní Technical Advisory Report, 2004). YNP is also home to 173 mammals including 10 primate species, two of which appear as Vulnerable on the IUCN Red List (*Ateles belzebuth* and *Lagothrix poeppigii*: Rylands et al., 2003a, b).

Geologic history

Geologic parent material is the mass from which a soil is formed and is primarily responsible for the chemical and mineralogical composition of soils. This parent material in YNP is relatively young alluvium from the Andean mountain range dating from the upper Miocene to perhaps even the Pliocene (Pitman, 2000). The region is dominated by massive blocks of upland or *terra firme* forest that is bisected by streams and rivers and interspersed with narrow bands of riparian forest (Pitman, 2000). Upland soils in YNP are characterized as reddish, acidic, and low in most cations but rich in iron and aluminum, and are tentatively classified as Ultisols (N. Pitman unpublished data).

According to a composite geologic map of the area published by the Ecuadorian Ministry of Energy and Mines in 1987, the dominant parent material in YNP is the Curaray (also known as Pebas) Formation, replaced in some places by the adjacent and possibly younger Chambira Formation (Hoorn, 1983; Räsänen, 1998). Both formations are essentially kilometer-thick slabs of clay and sandstones

(INEMIN, 1987; HBT AGRA, 1993), however they are not homogeneous. Rather, due to a pattern of deposition that resulted in a network of rivers and lakes over millions of years, they are small-scale mixtures of ancient sandbars, silty floodplains, and clayey lake bottoms (Pitman, 2000).

Yasuní is bounded to the north by the Rio Napo and to the south by Rio Curaray, two large so-called white-water rivers originating in or near the Andes (Pitman, 2000). These rivers differ from those originating in the lowlands in that they carry a higher sediment load, follow a slightly more seasonal flooding regime (because seasonality of rainfall on the eastern slopes of the Andes increases with elevation), and show higher nutrient concentrations, though quantitative comparisons have yet to be made (Balslev et al., 1987; Colinvaux,1988; Pitman, 2000).

The interior landscape is drained by intermediate-sized rivers originating in the lowlands (e.g., the Tiputini) that are referred to as black-water rivers (Balslev and Renner, 1989; Herrera-MacBryde and Neill, 1997). However, their relatively high sediment load makes them intermediate between white and black (Kalliola and Puhakka, 1993; Pitman, 2000). True black-water —sediment-free and with extremely low pH— does occur in Yasuní, but mostly in the form of small streams (Pitman, 2000).

The elevation in YNP is between 190 and 350 m above sea level and includes a variety of topographic elements (Di Fiore, 1997). For example, the region has been characterized as ranging from completely flat areas in swamps and floodplains to terraces separated by narrow ravines to rolling hills as well as ridge systems characterized by near-vertical cliff-faces (Pitman, 2000). These topographic features do not generally occur together in a small area, but form large and rather uniform patches on satellite images of the area (Pitman, 2000).

Soils

Generally speaking, soils in YNP appear to be rather homogeneous (Pitman, 2000). Previous published surveys classify soil in the same order and suborder of the Soil Taxonomy system, as Ultisols and Udults respectively (Kapos et al., 1990; Korning et al.,1994; Pitman, 2000; Woodward, 1996). These surveys were almost exclusively conducted in upland areas (~90% of the landscape) and indicate that while color and texture can vary dramatically on scales of just a few meters, most samples are clayey, acidic, low in most cations but rich in aluminum and iron, and lacking rocks and pebbles (Kapos et al., 1990; Korning et al., 1994; Woodward, 1996; N. Pitman, unpublished data).

However, site differences can occur and are largely influenced by proximity to rivers and flooding, either in swamps or in floodplains (Pitman, 2000). For example, soils from a floodplain forest along the Napo River were found to be less acidic than those from *terra firme* sites, not as rich in aluminum and iron but richer in other nutrients, and with more organic carbon (Kapos et al., 1990). Soils in swamps are likely classified as Histosols, i.e., peaty soils with a high proportion of organic matter (Pitman, 2000).

Climate

YNP is a moist, aseasonal, hyperdiverse lowland forest near the equator (Clinebell et al., 1995; Pitman 2000). Rainfall averages ~3,200 mm annually and is technically aseasonal, with monthly means not falling below 100 mm (Pitman, 2000, Di Fiore and Rodman, 2001). Precipitation does, however, show a clear seasonal variation, with two peaks (from April to May and October to November) and two troughs (from January to February and August to September) per year and the rainiest month (May) averaging 72% more rain than the driest month (January; Pitman, 2000). Mean annual temperature is ~ 27 °C and is relatively constant throughout the year (Di Fiore and Rodman, 2001).

Tree diversity & structure

Recent studies looking at large scale diversity patterns of tree species within YNP (e.g., Balslev, 1988; Tuomisto, 1994; Pitman, 2000; Condit et al., 2002; Valencia et al., 1994, 2004) characterize the region as having ordinary gamma-diversity, which is the total number of species on a regional scale, with respect to other Amazonian regions and low rates of endemism with incredibly high alpha-diversity, defined as the total number of species in relatively small areas, such as 25 ha or less. Specifically, free-standing trees ≥ 10 cm DBH (diameter at breast height) number ~1,500 species, with only 1-2 % endemism, while at local scales the diversity of woody plants is among the highest in the world, averaging 229 species per hectare (range: 114-307, Losos and Leigh, 2004; Valencia et al., 2004).

The structure is a tall, generally around 30 m, closed-canopy forest and the important woody plant families in YNP are similar to those that hold sway over other forests throughout the Neotropics —Fabaceae *sensu latu,* Arecaceae, Rubiaceae, Melastomataceae, Lauraceae, Annonaceae, Moraceae, Sapotaceae, etc — (Gentry, 1988;

Gentry, 1990, Pitman, 2000). The floristic composition indicates that trees, treelets, lianas, and shrubs dominate the flora, complimented by a relatively weak herbaceous and epiphytic community (Pitman, 2000).

Anthropogenic influence

YNP is categorized as a 'strict protected area' under the IUCN (Franzen, 2006). However, in addition to oil development permitted inside the boundaries, there are no restrictions on colonization or use of resources by indigenous inhabitants (Franzen, 2006). Adjacent to YNP there are 6100 km^2 designated as the Waorani Ethnic Territory in which earlier studies have estimated the population to be between 1500-2000 individuals (Lu, 1999, 2001). However, this figure likely underestimates the current population due to the increase in human colonization by indigenous ethnic groups that YNP has experienced over the last decade (Koester, personal communication; Derby personal observation, this study).

The influx of human habitation is largely due to the construction of a road built in the early 1990's by the oil company Maxus Energy Corporation, attracting people from other areas who established permanent settlements along it because of the ease of mobility it provides (Franzen, 2006). Rural development, and roads in particular, provide greater access to areas of the forest that otherwise would not have been accessible to hunters (Peres, 1999; Wilkie et al., 2000). Recent data indicate this is occurring within YNP and that the Maxus road has led to increased subsistence hunting, threatening the local depletion of large bodied primates in areas of persistent hunting (Franzen, 2006). Data from this study indicates that areas closer in proximity to indigenous communities where hunting is known to occur have slightly lower densities of most species, and significantly lower densities of large bodied taxa versus small and medium size taxa, compared to areas where no hunting has been observed (see Chapter 2). However, when all species are compared, there is not a significant relationship between, on the one hand, the comparative density ratio for each of the species in the hunted versus the non-hunted region and, on the other, annual hunting rates recorded by Franzen (2006), as would be expected if larger-bodied primates were differentially harvested to the point where that harvest has a measurable effect on the population.

3.4 Methods

Study Sites

The study was conducted at two sites within YNP. The first is located 47 km along the petroleum access road (75°28'W, 0°42'S) and is the long-term primate field site Proyecto Primates Research Area (PPRA) that was established in the mid-nineties (Dew, 2001; Di Fiore, 1997; Di Fiore and Rodman, 2001; Spehar, 2006; Suarez, 2003). PPRA is approximately 11 km inland from the nearest major river and encompasses approximately 650 hectares. It is comprised almost entirely of primary *terra firme* tropical rainforest with a road that borders the area on two sides (Di Fiore, 1997); however it is spread out over a series of ridges and minor drainages that feed several small but permanent streams (Di Fiore, 1997). During the rainy season, these streams can swell and inundate the areas in immediate proximity to the streambeds for several weeks per year (personal observation, this study). Due to regular researcher presence and a long-standing agreement with two nearby Waorani communities, this site has experienced very low levels of hunting over the last decade compared to that of the surrounding area. This low level of hunting has mainly occurred during periods of researcher absence (A. Di Fiore, personal communication).

The second site, Tiputini Biodiversity Station (TBS), is also a 650 ha area bordering the Tiputini River which is considered a hybrid of both white and black water sources (Pitman, 2000). TBS contains some areas that are periodically flooded for up to two months per year by the river. It is located further from the Waorani communities and thus far hunting has not been reported at TBS. The PPRA and TBS study sites are approximately 40 km apart from each other (Figure 1) and part of larger, contiguous tracts of land in the region. They contain the same 10 species of primates, but the overall population density and biomass of the primate community is lower at PPRA compared to TBS (see Chapter 2). Total primate biomass at PPRA is 284.19 kg/km^2, with 33.3 kg/km^2 represented by howler monkeys, while at TBS it is 410.54kg/km^2 with howler monkeys comprising 76.26 kg/km^2. The difference reflects a howler monkey biomass that is 2.3 times higher at TBS than at PPRA (see Chapter 2).

Botanical Plot Sampling

A total of six 500m x 10m phenological transects were randomly placed at PPRA and TBS, with three transects (totaling one and half hectares) located in each site. Along each transect, 10m x 10m blocks were measured out and all trees ≥ 10 DBH (130 cm from the upslope base of the tree), a minimum size shown to be used by howler monkeys (Milton, 1980), were tagged, mapped, and measured. Trees were identified by botanists with long term expertise of YNP woody plant species (M. Zambora, P. Alvia, S. Queenborough), and monitored for phenological activity.

Tree Phenology

To determine the productivity and seasonal availability of resources, phenological transects were walked once monthly (N = 11 months; February-December 2005) to monitor for phenological activity during approximately the same time period at both sites. Every tree was given qualitative scores for each visible phenophase and the amount of each phenophase was then recorded using both a semi-quantitative index for fruit (i.e., $\log_{10}$ scale following Janson and Chapman, 1999) and a percentage scale for new leaves (i.e., 1-5, 6-10, 11-25, 26-50, 51-75, 76-100), flower buds and mature flowers (i.e., 0-25, 26-50, 51-75, 76-100). Fruit quantifications were done by counting the total number of fruits in a portion of the crown and extrapolating this to the whole crown volume, while percentages for new leaves, flowers and flower buds were evaluated by the proportion of flushing or flowering exhibited in comparison to the total tree crown.

Soil Collection and Analysis

Soil samples were taken from 10 random locations along the botanical transects at each site, following the guidelines recommended by the Cornell Nutrient Analysis Laboratory (CNAL). A stainless steel soil probe was used to obtain 2 samples at each location (each at least 1.5 cups of soil): 1) a surface sample from 0- to 8-inch depth and 2) a subsoil sample from the 8- to 24-inch depth that were combined and analyzed together. Samples were spread into a thin layer on waxed paper and allowed to dry at room temperature before being stored in sealed plastics bags. They were then transported to the US and analyzed at Cornell Nutrient Analysis Laboratory upon return from the field for levels of pH, P, K, Ca, Mg, Fe, Mn, Cu, Zn, Al, NO_3, and organic matter (OM) (following Peres, 1997).

Samples were taken on two occasions at similar times at both sites during the 12-month study period. One sample was taken prior to the seasonal flooding that occurred (March) and the second was taken directly after inundation had subsided (August). Although only TBS was seasonally flooded by the large Tiputini River, inundating parts of the forest for up to two months throughout year, there were areas at PPRA that were in close proximity to small streambeds that also swelled during the rainy season and covered the immediate surrounding substrate with water for several weeks during the year. Areas flooded by water at both sites, regardless of the source or for how long, were regarded as riparian microhabitats. Generally speaking, the term riparian refers to land adjacent to a body of water such as a river, stream, pond, lake, etc. (Cooper, 1990), and samples from these areas were distinguished from others collected from forest areas that were not ever flooded. Although there were three transects at each site, samples from the pre-flooding period at PPRA were only analyzed from transects one and three (Pre-flooding samples from PPRA: T1, T3; TBS: T1, T2, T3). In addition to re-sampling the same areas during the post-flooding period, samples were collected from T2 at PPRA as well. Furthermore, samples were also collected from an area that occurred near a streambed along T1 and analyzed separately from the rest of the samples from this transect which came from non-flooded areas (Post-flooding samples from PPRA: T1, T1a, T2, T3; TBS: T1, T2, T3).

The specific analytical methods for soil nutrients were as follows: 1) pH was determined on a 1:1 (by volume) soil: water or soil:1.01 M CaCl2 suspension, 2) all major and minor nutrients were extracted by Morgan's solution, 10% sodium acetate in 3% acetic acid buffered to pH 4.8, using a 1:5 (by volume) soil: solution ratio; all results are reported in standard units ppm (parts per million), 3) P was colorimetrically determined using stannous chloride and ammonium molybate reagents, 4) NO_3 levels were colorimetrically determined using a cadmium reduction, and 5) organic matter (OM) was determined by loss on ignition (LOI). Lastly, soil content was examined in several different contexts. The first was to test for differences between pre-flooding and post-flooding periods. Next, the pre-flooding and post-flooding data sets were separately tested for differences between 1) sites (TBS and PPRA) and 2) microhabitats (Riparian versus Non-riparian).

Statistical Testing

To examine differences in total stem density, tree DBH and total basal area, Mann Whitney U Tests (Siegel and Castellan, 1988) were performed on these data sets. Non-parametric tests were used in these cases because their distributions differed significantly from the expected normal distribution due to a higher number of small and medium trees compared to larger trees within the plots.

The Simpson's Diversity Index (D) was used to calculate the diversity of species at the sites (Simpson, 1949). This index ranges from 0-1, representing infinite diversity to no diversity, respectively, and thus smaller D values are indicative of higher diversity levels. This diversity index takes into account the number of species present as well as the abundance of each species by measuring the probability that two individuals randomly selected from a sample will belong to the same species. A Mann Whitney U Test (Siegel and Castellan, 1988) comparing the three transects at each site was then applied to these data in order to examine differences in total site diversity.

Phenological patterns were analyzed in three ways. The first was to compare the percentage of trees scored in each phenophase per month between sites and the second was to compare the total amount of each phenophase produced per month between sites. A Wilcoxon Matched Pairs Test (Siegel and Castellan, 1988) was applied to both of these data sets. The third analysis used a three-way factorial ANOVA to look at the main, as well as the interactive effects, of flooded versus non-flooded transects, months, and sites on phenological patterns (Sokal and Rohlf, 1995).

Finally, soil nutrients were analyzed in several different ways. First, a Wilcoxon Matched Pairs Test was performed (Siegel and Castellan, 1988) in order to examine whether overall differences between pre-flooding and post-flooding period occurred. Next, pre-flooding and post-flooding periods were then analyzed separately for differences between 1) sites and 2) riparian and non-riparian microhabitats and multiple Mann Whitney U Tests (Siegel and Castellan, 1988) were applied to the soil nutrients within these data sets.

3.5 Results

Forest Structure

The total number of stems occurring per 1.5 ha at TBS was 909 versus 738 at PPRA and there was an overall higher mean stem count per 0.5 ha (or per transect) at TBS (mean = 303, SD = 51.5) compared to PPRA (mean = 246, SD = 65.9). The latter, however, did not differ significantly between sites (Mann-Whitney U Test: N = 6, U = 2.00, Z = -1.09, $P > 0.05$). Overall, there was an overlap between the sites in the number of stems per transect (Table 1: TBS range: 251-354; PPRA range: 185-316). At TBS, the mean tree DBH was found to be significantly larger (Figure 2: Mann Whitney U Test, U = 289986.00, Z = -2.54, P = 0.01, Mean_{TBS}: 22.02 (SD = 14.91) N = 870; $\text{Mean}_{\text{PPRA}}$: 20.73 (SD = 14.07), N = 738). Additionally, the total basal area for all trees (m^2/1.5 ha) was also higher at TBS (48.7 m^2/1.5 ha) versus PPRA (35.3 m^2/1.5 ha) and the difference in mean tree basal area was significant between sites (Mann Whitney U Test, U = 289651.00, Z = -2.58, P = .01, Tree Mean_{TBS} = .056 ha/m^2 (SD = 0.11), N = 870; Tree $\text{Mean}_{\text{PPRA}}$ = 0.49 (SD = 0.10), N = 738).

Forest Diversity

The same number of plant families occurred at TBS and PPRA (N = 47), with an 81% overlap of families between sites (Table 2). The number of genera was similar (TBS: 153 genera; PPRA: 155 genera), but there was a slightly higher number of species occurring at TBS (N = 295 species) compared to PPRA (N = 261 species). When a Simpson's Diversity Index is applied, values at both sites were indicative of hyperdiversity at the species level (Table 2: Simpson's Index (D): D_{TBS}: 0.025; D_{PPRA}: 0.013, $P < 0.05$), overall as well as per transect, although this diversity is significantly higher at PPRA, reflected by its lower D value (Mann Whitney U Test: U = 0.00 Z = -1.96, $P < 0.05$).

Importance Values (IV's), which are the summed values of the relative frequency, relative density, and relative basal area, calculated at the family level found the two sites shared eight of their top ten families with the highest values (Figure 3: IV range for all families at TBS: 0.23 - 75.5; PPRA: 0.32 - 24.80). However, among the top ten highest values at the species level, the sites shared only three taxa (Figure 4: IV range for all species at TBS: 0.23-21.30; PPRA: 0.31-21.10). The species with the highest IV at both sites was *Iriartea deltoidea* (Palmae: TBS IV: 21.30; PPRA IV: 21.10), while the second was *Otoba glycicarpa* (Myristicaceae) which was ranked number two at TBS (IV = 9.38) and seven at PPRA (IV = 4.15) and the third was *Brownea grandiceps* (Fabaceae: TBS IV = 8.08, PPRA IV: 4.23) which ranked fourth at TBS and fifth at PPRA (Figure 4). Over half of the species, 52.2%, at TBS occur only once per 1.5 ha (154 of the 295 species) while 95% of them occurred 10 or fewer times (279 species). A similar pattern characterized the floristic diversity at PPRA, showing 55.5% of the species occurred only once within the plots (145 of the 261 species) and 98.5% occurred 10 or fewer times.

Forest Phenology

In the first comparison, the monthly percentage of individuals in each phenophase did not differ significantly between sites, although it was found to be higher or the same at PPRA compared to TBS (Wilcoxon Matched Pairs Test, N = 11 months, new leaves: T = 18, Z = 1.33, P = 0.18, flower buds: T = 18, Z = 1.33, P = 0.18, mature flowers: T = 27, Z = 0.53, P = 0.59, fruits: T = 28, Z = 0.44, P = 0.65), although the temporal patterns of when the peak percentage of trees in each phase occurred were rather different. For example, while the percentage of trees observed to have new leaves and flowers present was highest in April at TBS, these phases did not peak until September and August, respectively, at PPRA. Additionally, the percentage of trees with flower buds and fruits were highest in October and February, respectively, at TBS while they both did not peak until December at PPRA (Figure 5a).

In contrast, the average monthly percentage of each phenophase in the canopy of all trees did differ significantly (calculated as the percentage of crown for new leaves, flower buds, and mature flowers and the total habitat-wide crop for fruits; Figure 5b). The total amount of new leaves, flower buds, and mature flowers were significantly higher at TBS (Wilcoxon Matched Pairs: N = 11 months, new leaves: T = 11.0, Z = 1.96, P = 0.05, flower buds: T = 0.0, Z = 2.93, P = 0.003, mature flowers: T = 8.0, Z = 2.22, P = 0.026) while the amount of fruit did not differ (Wilcoxon Matched Pairs: N = 11 months, fruit: T = 23, Z = .89, P = 0.37).

When a three-way factorial ANOVA is performed on the data, with flooding, months, and sites as independent variables and phenology as the dependent variable, the overall model is significant in all cases (Table 5). Looking first at the main effects, the variable of flooded versus non-flooded transects is significantly different for the average monthly percentage of trees with mature flowers ($P < 0.05$) and the average monthly percentage of trees fruiting ($P < 0.05$), as well as the average monthly percentage of fruit produced ($P < 0.01$). There was a higher average monthly percentage of fruit produced on flooded transects at both sites, but the pattern for flowers was different between sites. At PPRA flooded transects had a significantly lower average monthly percentage of trees flowering, while this was higher on flooded transects at TBS. Next, looking at months, all phenological categories are significantly different ($P < 0.05$), except for the average percentage of flower buds produced. This indicates that there is an overall trend for phenological differences between months, which is not surprising given that phenophases are, at least to some degree, seasonal. There are significant differences between sites in all categories as well, except for the average monthly percentage of trees with flower buds and with fruit. These results indicate that the phenology between sites differs, corresponding with earlier results showing the average amount of new leaves, flower buds, and mature flowers produced to be significantly higher at TBS (see above).

The interaction effect of flooding and months is not significant for any phenological category, although it approaches significance for the average monthly percentage of fruit produced ($P = 0.050$). The effect of transect flooding and sites is significantly different for only two variables, the average monthly percentage of trees with flower buds and mature flowers ($P < 0.05$), shown to be lower in flooded sites at PPRA but higher in flooded sites at TBS. The overall pattern in the flooded transects at PPRA is a lower average monthly percentage of trees in all phenophases and a lower or similar average percentage of each phenophase produced with the exception of fruit, which was higher (Table 5). The flooded transects at TBS showed a slightly higher or similar average monthly percentage of trees in all phenophases and, like PPRA, the average percentage of each phenophase produced is lower or similar, with the exception of fruit which was also high. There is a mixed signal when examining the interaction effect of months and sites. Four out of the eight variables are significantly different ($P < 0.01$; as well as the average percentage of leaves approaching significance, $P = 0.058$), but the remaining 3 variables have P values greater than 0.10. Finally, when considering the combined effect of flooding, months and sites together, only the average monthly percentage of fruit produced approaches significance ($P = 0.058$) while all categories have P values greater than 0.10.

Soil Nutrients

The nutrient content of the soil was first examined for overall differences between pre-flooding and post-flooding periods. There were five transect pairs that could be analyzed and compared (PPRA: T1, T3; TBA: T1, T2, T3). The results showed that levels of Mn were significantly higher and Al significantly lower after flooding occurred at both sites (Table 3, Figure 6: Wilcoxon Matched Pairs Test: N = 5 transects; T = 0.00, Z = 2.02, P = 0.04)

Soil nutrients from pre-flooding and post-flooding periods were then analyzed separately for differences between 1) sites and 2) riparian and non-riparian microhabitats (Table 4). During the pre-flooding period, no differences in soil nutrients between sites or microhabitats were found. However, the post-flooding samples from riparian microhabitats were found to be higher in pH, Ca, and Mg than non-riparian at both sites (Figure 7a-c: Riparian mean pH = 4.76 (SD = 0.26), mean Ca = 2814.33 (SD = 677.07), mean Mg = 543.23 (SD = 157.42); Non-riparian mean pH: 4.27 (SD = 0.19), mean Ca = 598.25 (SD = 403.44), mean Mg = 118.80 (SD = 58.14)). Furthermore, when the post-flooding samples from riparian transects at both sites were combined and compared to all non-riparian transects, the levels of pH, Ca, and Mg were significantly higher (Table 4). It is also noteworthy that even though non-significant, many of the pre-flooding comparisons indicated a difference shown by P-values below 0.1. Thus, while no overall significant differences were found between sites, the riparian transects at both sites were significantly higher in several macronutrients.

3.6 Discussion

Forest Ecology

The first aim of this paper was to present comparative ecological data from a small scale micro-habitat perspective on the vegetation structure and diversity, phenology and soil nutritional content. The data suggest that several differences occur between the two sites, despite being geographically close in proximity. TBS had a significantly higher tree DBH, basal area, and annual production of leaves, flower buds, and flowers. In addition, while plant diversity at the family and genus level was similar between sites, PPRA had significantly higher species diversity. The diversity values at both sites are indicative of hyperdiversity (Losos and Leigh, 2004), but PPRA's higher index supports previous research showing *terra firme* habitats were typically higher in species diversity compared to seasonally flooded, or varzea, habitats (e.g., Campbell et al., 1986). It is evident, however, that the habitats at TBS and PPRA are dominated by the same species, *Iriartea deltoidea* (Palmae), which has almost identical IV's values at both sites (TBS IV: 21.30; PPRA IV: 21.10). This species produces large quantities of fruit that most primate taxa, and other mammals, were observed to feed on throughout the year. This species not only dominates these sites in Ecuador, but apparently other regions in Western Amazonia, such as Peru, as well (Pitman, 2000). This pattern raises several questions, for example: why is the population density of the species so constant over such large areas of forest in western Amazonia, why is a species that is dominant over large areas of upper Amazonia sparse or absent in the central and eastern portions of the basin, and do the same animals disperse the fruits and pollinate the flowers of *Iriartea* across different forests (Pitman, 2000). Lastly, while there were no overall significant differences in soil nutrients between sites, there were differences between the microhabitats within the sites.

Specifically, soil samples were collected along phenological transects that were placed randomly throughout the habitats and encompassed both flooded and non-flooded areas throughout each study site. Although only TBS, situated on the Tiputini River, had areas which were flooded for approximately two months, there were sections along two of the transects at PPRA that were situated near streambeds that swelled and flooded the immediate adjacent area for several weeks. Samples from these areas, termed riparian, were higher in pH, Ca, and Mg than samples from non-riparian areas. When the riparian samples from both sites were combined and compared to all non-riparian samples, these differences were significant. This implies that areas flooded with water, regardless of how long, appear to have higher levels of certain secondary macronutrients and a higher pH level, which can all affect plant growth and productivity (Campbell et al., 1986).

Both Ca and Mg are important to plant growth, for example Ca is an essential part of plant cell wall structure, provides normal transport and retention of elements as well as strength in the plant, and it is thought to counteract the effect of alkali salts and organic acids within a plant (Mengel and Kirkby, 2001). On the other hand Mg is part of the chlorophyll in all green plants and essential for photosynthesis, it also helps activate many plant enzymes needed for growth (Mengel and Kirkby, 2001). The soil pH can greatly affect the solubility of minerals or nutrients such that strongly acid soils (pH 4.0-5.0) can have high concentrations of soluble Al, Fe and Mn which may be toxic to the growth of some plants (Mengel and Kirkby, 2001). Thus, a pH range of approximately 6 to 6.5 promotes the most ready availability of plant nutrients (Mengel and Kirkby, 2001).

Additionally, soil pH can influence plant growth by its effect on the activity of beneficial microorganisms. Bacteria known to decompose soil organic matter are hindered in strongly acidic soils, preventing organic matter from breaking down and resulting in an accumulation of organic matter and the tie up of nutrients, particularly nitrogen, that are held in the organic matter (Mengel and Kirkby, 2001).

Soils from this study were not only found to be lower in Al post-flooding, but riparian areas had a higher average pH (Mean: 4.76, Range: 4.55-5.05, N = 3) than non-riparian areas (Mean: 4.27, Range: 4.00-4.41, N = 4) which may make them a more hospitable substrate for plant growth. It is possible that because TBS has a more extensive area of flooded forest, and thus a larger area characterized by higher soil fertility and more hospitable pH levels, there is higher nutrient availability which may contribute to the higher plant growth (DBH and basal area) and phenological productivity (leaves, flower buds, and flowers) observed at this site, and thus supporting a howler monkey population density.

In order to directly evaluate whether higher soil fertility in flooded areas actually correlates to higher phenological productivity, we can examine the results from the three-way factorial ANOVA. This analysis showed that the flooded transects at PPRA had lower percentages of trees in each phenophase, while those at TBS had higher. On the other hand, flooded transects at both sites were found to actually have either lower or similar average monthly percentage of each phenophase produced compared to the non-flooded transects. With the exception of the average amount of fruit, which was higher in flooded transects at both sites, there is little support from this study to suggest that the small-scale variation in nutrients/pH on flooded transects has a large effect on overall food availability.

Possible Ecological Influences on Howler Monkey Population Densities

The second aim of this paper was to test the following hypotheses regarding ecological influences on howler monkey density: Higher howler monkey population density should be associated with 1) higher overall stem density indicative of higher food abundance and hence a greater carrying capacity of the habitat, 2) higher floristic diversity (as a proxy for a more heterogeneous habitat) indicative of a high diversity of successional habitats and thus a greater availability of alternative resources during times of low food abundance, 3) higher annual phenological productivity reflecting higher food productivity throughout the year and 4) higher soil fertility as evidenced by higher levels of macronutrients and a pH level hospitable for growth and production (i.e., closer to the range of 6- 6.5).

At the site with a higher howler monkey population density, TBS, the ecological data show support for hypothesis three and, to some extent, hypothesis four. Resource abundance, proposed to be the primary determinants of mammalian, including primate, abundance (Terborgh and van Schaik, 1987; Davies, 1994) was higher in the form of leaves, flower buds and flowers at TBS. Additionally, a significantly higher DBH (and basal area) was found at TBS, which may contribute to higher resource productivity. Although the inferential link between primate biomass and food productivity when using rainfall as a correlate is somewhat weak (for a review, see Janson and Chapman, 1999) several studies have found that primate biomass is positively related to food abundance using other ecological variables. For example, the biomass of gibbons (including siamangs) in south-east Asia was shown to be almost perfectly correlated with the density of fig trees (Mather, 1992). In addition, howler monkey densities in particular have been found to be positively correlated with food abundance, estimated using the average DBH, in regenerating forests of Central America (*A. palliata*: Sorensen and Fedigan, 2000). Thus it appears that higher resource abundance, and greater tree DBH, may be influencing the differences in howler monkey density at Yasuní as well.

In addition, while there are no differences in soil nutrients between sites, TBS has a larger area characterized by riparian or flooded forest, which were found to be higher in important macronutrients along with a more hospitable pH. These data illustrate partial support for work showing that the single best predictor of *Alouatta* densities in central lowland Amazonia is the distance to major white water rivers (Peres, 1997; Haugaasen and Peres, 2005). There was some evidence found to support the idea that areas with higher soil fertility have greater food productivity. In particular, flooded transects had significantly higher percentage of fruit production, and the flooded transect at TBS was significant higher than PPRA, but no differences were found for young leaves, flower buds, or flowers. It raises the question whether fruit, versus leaf, production is more influential for howler monkeys. However, there is no strong evidence to support this based on the diets of focal groups that were studied at the two sites (see Chapter 4).

There are two possible reasons that distinct site differences were not found in this study. One may be because the Tiputini River is a white- and black-water hybrid, and the content of nutrient rich suspended sediments may not be as high as that of pure white-water rivers (Peres, 1997). Also, the forest at TBS is only flooded for about two months per year, compared to true varzea habitats which annually flood up to six months (Peres, 1997; Haugaasen and Peres, 2005). However, regardless of the inundation period in this study (PPRA: 2 weeks; TBS: 2 months) riparian habitats had significantly higher soil fertility than did non-riparian. It has been suggested that the more fertile soils in varzea forests may result in lower levels of secondary defenses in the leaves because nutrient uptake is less limited (Janzen, 1974). Furthermore, the availability of mineral nutrients in tropical soils generally correlates well with nutrient availability in the plants growing on them (Vitousek and Sanford, 1986; Janson and Chapman, 1999). This aspect of plant nutrition will be presented and discussed in the following chapter, along with a multivariate approach that tests the predictive power of multiple ecological variables on the observed patterns of *Alouatta* behavior.

Recent research comparing patterns of plant diversity and distribution at a larger regional spatial scale within Amazonian forests characterized as lowland *terra firme*, such as Yasuní, Ecuador and Manu Peru, described the forest structure of Yasuní as homogeneous (Pitman et al., 2002). While this may reflect the large scale pattern when compared to other Amazonian regions, it is important to recognize that small scale local patterns within Yasuní also occur and can potentially influence the floral and faunal communities associated with them. This study not only provides evidence that small scale ecological differences occur in lowland Ecuadorian Amazon, but that red howler monkey population densities may be affected by these differences in phenological productivity.

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3.8 Tables and Figures

TABLE 1: Forest structure at the two sites PPRA and TBS. Given are mean total stem density, total basal area, and Simpson's Diversity Index for the individual transects at each site.

Forest structure variable	**Site**					
	TBS			**PPRA**		
	T1	**T2**	**T3**	**T1**	**T2**	**T3**
Total # stems (0.5 ha)	251	304	354	237	185	316
Total basal area (m^2/0.5 ha)	10.9	19.2	18.6	12.5	8.0	15.0
Simpson's diversity index	0.027	0.029	0.030	0.014	0.018	0.019

TABLE 2: Comparative plant family diversity. X's indicate that species is present and dashes indicate a species is absent at a site.

FAMILY	TBS	PPRA
1. ANACARDIACEAE	X	X
2. ANNONACEAE	X	X
3. APOCYNACEAE	X	X
4. ARALIACEAE	X	X
5. ARECACEAE	-	X
6. BIGNONIACEAE	X	-
7. BOMBACACEAE	X	X
8. BURSERACEAE	X	X
9. CAPPARIDACEA	-	X
10. CARICACEAE	X	X
11. CECROPIACEAE	X	X
12. CELASTRACEAE	X	X
13. CHRYSOBALANACEAE	X	X
14. CLUSIACEAE	X	X
15. DICHAPETALACEAE	X	X
16. EBENACEAE	X	-
17. ELAEOCARPACEAE	X	X
18. EUPHORBIACEAE	X	X
19. FABACEAE	X	X
20. FLACOURTIACEAE	X	X
21. HIPPOCRATEACEAE	-	X
22. ICACINACEAE	X	X
23. LACISTEMATACEAE	-	X
24. LAURACEAE	X	X
25. LECYTHIDACEAE	X	X
26. LYTHRACEAE	-	X
27. MARCGRAVIACEAE	X	-
28. MELASTOMATACEAE	X	X
29. MELIACEAE	X	X
30. MEMECYLACEAE	X	-
31. MONIMIACEAE	X	X
32. MORACEAE	X	X
33. MYRISTICACEAE	X	X
34. MYRTACEAE	X	X
35. NYCTAGENACEAE	X	X
36. OLACACEAE	X	X
37. OPILIACEAE	-	X
38. PALMAE	X	X
39. PHYTELEPHAS	X	-
40. POLYGONACEAE	X	X
41. QUIINACEAE	X	X
42. ROSACEAE	-	X
43. RHAMNACEAE	X	-

44. RUBIACEAE	X	X
45. RUTACEAE	X	-
46. SABIACEAE	X	X
47. SAPINDACEAE	X	X
48. SAPOTACEAE	X	X
49. SIMAROUBACEAE	X	-
50. STAPHYLEACEAE	X	-
51. STERCULIACEAE	X	X
52. TILIACEAE	X	X
53. ULMACAEA	X	X
54. URTICACEAE	-	X
55. VERBENACEAE	-	X
56. VIOLACEAE	X	X
57. VOCHYSIACEAE	-	X

TABLE 3: Soil nutrient values for samples pre- versus post flooding

	Pre-Flooding (N = 5 transects)					Post-Flooding (N = 7 transects)						
Nutrients	**PPRA (1)**	**PPRA (3)**	**TBS (1)**	**TBS (2)**	**TBS (3)**	**PPRA (1)**	**PPRA (1a)**	**PPRA (2)**	**PPRA (3)**	**TBS (1)**	**TBS (2)**	**TBS (3)**
pH	4.84	4.66	5.02	4.17	4.55	4.41	4.68	4.37	4.55	5.05	4.00	4.31
P	0.97	1.08	0.00	0.00	1.91							
K	58.38	49.01	45.62	57.63	59.34	63.00	81.00	70.00	71.00	67.00	54.00	50.00
Ca	308.44	2228.96	1891.17	185.04	757.26	525.00	3560.00	1130.00	2238.00	2645.00	151.00	587.00
Mg	53.49	378.44	445.48	65.08	192.81	123.30	717.90	186.70	412.30	499.50	44.60	120.60
Fe	48.28	118.15	22.88	190.71	102.78	101.00	32.50	27.40	44.20	22.80	176.90	109.60
Mn*	13.64	102.12	83.14	10.42	35.14	40.40	151.30	169.20	113.30	141.10	13.40	96.90
Cu	1.16	2.91	2.67	0.63	0.57	0.00	0.40	0.00	0.00	1.00	0.00	0.00
Zn	0.61	2.19	1.14	0.56	3.11	1.29	2.58	2.28	1.02	2.78	2.33	1.16
Al*	908.54	448.06	248.47	563.73	822.94	531.60	246.30	160.60	249.60	133.30	536.80	475.10
NO3	8.22	0.00	0.00	19.17	9.82							
OM (LOI)	8.56	5.26	7.55	8.48	9.04	10.03	7.63	12.37	6.16	8.28	7.15	7.28

TABLE 4: Statistical values for comparisons of pre- and post-flooding soil nutrients between sites and microhabitats (Mann Whitney U Test)

Nutrients	Between Sites (TBS vs. PPRA)						Between Microhabitats (Riparian vs. Non-riparian)					
	Pre-flooding			Post-flooding			Pre-flooding			Post-flooding		
	U	Z	P level	U	Z	P level	U	Z	P level	U	Z	P level
pH	2.00	0.58	0.56	4.00	0.71	0.48	1.00	-1.15	0.25	0.00	-2.12	0.03*
P	2.00	0.58	0.56	1.00	1.77	0.08	2.50	0.29	0.77			
K	3.00	0.00	1.00	4.00	0.71	0.48	0.00	1.73	0.08	1.00	-1.77	0.08
Ca	2.00	0.58	0.56	3.00	1.06	0.29	0.00	-1.73	0.08	0.00	-2.12	0.03*
Mg	2.00	-0.58	0.56	4.00	-0.71	0.48	0.00	-1.73	0.08	0.00	-2.12	0.03*
Fe	3.00	0.00	1.00	3.00	1.06	0.29	2.00	0.58	0.56	2.00	1.41	0.16
Mn	2.00	0.58	0.56	1.50	-0.39	0.70	0.00	-1.73	0.08	3.00	-1.06	0.29
Cu	1.00	1.15	0.25	4.00	-0.71	0.48	0.00	-1.73	0.08	0.00	0.00	1.00
Zn	3.00	0.00	1.00	5.00	-0.35	0.72	2.00	-0.58	0.56	4.00	-0.71	0.48
Al	2.00	0.58	0.56	4.00	0.71	0.48	0.00	1.73	0.08	2.00	1.41	0.16
NO3	1.50	-0.87	0.39	4.00	0.71	0.48	0.00	1.73	0.08			
OM (LOI)	2.00	-0.58	0.56	1.00	1.77	0.08	0.00	1.73	0.08	4.00	0.71	0.48

TABLE 5: Comparative monthly phenology for all transects and flooded versus non-flooded at both sites. Values represent the percentage of 1) individual trees in each phenophase and 2) the average percentage of each phenophase in the canopy of all trees for leaves, flower buds and flowers; average number of fruits in the canopy of all trees.

		Total Monthly Average		Monthly Average Non-Flooded (NF) versus Flooded (F)			
Phenological Category		**PPRA**	**TBS**	**NF PPRA**	**F PPRA**	**NF TBS**	**F TBS**
Leaves	**% Trees:**	27.33	19.31	37.27	27.29	18.90	20.58
	Avg % produced:	7.79	12.52*	7.95	6.66	13.98	10.79
Flower buds	**% Trees:**	4.72	3.86	7.31	3.04*	3.64	4.43*
	Avg % produced:	20.49	30.21*	21.60	21.07	31.35	25.61
Mature flowers	**% Trees:**	1.67	2.01	2.54	0.79	1.78	2.59
	Avg % produced:	16.13	33.50*	21.47	7.54	32.26	33.56
Fruit	**% Trees:**	5.64	5.34	5.92	4.52*	5.49	4.81*
	Avg # produced:	749.88	1143.17	512.44	962.69*	1071.90	1334.11*

TABLE 6: Statistical values for comparisons of the effects that flooding, months, and sites have on phenological patterns (Three-way Factorial ANOVA). The quantitative categories for phenophase are1) the percentage of individual trees in each phenophase and 2) the average percentage of each phenophase in the canopy of all trees for leaves, flower buds and flowers; average number of fruits in the canopy of all trees.

Phenological Category		**Flood**	**Month**	**Site**	**Flooding X Month**	**Flooding X Site**	**Month X Site**	**Flooding X Month X Site**
Leaves	**% Trees:**	0.79	0.02*	0.01**	0.37	0.29	0.01**	0.43
	Avg % produced:	0.07	0.01*	0.01**	0.11	0.61	**0.06**	0.65
Flower buds	**% Trees:**	0.05*	0.01**	0.65	0.83	0.01**	0.16	0.87
	Avg % produced:	0.27	0.16	0.01**	0.6416	0.12	0.11	0.28
Mature flowers	**% Trees:**	0.19	0.01**	0.01**	**0.08**	0.03*	0.01**	0.67
	Avg % produced:	0.95	0.02*	0.01**	0.85	0.33	0.14	0.18
Fruit	**% Trees:**	0.02*	0.01**	0.68	0.88	0.42	0.01**	0.54
	Avg # produced:	0.01**	0.01**	0.01**	0.05*	0.98	0.01**	**0.06**

FIGURE 1: Map of the study sites in YNP

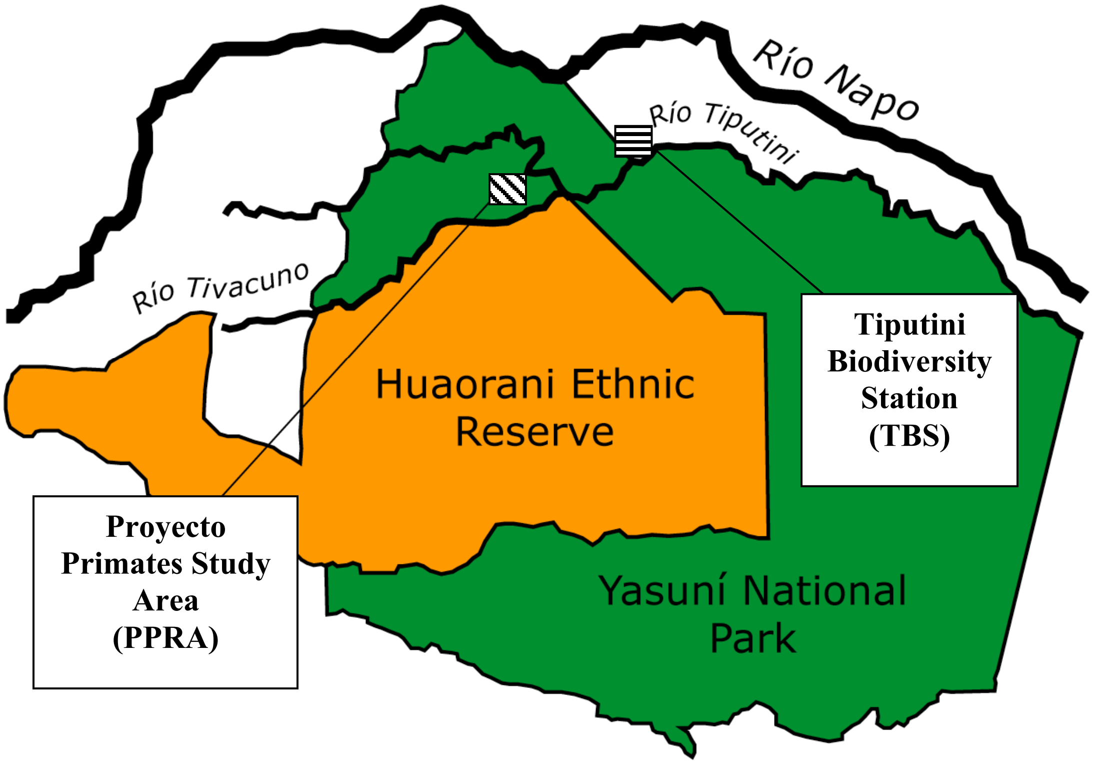


FIGURE 2: Mean tree DBH (trees ≥ 10 DBH) at the two study sites TBS and PPRA

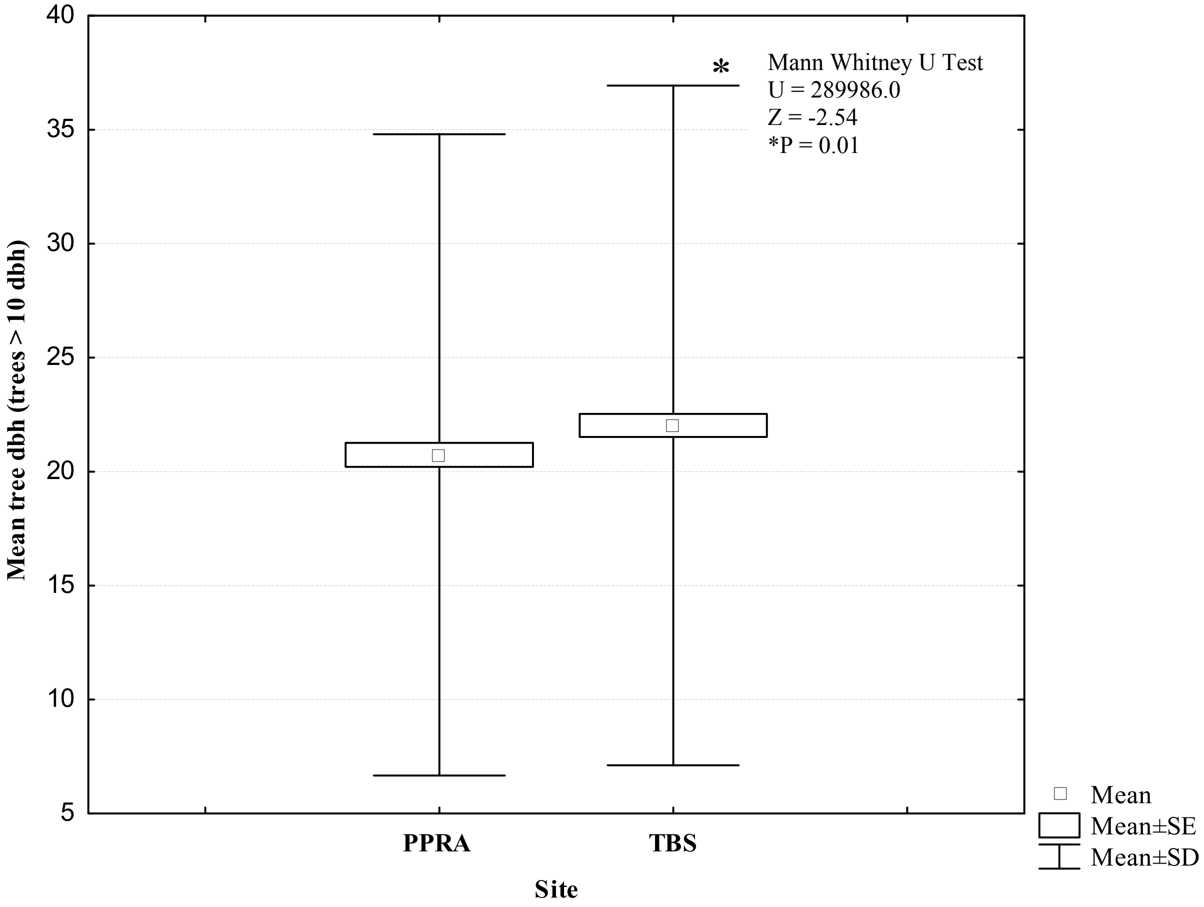


FIGURE 3: Top 10 families at each site with highest Importance Values (IV) calculated by summing the values of the relative frequency, relative density, and relative basal area. Families are ordered from highest to lowest IV, regardless of site occurrence.

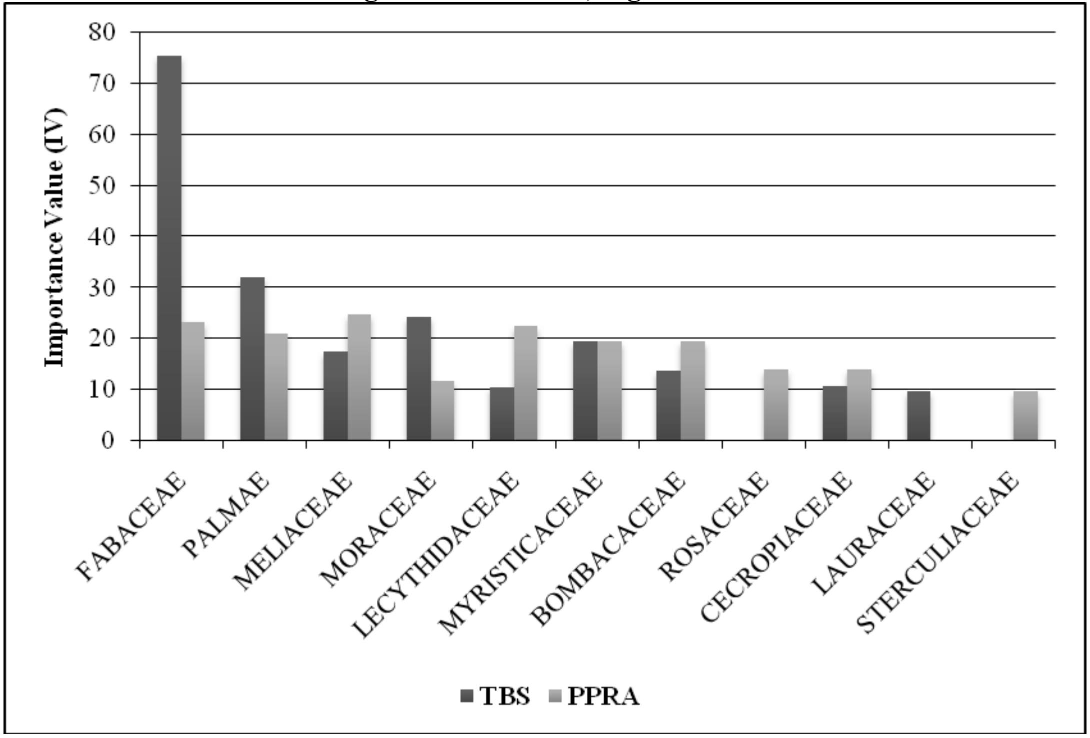


FIGURE 4: Top 10 species at each site with highest Important Values (IV) calculated by summing the values of the relative frequency, relative density, and relative basal area. Species are ordered from highest to lowest IV, regardless of site occurrence.

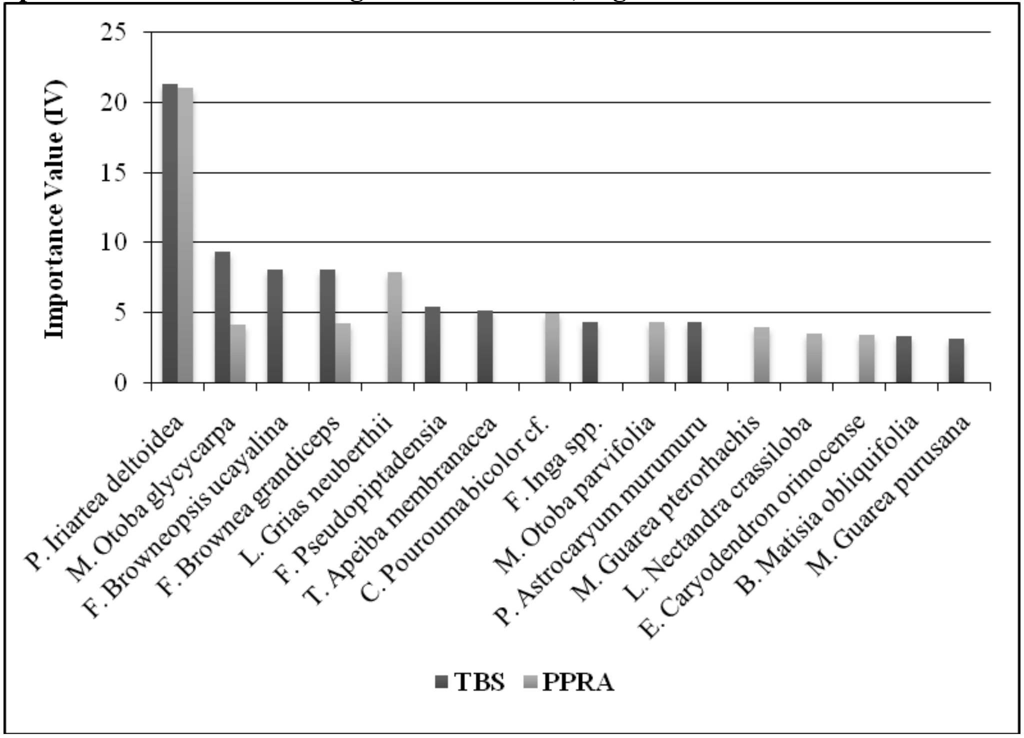


FIGURE 5a: Comparative monthly phenology shown as the a) percentage of individual trees in each phenophase and b) average percentage of each phenophase in the canopy of all trees for leaves, flower buds and flowers; average number of fruits in the canopy of all trees

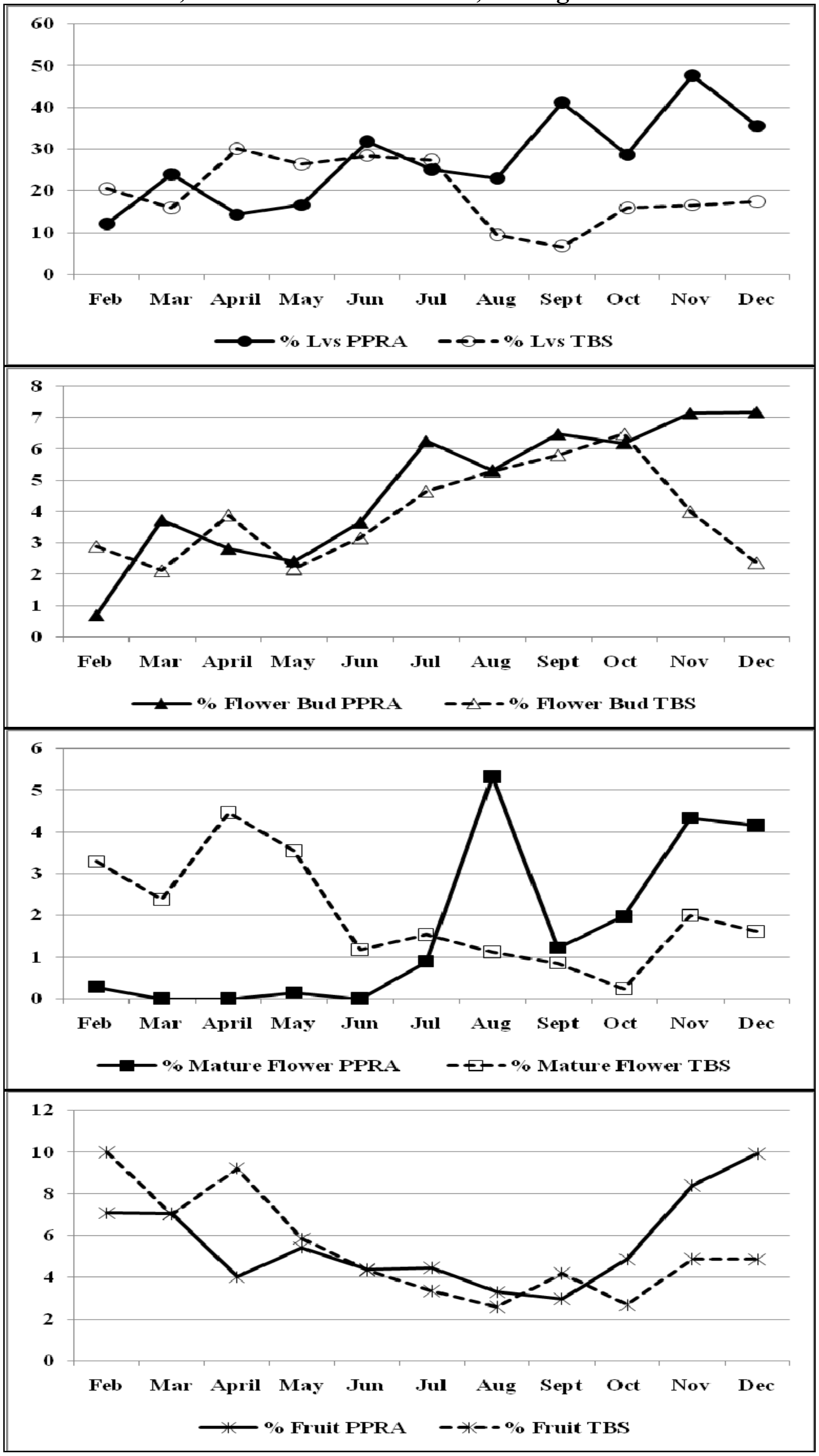
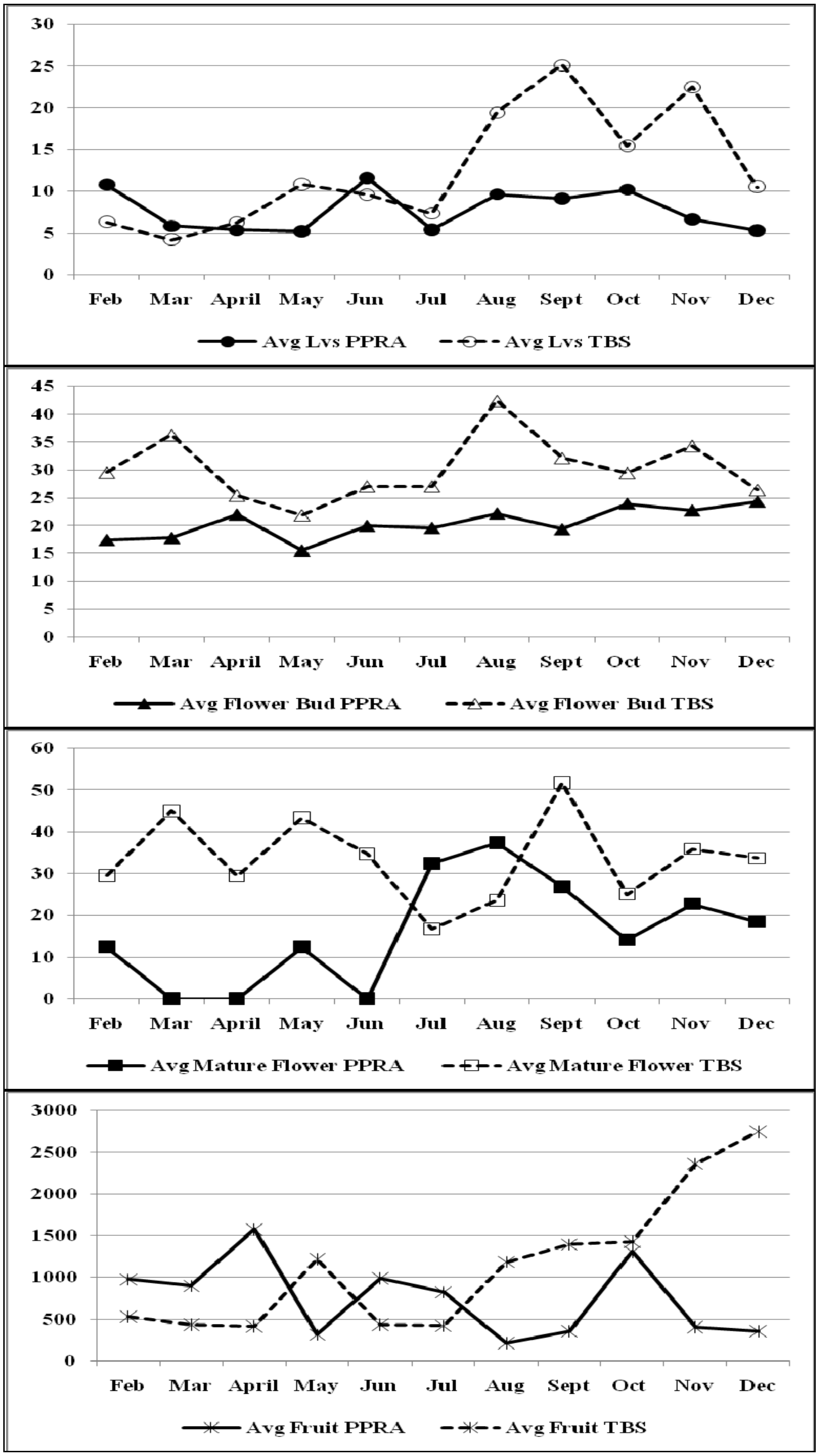


FIGURE 5b



30
25
20
15
10
5
0
Feb
Mar
April
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
Avg Lvs PPRA
Avg Lvs TBS
45
40
35
30
25
20
15
10
5
0
Feb
Mar
April
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
Avg Flower Bud PPRA
Avg Flower Bud TBS
60
50
40
30
20
10
0
Feb
Mar
April
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
Avg Mature Flower PPRA
Avg Mature Flower TBS
3000
2500
2000
1500
1000
500
0
Feb
Mar
April
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
Avg Fruit PPRA
Avg Fruit TBS

FIGURE 6: Significant differences in pre- versus post-flooding soil nutrient levels for Mn and Al (levels shown on Y axis as ppm).

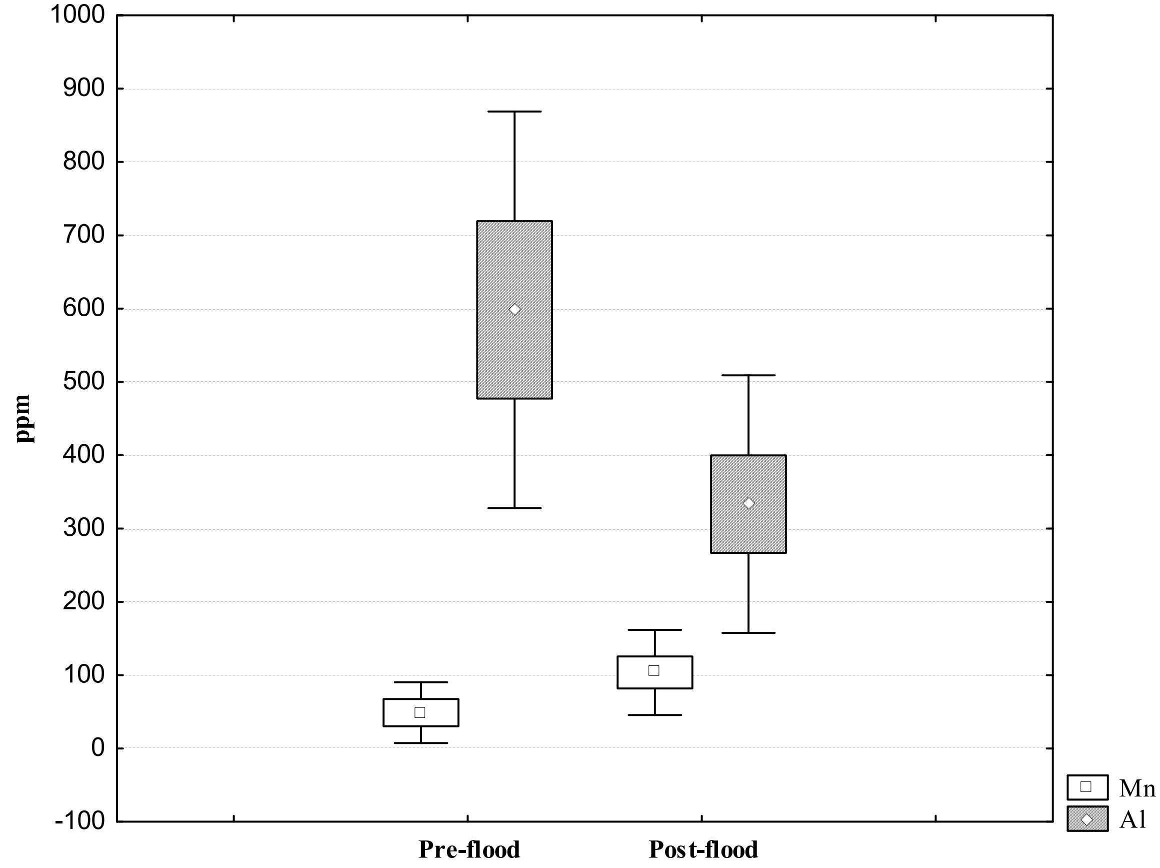


FIGURE 7a: Significant post-flooding differences in a) pH level b) Ca and c) Mg between site (PPRA versus TBS) and microhabitat (Non-riparian versus Riparian).

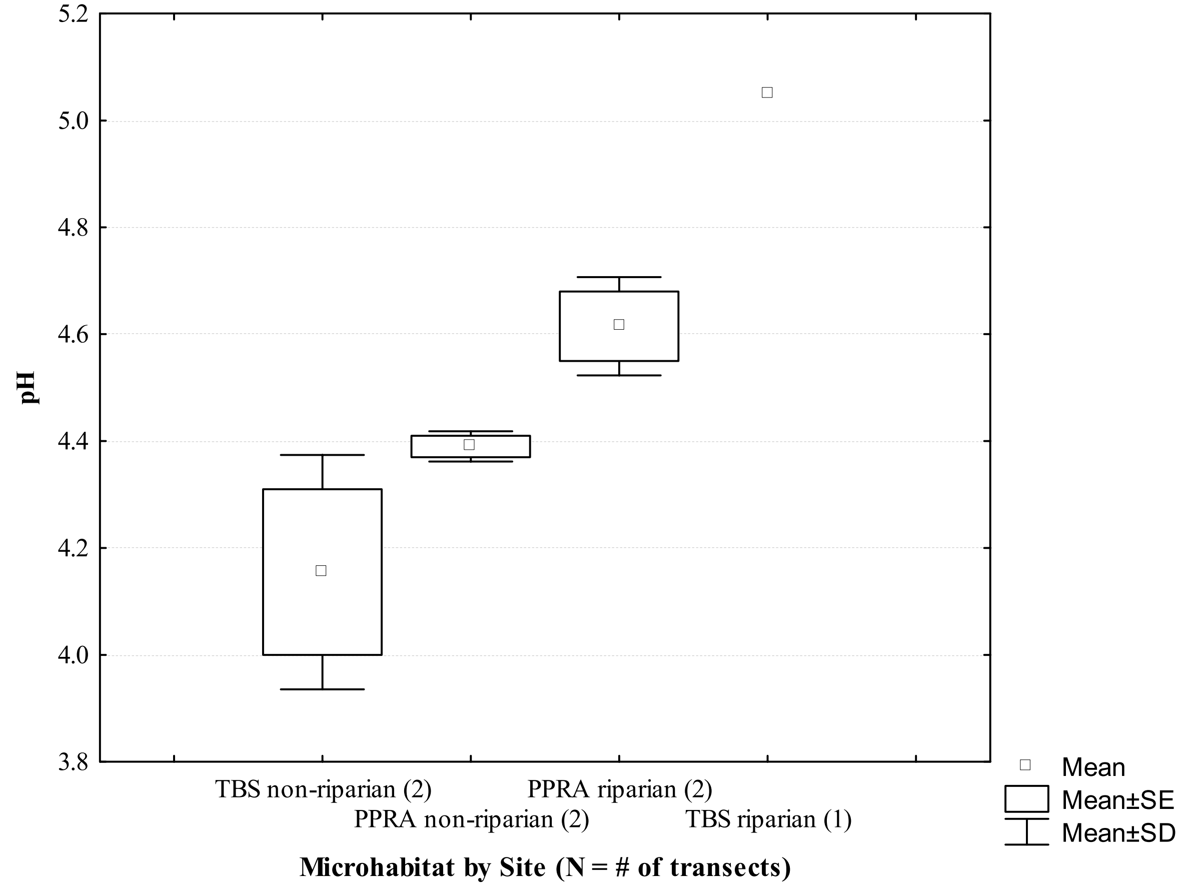
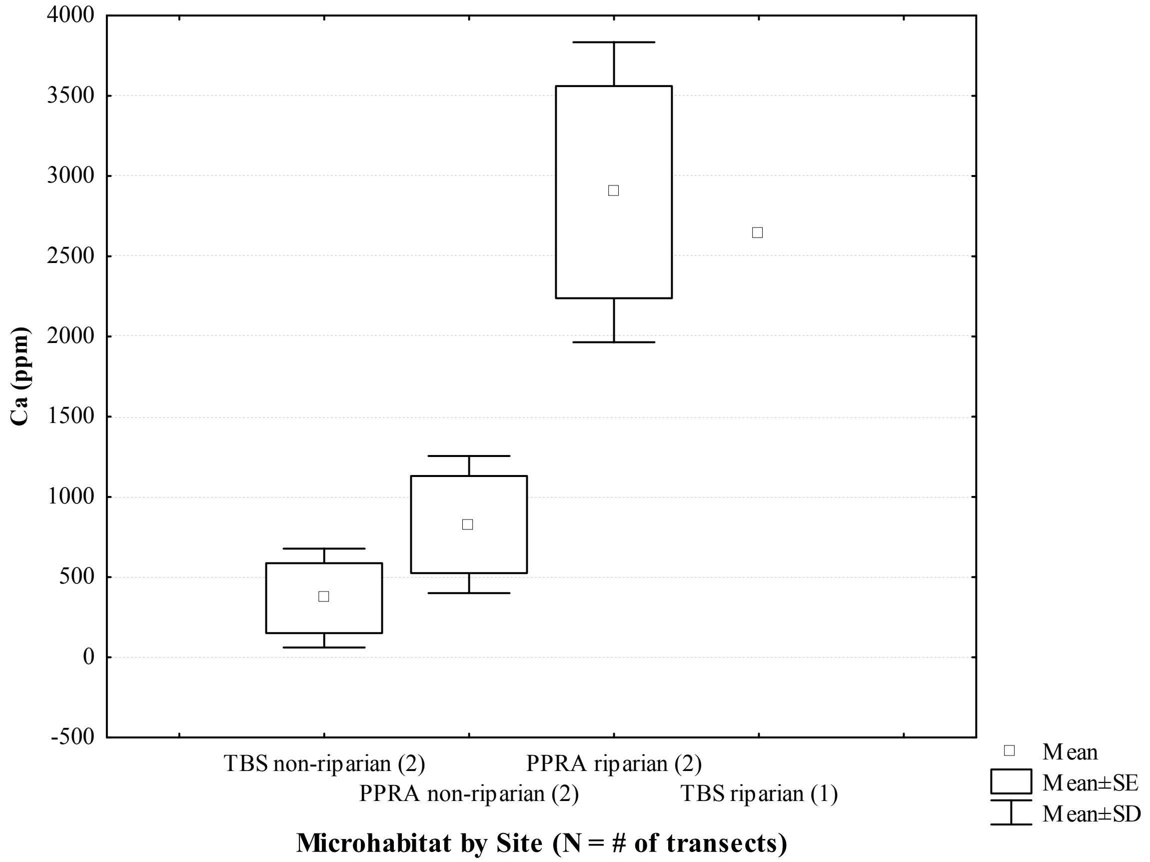
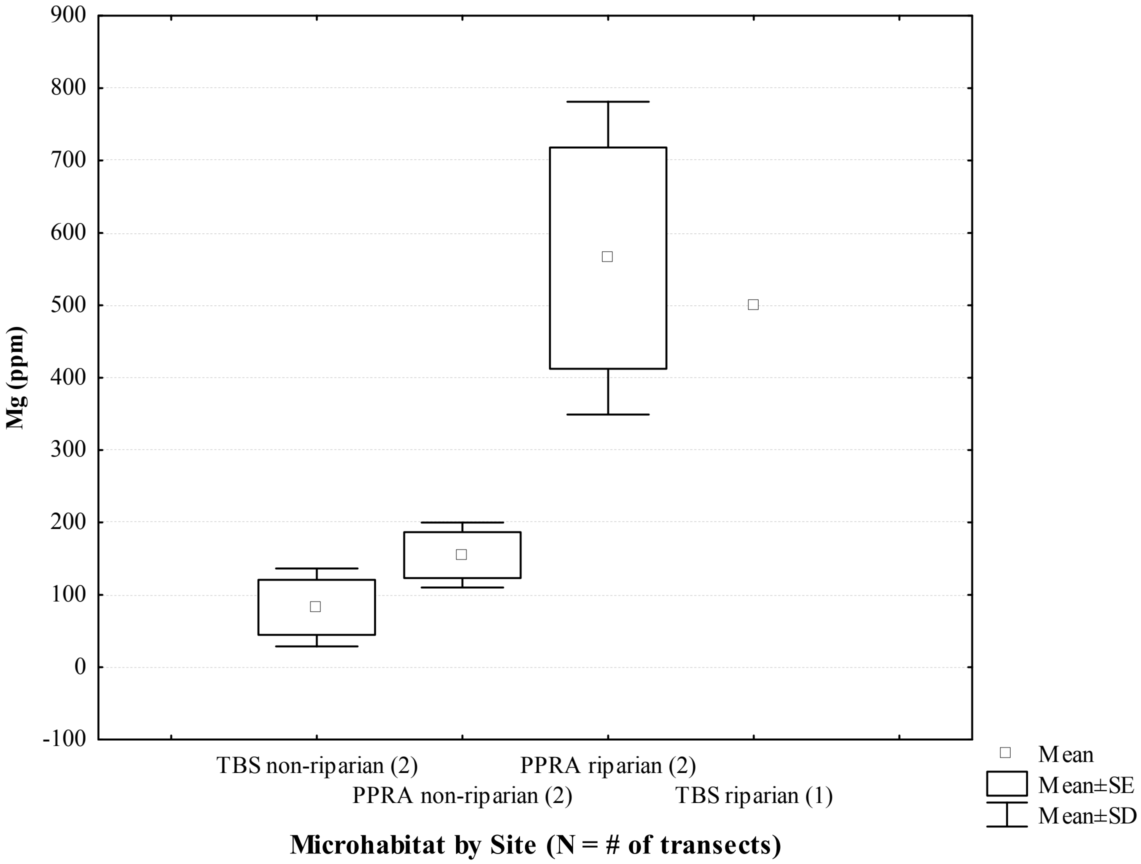


FIGURE 7b



4000
3500
3000
2500
2000
1500
1000
500
0
-500
Ca (ppm)
TBS non-riparian (2)
PPRA non-riparian (2)
PPRA riparian (2)
TBS riparian (1)
Microhabitat by Site (N = # of transects)
□ Mean
Mean±SE
Mean±SD

FIGURE 7c



900
800
700
600
500
400
300
200
100
0
-100
Mg (ppm)
TBS non-riparian (2)
PPRA non-riparian (2)
PPRA riparian (2)
TBS riparian (1)
Microhabitat by Site (N = # of transects)
□ Mean
Mean±SE
Mean±SD

CHAPTER 4

The Interrelationship Between Forest Ecology, Population Structure and Behavior in Red Howler Monkeys (*Alouatta seniculus*)

4.1 Abstract

This chapter investigated how differences in howler monkey population density may relate to food resources, demographic patterns, and behavior. There were three main goals. The first was to test whether there were differences in the quality of resources available between the sites by looking at 1) the digestibility of leaves as measured by the presence of total phenolic content, 2) the ratio of protein-to-fiber in leaves, and 3) the densities of resources with leaves that have the lowest content of phenolics and the highest ratios of protein-to-fiber. The second goal was to identify whether high population density was linked to the particular differences in demography as proposed for other primates. Finally, a comparison was done to test which of the above ecological variables had behavioral predictive sets that best matched the observed patterns of *Alouatta* behavior.

This study showed that the factors likely to be playing the largest roles influencing the differences in howler monkey population density in Yasuní N.P. are a combination of higher protein content in leaves and a higher density of these resources, along with a higher density of resources low in phenolics. This study illustrates that testing multiple ecological factors, that can be distinguished by how they should affect

the behavior of folivorous primates, is a step in the right direction to help tease apart which closely related biological factors are contributing to differences in folivore density.

4.2 Introduction

There has been considerable work done to address the question of which factors influence primate population density in an effort to better understand the process of behavioral adaptations (e.g., Oates et al., 1990; Davies, 1994) as well as to aid conservation endeavors (e.g., Chapman et al., 2002; Struhsaker et al., 2004). Several factors are thought to affect primate density such as **food quality** (Waterman et al., 1988; Oates et al., 1990, Ganzhorn, 1992), **seasonality** (Janzen, 1975; Davies, 1994; for a recent review see Brockman and van Schaik, 2005), **habitat heterogeneity** (Bourliere, 1985; Terborgh and van Schaik, 1987), and **density and availability of food resources** (e.g., Terborgh and van Schaik, 1987; Davies, 1994).

Among these, the density of food resources has been suggested to be the primary determinant of primate population density (e.g., Terborgh and van Schaik, 1987; Davies, 1994). This hypothesis has gained much support from studies that have looked at either closely related species or the same species at locations that differed in availability of resources and in primate density (e.g., Chapman and Chapman, 1999) or populations that have illustrated dramatic declines as a result of regional ecological changes and a reduction of available resources over time (e.g., yellow baboons: Hausfater, 1975, Altmann et al., 1985; vervets: Struhsaker, 1973; toque macaques: Dittus, 1979; mangabeys: Olupot et al., 1994).

Chapman and Chapman (1999) suggest the basis for this is that a greater abundance of food availability translates into a greater maximum availability of energy, ultimately enabling higher reproductive rates. More specifically, while population density is a function of emigration, immigration, birth and death rates, it is the latter two which are most closely linked to food availability. Based on this, areas with higher food availability, and thus a higher carrying capacity, should enable populations to have higher birth rates and/or lower death rates or birth rates that experience a stronger increase than death rates. The resulting pattern thus leads to a higher net recruitment and ultimately to a higher population density in areas with higher food availability. Therefore it is hypothesized that areas with higher availability of resources should maintain a higher primate density than areas with lower availability.

Most of the variation in biomass exhibited in primate communities is accounted for by folivores (Terborgh and van Schaik, 1987) and hence a great deal of research has specifically focused on these species. Due to the challenges that leaf consumption can pose, such as difficult to digest cellulose and high levels of potentially toxic secondary compounds (Waterman et al., 1988; Oates et al., 1990; Ganzhorn, 1992), data on resource quality, as well as resource density, have been the main foci of research. For instance, it has been suggested that folivorous primate population density is positively correlated with the average leaf quality of a habitat, reflected as the digestibility (either in low levels of fiber or secondary compounds) or the ratio of protein to fiber in leaves. While this is by no means a hard and fast rule, the idea has been well supported in an array of folivorous taxa and in each of the major primate radiations (Strepsirhini: Ganzhorn, 1992; Cercopithecoidea: Oates and Davies, 1990, Chapman et al., 2002, 2004, Wasserman and

Chapman, 2003; Platyrhini: Peres, 1997). However most of these efforts have been concentrated on African and Asian folivores while less attention has been paid to New World folivores characterized by a different digestive morphology (but see Milton, 1979; Rylands, 1987; Reed, 1999; Peres, 1997a, b; Chapman and Balcomb, 1998; Peres and Janson, 1999).

The ecology of a habitat can also affect the demography, and not just the density, of a population. For example, increasing both food availability and food quality can provide a diet higher in protein, and better nutrition can in turn influence aspects such as shorter inter-birth intervals and higher overall reproductive output. Thus demography may be viewed as a proxy for fertility and survivorship, the two main components that contribute to population density (Gotelli, 1998). In order to understand the way in which changes in density arise as a result of this variation in demography and which factors most greatly affect density, it is necessary to examine both the mechanisms that influence changes in population density and the ecology of a habitat. Some of the trends in demography at high versus low population density observed for other primate populations are: 1) The average number of males per group is **higher** (Crockett, 1996), 2) The average number of adult female howler monkey per group is **higher** (Crockett, 1996), but does **not exceed four** (Crockett, 1996; Crockett and Janson, 2000; Horwich et al., 2001), 3) The average group size is **larger** (Crockett, 1996) and 4) The ratio of infants and juveniles to adult females is **higher**, (Sadlier, 1969; Jorde and Spuhler, 1974). It is possible that factors such as sex biased dispersal may influence these patterns. For example, male biased dispersal, which is the most common pattern within Cercopithecidae (Lawson Handley and Perrin, 2007), may increase the number of females but not males per group. Furthermore, if dispersal distance is relatively great in this scenario and/or the males become solitary they may experience higher mortality (e.g., due to predation) which could potentially decrease the percentage of males in the population as well.

The cumulative information gained from the comparative studies discussed thus far has been essential to uncovering the patterns that exist between ecology and folivore density, but most studies have been univariate in nature, correlating one aspect of habitat ecology with folivore density. Furthermore while there is information that suggests habitat quality also influences demographic patterns, it is possible that different ecological variables could produce the same observable patterns. Therefore focusing on ecology and demography alone may not provide enough information to fully distinguish which factor(s) play the largest role in affecting differences in folivore density.

One way to address these issues is to look at the behavior of primates, which can be influenced by the ecology of a habitat as well as the density and demography of a population. Behavioral predictions about how primates should respond to differences in resource availability can be derived from a theoretical perspective, such as optimal foraging theory (MacArthur and Pianka, 1966; Charnov, 1979; Hume, 1989), and from data in the literature indicating that differences in the activity budgets of folivorous primates can arise in response to variation in food availability (e.g., Dasilva, 1992; Fashing et al., 2007; Korstjens and Dunbar, 2007). For example, optimal foraging theory makes predictions regarding patch residency times. However, these predictions are based on the assumption that feeding rates decline gradually with time spent in a patch. In practice, however, feeding rates are likely to remain rather constant for more conspicuous items such as fruit, flowers, and young leaves. In these cases, patch residency time will not depend on either Energy/Time or the mean rate of food intake in the patch. Therefore there is strong reason to argue that predictions made for patch residency time by optimal foraging theory may not hold in folivorous primates and are thus not considered here.

Comparative studies may be more useful and applicable in making predictions for activity budgets of folivorous primates in response to variation in food availability. Several studies have shown that primates may spend more time feeding per day as per capita food quality diminishes with an increase in the number of competitors and spend more time moving as food patches are depleted (van Schaik et al., 1983; Janson and van Schaik, 1988; Janson and Goldsmith, 1995). However this relationship in time allocations is expected only if there are no differences in food quality and density between sites (Gillespie and Chapman, 2001). In the context where one habitat is characterized by higher resource quality, for example in the form of leaves with higher ratios of protein-to-fiber, this relationship at the higher quality site may still reflect more time feeding but there may be less time spent resting due to less time required for the digestion of high-protein-to-low fiber items (Milton, 1980; Coley and Barton, 1996). Furthermore, if the density of these high quality resources were increased, the behavioral predictions for increased quality would still hold, but animals might instead spend less time moving because between patch distances would decrease as resource density increased. This is a pattern that has been observed in large herbaceous terrestrial mammals (e.g., goats: de Knegt et al., 2007) and in folivorous primates (howler monkeys: Milton, 2000).

Finally, it has been suggested that population density may also affect primate behavior. For example, it has shown that Neotropical howler monkeys that live at high population densities have shorter day ranges and smaller home ranges (Chivers, 1969; Crockett and Eisenberg, 1987) and engage in higher rates of long call vocalizations (Chiarello, 1995).

A new perspective on how to tease apart which closely related biological factors are influencing density may therefore be gained by considering the ecological, demographic and behavioral information together. A way to do this is to employ a multivariate approach which tests multiple ecological factors that can be distinguished by how they would affect the behavior of folivorous primates. Specifically, each factor would be accompanied by a set of mutually exclusive *a priori* predictions regarding how each should, all other aspects remaining equal, affect the behavior of folivorous primates in areas of high versus low population density.

This study will examine the relationships between ecology, demography and behavior in order to address the question of which factors influence folivore density in two populations of howler monkeys (*Alouatta seniculus*). The two populations are geographically close, but occur in different forest types and at different densities. Howler monkeys (genus *Alouatta*) are among the most folivorous Neotropical primates (*e.g.*, Milton 1980, Braza *et al.*, 1981) and have a wide geographic range. Seven species occur from southern Mexico to northern Argentina (Groves, 2001) but their densities are variable throughout this distribution (for review see Chapman & Balcomb, 1998).

There are three main goals to this paper; the first is to test whether there are differences in the quality of resources available between the sites by looking at 1) the digestibility of leaves as measured by the presence of total phenolic content, 2) the ratio of protein-to-fiber in leaves, and 3) the densities of resources with leaves that have the lowest content of phenolics and the highest ratios of protein-to-fiber. The second goal is to identify whether high population density was linked to the following differences in demography as proposed for other primates: 1) The average number of males per group is **higher**, 2) The average number of adult female howler monkey per group is **higher** but does **not exceed four**, 3) The average group size is **larger** and 4) The ratio of infants and juveniles to adult females is **higher**. Additionally the predictions that howlers living at higher population densities should have shorter day ranges and smaller home ranges (Chivers, 1969; Crockett and Eisenberg, 1987) and engage in higher rates of long call vocalizations (Chiarello, 1995) will be tested. Finally, in order to try and tease apart which ecological factor(s) influence howler monkey density, a comparison was done to test which ecological variable(s) had behavioral predictive sets best matched to the observed patterns of *Alouatta* behavior.

The first two hypotheses regarding resource quality reflect solely plant quality, while the last two reflect the combined effects of both quality and density. The ecological hypotheses have mutually exclusive sets of *a priori* predictions based on how each of the variables, with all other aspects remaining equal, should **affect the behavior of howler monkeys in terms of percentage of time spent resting, feeding, and moving, between patch distance and number of patches fed upon per day, in a high versus a low population density region.** The ecological hypotheses and their corresponding predictions are as follows:

H1 A lower level of total phenolics in leaves supports a high *Alouatta* density. This is based on the idea that phenolics, such as tannins, can act as digestion inhibitors and have been shown to reduce feeding time (Wrangham and Waterman, 1981). Thus, leaves containing a lower phenolic content should allow howler monkeys to spend a lower percentage of time resting and a greater percentage of time feeding. The percentage of time spent moving and the between patch distance are not predicted to differ between a high versus a low population density.

H2 A high protein-to-fiber ratio in the leaves supports a high *Alouatta* density. The foraging strategy of howler monkeys should be to select food of a relatively high quality, to minimize the costs of procuring such foods and generally to conserve energy (Milton, 1980). Leaves that have a higher ratio of protein-to-fiber enable howlers to acquire a greater nutritional amount per feeding bout and thus they should spend a greater percentage of time feeding as well as have a longer period of time to rest.

H3 A high density of resources low in phenolic content supports a high *Alouatta* density. The combined effect of resources lower in phenolic content and a higher density of these resources available differs from H1 in that higher density decreases the distance between patches, and thus the percentage of time spent moving.

H4 A high density of resources with high protein-to-fiber ratios supports a high *Alouatta* density. The combined effect of having resources higher in protein-to-fiber and a higher density of these resources differs from H2 in that higher density decreases the distance between patches thus decreasing the percentage of time spent moving. It is also predicted that howler monkeys will be able to feed on a higher number of trees per day. This prediction is based on the assumption that under these conditions individuals may be less nutritionally limited due to a diet higher in protein, enabling them to travel to more patches per day facilitated by the decreased distance between those patches.

4.3 Methods

Study Area

Research took place from February-December 2005 in the Yasuní National Park and Biosphere Reserve, a primary Neotropical rainforest located south of the Rio Napo in the Amazon region of Ecuador (Koester, 2001). This region has been designated as an UNESCO Man and the Biosphere reserve due to its extremely high species diversity (Di Fiore, 1997). The region is moist tropical forest composed primarily of *terra firme* forest and smaller areas of riparian forest and swamp with a mean annual temperature of 26˚C that is relatively constant throughout the year (Di Fiore, 1997, 2003; Di Fiore and Rodman, 2001). The elevation ranges from 190-350 m and there is a mean annual rainfall of ca. 3,200 mm with no distinct dry season (Di Fiore, 1997, 2003; Di Fiore and Rodman, 2001). Until recently, much of the park remained pristine, but human subsistence practices and resource extraction have altered portions of the reserve (Di Fiore, 1997), including a road that was built in the early 1990's by Maxus Ecuador Corporation, which now stretches over 100 km inside YNP (Franzen, 2006).

Study Sites

The study was conducted at two sites within YNP. The first location is the Proyecto Primates Research Area (PPRA) established in the mid-nineties (Di Fiore, 1997, 2001; Dew, 2001; Suarez, 2003; Spehar, 2006). The PPRA site is approximately 650 ha in size and is characterized by primary, non-flooded *terra firme* forest with a road that borders the area on two sides. The second site, bordering the Tiputini River near the Tiputini Biodiversity Station (TBS), is also roughly 650 ha area and consists of a mix of *terra firme* and seasonally flooded habitat. It is located further from the Waorani communities and thus far hunting has not been reported at TBS. The PPRA and TBS study sites are located approximately 36 km apart from each other (Figure 1) and both are contiguous with large tracts of unfragmented tropical rainforest. Total primate biomass at PPRA is 284.2 kg/km^2, with 33.3 kg/km^2 composed of howler monkeys, while at TBS it is 410.5 kg/km^2 with howler monkeys comprising 76.3 kg/km^2. The difference reflects a howler monkey biomass that is 2.3 times higher at TBS than at PPRA (Derby in preparation).

Nutritional Analysis

Plant samples representing both food and non-food items were collected from the study sites between November 2004-December 2005 (N= 127; 55 at PPRA, 72 at TBS). Food samples were acquired in two ways, either from the exact branch location within three days of when the monkeys fed from the patch using a modified crossbow or from collecting the remains on the ground that fell from the animals' mouths while eating. Samples were identified, weighed (wet), dried, re-weighed (dry), and sent to the University of Hamburg, Germany for nutritional analysis. Table 1 lists the extraction procedures used in this study.

In addition, the top ten species with the highest percentage of protein and the top four species with the lowest content of phenolics were identified at each site and existing data on these species' corresponding density frequencies were then compared between the sites (Derby in preparation). Ideally the top ten species would have also been selected to investigate the density of trees with the lowest levels of phenolics, however because not all samples were able to be identified only the top four species were used. Data on the tree species density comes from stratified botanical plots that represented a total of 1.5 ha at each site with all trees > 10 DBH identified. The total number of stems per 1.5 ha at TBS was 909 and 738 at PPRA.

Demographic Data

All data were collected between February and December 2005 at the PPRA and the TBS study sites. Demographic information on howler monkey group size and composition was collected during full day follows on habituated focal groups two to three days per month (N= 1 group at PPRA; 2 groups at TBS). During full day follows, data on group size and composition were recorded for the focal group and any additional howler group that was encountered while with the focal group. Group composition was defined as all adult and immature members (following Peres, 1999) and the sex and age class of all group members was recorded. In addition to group follows, weekly distributional surveys and monthly line transect sampling were done with the intent to search and conduct a complete count of howler groups in the study sites (Derby in preparation). Data on the group size and composition of howler groups at each site were derived either from follows with focal groups, surveys or transect walks. In the latter two cases, a full year of survey and transect data were examined, along with the general knowledge of howler monkey home ranges from these sites, to determine the general location and range of each group within the study sites and their size and composition.

Group Encounters and Relative Vocalization Rate

Group encounters and vocalization rates were recorded in an all occurrence manner (Martin and Bateson, 1993). When group encounters occurred the following information was taken: species, number of individuals, age class and sex of individuals, location, duration, and nature of encounter (affiliative, neutral, agonistic). All long call vocalizations heard throughout the course of the day from both focal and unknown groups were recorded. For each occurrence the date and time together with the duration were noted. A relative vocalization rate was calculated using the following formula:

(Total number of long call events/Total observation days)

Behavioral Data

Home range, daily path length, and activity pattern

In order to assess home range, daily path length, and activity patterns of the red howler monkeys, full day follows were conducted on habituated focal groups (N= 1 group at PPRA; 2 groups at TBS) two to three days per month at each site. Size and composition of the PPRA focal group was 7 individuals, including 1 adult male, 1 sub-adult male, 2 adult females, 1 sub-adult female, 1 juvenile and 1 infant. Group 1 at TBS had a total of 10 individuals including 1 adult male, 1 sub-adult male, 4 adult females, 1 sub-adult female, 2 juveniles, and 1 infant while Group 2 had a total of 5 individuals with 1 adult male, 1 sub-adult male, 2 adult females, and 1 juvenile.

Although the intention of this study was to monitor focal groups at both sites for the duration of the project, this was only achieved at the TBS site. It was not possible to locate and habituate a study group at the PPRA site until September of 2005. In large part this was due to the low density of howler monkeys at this site and the virtual non-existence of long call vocalizations that typically aid in the endeavor to locate and follow groups. Therefore, the behavioral data comparisons were restricted to the months of overlap between the focal group follows at the two sites (N= 3 months).

Monthly day range data collection began by finding the monkeys in their sleep site from the previous evening and recording its location. The angle of all subsequent travel movements and the location of each resting and feeding tree (defined below) were then recorded along with their distance and angle from the nearest marked trails and trees mapped with Global Positioning System (GPS) coordinates (DiFiore, 1997; Suarez, 2003). All points were converted into Universal Transverse Mercator (UTM) coordinates and entered into ArcView 3.3. Home range was determined using the ArcView 3.3 Spatial Analyst which calculated both a minimum convex polygon and a 95% Kernel from all day range data points for each group. Daily path length was then calculated by summing the straight line distances between each recorded location using the ArcView 3.3 Movement software. Activity budget data were derived from fifteen minute behavioral scan sampling (Martin and Bateson, 1993) that recorded the following four categories: feeding, resting, moving and socializing.

<u>Between patch distance and number of feeding trees used per day</u>

A patch, or feeding tree, was defined as a tree or liana within a tree where feeding occurred for more than five minutes (Di Fiore, 1997). Between patch distance was measured by taking the GPS points from each feeding tree the howler monkeys entered and calculating the straight line distance between sequential patches in ArcView 3.3 (see above). Patch feeding time was defined as the length of time from when the first monkey in a group entered a patch until the last monkey left the same patch.

Statistical Testing

The following statistical tests were applied to the data. In order to compare the nutritional components of plant items between the sites, Independent T-tests were used. Due to the small sizes of the behavioral data set, several tests were performed on these scores in order to look at the variance within the data both on the daily and the monthly level between the two sites. First, a Mann-Whitney U Test (Siegel and Castellan, 1988) was performed on the daily scores for the activity budgets and then again on the monthly averages. Second, a Wilcoxon Matched Pairs Test (Siegel and Castellan, 1988) was applied to the monthly averages. In addition, between patch distances were tested using a One-way ANOVA (Sokal and Rohlf, 1995) and 95% Confidence Limits were applied to the number of feeding trees used per day at both sites. Lastly, a Mann-Whitney U Test was used to look at the demographic characters of the groups at both sites, while a Chi Square Test was used to test the number of days with long call vocalizations versus without vocalizations between the two populations.

4.4 Results

Resource Quality and Density

The plant samples were tested for six nutritional components (Table 1) and the leaves from the two sites were found to have two significant differences (Table 2), while no differences were found in the fruit content. The total percent protein in the mature and young leaves combined was found to be significantly higher at TBS (Independent T-test; df = 60, t = 2.56, P= 0.01), while the protein to fiber (acid detergent fiber) ratio was found to be significantly higher in the mature leaves at TBS (Independent T-test; df = 16, t = -2.33 P = 0.03).

Additionally, the top ten species with the highest percentage of protein were identified at each site and existing data on these species' corresponding density frequencies were then compared between the sites. It was found that the average protein percentage of the top ten species at TBS was 9.08 (SD = 2.3) and that there were 46 individuals of these species found within 1.5 ha of botanical plots, representing 5.1% of the total tree density. The average percentage protein of the top ten species at PPRA was 7.88 (SD = 2.7), and there were only 11 individuals of these species found within 1.5 ha of botanical plots, representing 1.5% of the total tree density. Furthermore, when the top ten species from each site are combined, there are 140 individuals (15.4% of total tree density) present within the botanical plots at TBS, while only 51 individuals (6.9% of total tree density) were found at PPRA (Table 3).

Although there were no significant differences found between sites in the average phenolic content within the leaves, a significant difference emerges if the density of the top four species with the lowest levels of secondary compounds is calculated for each site. There were 105 trees at TBS with the lowest phenolic content (Average = 0.50, SD = 0.21), or 11.6% of the total tree density within the botanical plots, whereas there were only 20 trees that occurred at PPRA. When the species are combined from both sites and the top eight are taken into consideration, there are a total of 127 individuals at TBS, or 13.9% of the tree density, versus 44 trees at PPRA which represents 5.9% of the total botanical plot density (Table 4).

Demography

Within the similar sized study sites, both approximately 650 ha, there were 3 groups found to occur at the PPRA site and 10 groups at the TBS site. The average group size was slightly larger at PPRA, reflected mainly in a higher number of females, but no group was found to have greater than four females per group (Table 5). The ratio of immature to females was slightly higher at TBS (1:0.88) compared to PPRA (1:0.62). However, neither the average group size nor any aspect of group composition differed significantly between the two sites (Table 5: Mann-Whitney U Test, $P > 0.05$).

Group Encounters and Relative Vocalization Frequency

Inter-group encounters were rarely witnessed at either site. However, five occurred while either searching for or with the focal groups at the TBS site and one occurred at the PPRA site. Howler monkeys at both sites have at least some part of their peripheral home range overlapping with adjacent group ranges, and it is these peripheral areas that encounters were observed. All encounters began with long call vocalizations by the male(s) in each group (females were not observed vocalizing) and four out of six encounters escalated to direct aggression. All of the direct aggression encounters occurred at the TBS site, resulting in rival male group members chasing each other through the canopy. The other two occasions were strictly “vocal battles” between group males located less than 50 m apart from one another (one at the TBS site, one at PPRA).

In contrast, long call vocalizations were much more common. At the TBS site a total of 140 long call vocalization events occurred on 58 of the 143 total observation days, or 40.6% of the time. The relative vocalization rate, which is the total number of long call events/total observation days, was 0.98 and throughout the study period there were, on average, 1.20 (SD= 0.85) long call vocalizations per day. This varied throughout the year however (Figure 2a), with a maximum number of 3.33 calls per day in May 2005 and a minimum of 0.20 in March 2005.

In contrast, there were significantly fewer long calls at the PPRA site (Chi Square, 54.63, $P < 0.001$; N= 58 days with vocalizations and 85 without for TBS; N= 7 days with vocalizations and 143 without for PPRA). A total of 8 long call vocalization events occurred during 7 of the 150 total observation days, or 4.7% of the time at PPRA. The relative vocalization rate was 0.05 and the overall average of long call vocalizations per day was 0.04 (SD= 0.11) for the study period, with the maximum number in November 2004 only reaching 0.28 and eight months with zero long calls recorded (Figure 2b).

Behavioral Data

Home range, daily path length, and activity pattern

When comparing the home range area for two similar sized howler monkey groups ($\text{Group}_{\text{PPRA}}$ = 7 individuals, N = 6 days and 32 ranging points; $\text{Group}_{\text{TBS}}$ = 10 individuals, N = 7 days and 64 ranging points), the PPRA group is found to have a smaller home range. The difference in area is 3.8 ha when using a Minimum Convex Polygon (MCP) to calculate home range (PPRA= 23.6 ha; TBS= 27.4 ha) and 2.2 ha when using a 95% Kernel (PPRA= 24.6; TBS = 26.8 ha). This similarity in home range size between two groups that occur at sites that are similar in size but differ in population and group density may be reflective of small sample sizes. Although the average daily path length at the PPRA site is shorter (448.3 m at PPRA, N= 6 days; 616.7m at TBS, N=

7 days), it does not significantly differ between the groups (Figure 3: 95% Confidence Limits).

However, results for group activity patterns indicate there are significant differences between the two populations. First, differences between the behavioral daily averages were tested, showing that howler monkeys at the TBS site spent significantly more time feeding (Mann-Whitney U Test, $U = 4.5$, $N_{PPRA} = 7$, $N_{TBS} = 9$, $P < 0.05$). There were no differences found in the time spent moving, resting, or socializing ($U_{move} = 21.5$, $U_{rest} = 27$, $U_{soc} = 31.5$, $N_{PPRA} = 7$, $N_{TBS} = 9$, all Ps > 0.1). When monthly averages are tested, time spent feeding is still significantly higher at TBS (Mann-Whitney U Test, $U = 0.0$, $N_{PPRA} = 3$, $N_{TBS} = 3$, $P < 0.05$) and, while not significant, the data indicated that they are also spending less time moving. To control for possible seasonal effects, a Wilcoxon Matched Pairs Test was also applied to the monthly averages, and it also indicated that monkeys at TBS are feeding more and moving less (Figure 4: $T_{feed} = 0.0$, $T_{move} = 0.0$, $N_{PPRA} = 3$, $N_{TBS} = 3$, $P > 0.05$). While the results from the Wilcoxon Matched Pairs Test cannot be significant due to small sample size, there was no exception to the direction of the average scores for each month between the sites, suggesting that the non-significant result was more likely due to sample size and not because of variation in the data.

In addition to the differences in time spent feeding, there are also a few differences in the amount and the type of foods being consumed. Monkeys at both sites have a high overall average of leaves in their diet, however it was slightly higher at TBS (TBS= 81.8%; PPRA= 73.2%). Within this category, at TBS the average amount of young leaves consumed was higher and conversely the average amount of mature leaves was lower (TBS: young leaves= 77%, mature leaves= 4.8; PPRA: young leaves= 59.9%, mature leaves= 13.3%). The diet at TBS also appears to be more diverse, reflected by the monthly inclusion of flowers, fruits, or pods while the diet at PPRA was restricted to only the inclusion of fruits (Figure 5).

Between patch distance and number of feeding trees used per day

The distance between feeding patches, or inter-patch distance, was found to be significantly longer at the PPRA site. The average inter-patch distance at the PPRA site was 99.62 meters compared to an average of 74.43 meters at the TBS site (Figure 6: 1-way ANOVA, F = 76.45, $P < 0.05$; $N_{PPRA} = 27$ and $N_{TBS} = 58$ feeding trees). While the average patch residency time did not differ between sites (Mann Whitney U, U = 820.5, P = 0.18, $N_{PPRA} = 28$, Average = 16.6 minutes, SD = 15.08 minutes; $N_{TBS} = 73$, Average = 20.83 minutes SD = 19.69), the number of feeding trees used per day did (Figure 7). On average, the howler monkeys at the PPRA site fed from 5.5 (SD = 1.04) trees per day, which is significantly lower than the 9.2 (SD = 4.57) trees fed upon per day at the TBS site (95% Confidence Limits; N = 6 days at PPRA for a total of 33 feeding trees and N = 7 days at TBS for a total of 65 feeding trees).

4.5 Discussion

Ecological Patterns

The data suggest that the site with a higher density of howler monkeys, TBS, is characterized by both a higher quality and density of resources compared to that of PPRA, which has a lower density of howler monkeys. At TBS, the mature and young leaves combined have a significantly higher total percent protein and mature leaves have a significantly higher ratio of protein-to-fiber (acid detergent fiber) than PPRA. However the fiber content (both acid detergent and neutral detergent) across species did not differ between sites, suggesting that it is the overall higher level of protein driving this pattern. In addition TBS has a higher stem density of these high quality resources, reflected by a greater number of stems representing the top ten species with the highest protein content present in the botanical plots (TBS: 15.4% of total botanical plot tree density; PPRA: 6.9% of total botanical plot tree density). Additionally, while there was no significant difference found in the phenolic content of leaves across species between sites, the data suggest that TBS also has a higher density of stems characterized by lower levels of total phenolics present in botanical plots (TBS: 13.9% versus PPRA: 5.9%). In both cases, the density of stems higher in protein levels and lower in phenolics, TBS had more than double the percentage of total tree density represented by these species compared to PPRA.

Thus it appears that three of the four ecological variables tested are supported at the high howler density site. The resources at TBS are higher quality, in the form of percent protein and protein-to-fiber ratio in the leaves, and there was a greater density of stems lower in phenolics at TBS suggesting that there is a greater availability of leaves at TBS that are higher in total energy and easier to digest.

Ecology and Demography

Given the higher quality of food at TBS as well as data from 1) previous studies illustrating primate responses to variation in food availability and 2) population characteristics of howler monkeys in high density sites, the following trends in demography should be present: 1) The average number of males per group is **higher**, 2) The average number of adult female howler monkey per group is **higher** but does **not exceed four**, 3) The average group size is **larger** and 4) The ratio of infants and juveniles to adult females is **higher**. Although the overall density is higher at TBS, there were no significant differences found in the demographic characteristics of average group size or group composition. The similarity in average group size between sites may be in large part due to the presence of newly formed groups, which were only observed at TBS. In fact two of the 10 groups at TBS were characterized as “new groups” or groups that had only one male and female with or without offspring (X= 2, 3), while PPRA had none. New groups are smaller than larger established ones and therefore lower the overall mean group size as well as the average number of males and females. Crockett (1996) also found that differences in the mean group size of *Alouatta seniculus* between two sites in Venezuela were reduced over time mainly due to differences in the proportion of newly formed groups created by dispersing individuals, rather than from fissioning groups, and emphasized the role of female dispersal in maintaining small group size. This is particularly relevant to the groups at PPRA because human hunting occurs in the region adjacent to the study site, and although it has been infrequent, it also occurs within the site which could make the prospect of forming new small groups a high risk behavior.

Furthermore, the average number of adult females per group (2.67 at PPRA versus 1.78 at TBS) was higher at PPRA instead of TBS. While these were not significantly different, it is contrary to the predicted demographic patterns for howlers occurring at higher population density. One reason there are more females per group at PPRA may be that there is less female-female aggression at this site. It has been suggested that *Alouatta seniculus* has high rates of infanticide and that groups with higher numbers of females are more at risk of a group takeover (Crockett, 1996; Crockett and Janson, 2000; Janson and van Schaik, 2000). This study showed similar results to other published data on red howler monkey group composition in that no group exceeded four females, a limitation thought to be imposed by infanticide avoidance in this species (Crockett, 1996; Crockett and Janson, 2000). Females are known to be highly aggressive towards immigrant females trying to join their group and will even evict their daughters as a way to reduce the number of females in their own group (Crockett, 1996; Janson and Crockett, 2000). At PPRA, however, the density may be so low that the threat of infanticidal behavior is less because there are fewer males that could take over groups. Under this circumstance female-female aggression may be relaxed and thus howlers can afford to have larger groups, as long as feeding competition is not too high.

A second reason for larger groups could be that the cost of dispersal is higher at PPRA due to the presence of occasional hunting in and around the study site. Hence, all else being equal, females should be less inclined to kick their daughters out of the group, resulting in larger groups. There is some evidence to support the first scenario from the vocalization rates observed between the sites. Howler long call vocalizations are thought to act both as an honest signal of male vitality and strength as well as a spacing mechanism (Sekulic, 1982; Crockett, 1998) and as such could be used as a proxy to indicate male-male competition. Therefore long call vocalizations might be expected to be lower in areas of lower male-male competition and lower population density, which is the case at PPRA (long calls occur 4.7% of the time at PPRA versus 40.6% of the time at TBS).

The ratio of immature to females also did not differ between sites, however it was slightly higher at TBS (1:0.88) compared to PPRA (1:0.62). When data on immatures are combined and related to the number of females in a population it is referred to as a "recruitment" rate and can reflect the general health of a population. It takes a snapshot of a population and the immatures that are counted are all infants and juveniles that were born minus those that have disappeared or died. To some degree it will relate to habitat quality (affecting birth rate and to some degree mortality), but since it also relates to mortality it represents other factors as well (e.g., predation). The higher ratio at TBS could be a possible indication that the overall health of this population is slightly higher. Although, considering this study is short term and can not adequately assess birth and death rates in the population, these ratios should be looked at with caution.

Lastly, there was no difference found between the percentage of infants and juveniles in the population, which suggests that the birth rates are similar between the two sites. Assuming that the reasons for this are not due to differences in mortality, but rather to differences in food availability, it is expected that populations of different densities at equilibrium will be equally constrained reproductively (Mangel and Clarke, 1989). It is therefore possible that both of the populations are at carrying capacity, which is likely to be lower at PPRA and higher at TBS due to differences in food quality and density. While a mortality rate per se could not be calculated, it can be qualitatively noted that only one disappearance (juvenile female) was recorded at TBS and none were recorded at PPRA. However, behavioral patterns of the howler monkeys at PPRA may be indicative of past hunting pressure that is affecting current population density. For example, howler monkeys at PPRA are very cryptic in their behavior, bridging through the canopy more quietly than those at TBS and rarely vocalizing, making them harder to find and follow. These behaviors could suggest that hunting pressure may be affecting the difference in population density between the two sites. However, it is uncertain whether hunting pressure alone is actually heavily impacting this difference. When the primate community is considered as a whole there is not a significant relationship between the comparative density ratio in the hunted versus the non-hunted region and annual harvest rates, as would be expected if primates were being harvested to the point where it has a measurable effect on the population (Derby in preparation). However, all of the primate species surveyed at PPRA were found to have larger group sizes than those at TBS, which could possibly be a predation avoidance response to hunting (Derby in preparation).

It is important to point out that demographic parameters vary over time and space, thus short term studies examining patterns of demography will only capture a specific static snapshot of this variation. It has been shown that aspects such as population density, group size, age-sex composition, natality and juvenile recruitment all vary considerably within populations over time (Struhsaker, 2008), requiring continued long-term monitoring from comparative studies in order to understand the full spectrum of variation that exists within and between populations.

Ecology and behavior

A summary of the ecological and behavioral variables is shown in Table 6. The data reveal that while H2 (A high protein-to-fiber ratio in the leaves supports a high *Alouatta* density), H3 (A high density of resources low in phenolic content supports a high *Alouatta* density) and H4 (A high density of resources with high protein-to-fiber ratios supports a high *Alouatta* density) are supported by the ecological data, none of the predictive sets of behavioral correlates for any of the hypotheses are fully supported (Table 7). The prediction that all of the hypotheses failed to support was a significantly different resting time. One possible explanation for this is that howler monkeys may be at the minimal resting time required for digestion. When the resting times of six *Alouatta* species from 14 separate studies are examined, the average percentage of time spent resting is 63.9%, ranging from 55.9%-79.7% (Table 7). Resting time reported for *Alouatta seniculus* in particular is on the higher end of this range (78.5%: Gaulin and Gaulin, 1982). This study found that the average time spent resting at TBS was 53.7%, and 59.4% at PPRA, which are at the low end of the range for this genus, but are much lower in comparison to the resting time reported for other red howler monkeys.

Other folivorous primates which are hindgut fermenters, however, have resting times reported to be lower than that of the howlers in this study (Table 7). For example, *Gorilla gorilla beringei* is reported to, on average, spend only about 40% of their time resting (Yamagiwa, 1986; Watts, 1988), while *Gorilla gorilla gorilla* spends a similar amount at 37.3% (Lodwick, unpublished data). In addition, folivorous lemurs such as sifakas (e.g., *Propithecus candidus*) spend on average 45% of their time resting (Santoreli et al., 2006). Thus, while it appears other genera with hind-gut digestion adaptations for folivory are able to spend a lower amount of time resting, the howler monkeys at TBS do have a slightly lower resting average than the range reported for six species of *Alouatta*, and a much lower resting average reported previously for this species. This suggests that there may be some support for the idea that the howler monkeys in this study are potentially at the minimal resting times required for digestion in this species, and perhaps why the prediction of a significantly different resting time was not met.

The remaining predictions for both H3 and H4 were supported by the data, suggesting these factors are likely playing the largest roles influencing the difference in howler population density between the sites. Only one of the predictions for H2 is supported, and thus it is not likely that the ratio of protein-to-fiber on its own is affecting howler density as much as the combined effects of resource quality and density. Due to the higher density of higher quality food resources at TBS the distance between patches is shorter, enabling howlers to spend less time moving between patches and to feed on a larger number of patches per day, ultimately resulting in a higher time spent feeding per day. There was no difference in daily path length between the sites, however, so the howlers at TBS are accomplishing this not by moving further each day but possibly by moving faster. This aspect can be looked at indirectly by taking the average time spent moving per day and converting it to a 12 hour day, which is representative of a howler monkey daily activity cycle. For example, howlers at PPRA spend on average 25.4% moving per day, if this converted to a 12 hour day they are spending 3.05 hrs moving. When the average daily path length is now divided by this time it equates to a movement rate of 147 m/hr (448.3 m/3.05 hrs = 147 m/hr). Contrast this with the much lower time spent moving at TBS, only 14.1%, and divide it by the longer daily path length and the resulting movement rate is nearly 2.5 times faster (616.7m/1.69 hrs = 364.9 m/hr). The ability to move more quickly between patches may again tie back in to the overall higher amount of protein, and thus energy, available in the leaves and allow howlers to be less energetically limited at TBS compared to PPRA. Furthermore, this behavior may be indicative of greater inter-group scramble competition at this site due to higher howler group density.

Interrelationships of Ecology, Demography, and Behavior

This study investigated the differences in howler monkey population densities and how it relates to food, demography, and behavior. Focusing on the factors which potentially or actually influence density, rather than just a numeric density value, may allow for a more complete understanding of the way in which the ecology of habitat affects population density. In addition, testing multiple ecological factors that can be distinguished by how they should affect the behavior of folivorous primates is a step in the right direction to help isolate which closely related biological factors are influencing differences in folivore density. This study showed that the factors likely to be playing the largest roles influencing the differences in howler monkey population density in Yasuní N.P. are a combination of higher protein content in leaves and a higher density of these resources, along with a higher density of resources low in phenolics. The possibility of hunting pressure, however, cannot be discounted in possibly affecting the difference in density between the two sites.

Although howler monkeys are characterized by a different digestive morphology then Old World folivores, these results support previous findings in both Asian and African leaf-eating monkeys (e.g., Waterman et al., 1988; Peres and Janson, 1999; Wasserman and Chapman, 2003; Chapman et al., 2004, 2002).

As with all short term studies however, it is important to view the population density and demographic patterns within and between sites as part of a larger construct of animal life history patterns that change over time and space (Struhsaker, 2008). There is no doubt that the best strategy for acquiring this information on primate populations, and the most relevant for conservation management strategies, is certainly long-term population monitoring. However, because many primate populations are now vulnerable to local extinction due to increased human disturbance activities in and around tropical habitats (e.g., Alvard et al., 1997; Peres, 1997a), there is an urgency to try and identify areas and populations that are at greatest risk. I suggest that short term studies, if approached from a multivariate and integrative viewpoint, may be helpful in identifying the factors that most greatly influence primate density and allow conservationists to target regions characterized by these parameters as high priority. In this way habitats that are capable of sustaining higher densities of primates will be conserved, which may foster the sustainability of vulnerable or at risk species or populations (as long as hunting pressure can remain low) and provide the opportunity for long-term studies to take place.

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4.7 Tables and Figures

TABLE 1: Plant nutritional analysis methods

Nutrient Variable	Procedure	Reference
Nitrogen	Kjeldahl procedure	Association of Official Analytical Chemists, 1984; Dumas, 1994
Protein (amino acids: soluble/extractable protein)	Pharmacia Biotech Ultrospec 1000, λ 595 nm	Ganzhorn, 1988; Koenig et al., 1998
Detergent Fiber Analysis	Van Soest method for NDF/ADF	Van Soest, 1994
Lipids	Ether extract using 200ml dry petrolether	Ganzhorn, 2004
Carbohydrates (sugars)	Pharmacia Biotech Ultrospec 1000, λ 490 nm	Ganzhorn 2004
Phenolics	Condensed (procyanidin) tannins	Oates et al.1980; Waterman et al. 1983; Ganzhorn 1988

TABLE 2: Plant nutritional data

	Flowers		Fruits		Leaves		Pods/Seeds	
	PPRA (N=2)	**TBS (N=7)**	**PPRA (N=20)**	**TBS (N=22)**	**PPRA (N=27)**	**TBS (N=37)**	**PPRA (N=6)**	**TBS (N=4)**
Nitrogen (%)	1.73 (1.58-1.88)	3.03 (2.02-4.47)	1.39 (0.70-2.55)	1.47 (0.51-4.24)	2.59 (1.42-5.67)	2.98 (1.34-4.96)	2.09 (0.88-3.29)	1.39 (0.73-2.01)
			t = -0.40, P = 0.68		t = -1.64, P = 0.10			
Protein (%)	8.35 (7.33-9.36)	4.21 (1.28-7.25)	4.86 (0.42-11.22)	4.75 (1.54-12.74)	4.93 (0.81-13.89)	6.78 (0.66-14.88)	4.74 (1.65-7.82)	7.85 (3.72-10.21)
			t = 0.11, P = 0.90		t = -2.45, *P = 0.01			
Sugar (%)	11.92 (6.38-17.47)	5.02 (2.10-10.52)	19.98 (2.74-55.78)	12.34 (2.04-33.61)	6.43 (0.75-22.83)	6.69 (1.30-36.72)	7.2 (3.74-10.66)	19.08 (3.05-32.87)
			t = 1.91, P = 0.06		t = -0.17, P = 0.86			
Fat (%)	1.44 (1.15-1.74)	1.03 (0.58-1.47)	6.56 (0.02-35.15)	6.32 (0.52-31.95)	1.41 (0.09-2.66)	2.18 (0.08-7.53)	0.63 (0.26-1.42)	1.04 (0.77-1.50)
			t = 0.08, P = 0.93		t = -1.67, P = 0.10			
Phenolics	3.99 (3.87-4.11)	1.21 (0.42-1.02)	1.66 (0.41-5.65)	1.68 (0.28-5.73)	4.89 (0.36-38.14)	4.15 (0.24-20.09)	1.04 (0.66-1.42)	8.75 (0.68-22.75)
			t = -0.05, P = 0.95		t = 0.48, P = 0.63			
Protein:Fiber (ADF)					0.07 (0.01-0.40)	0.10 (0.01-0.23)		
					t = -2.33, *P = 0.03			

TABLE 3: Tree species density: protein content. Table shows the top ten tree species at each site that have the highest average protein content (TBS: #1-10; PPRA: #11-20) and how many individual trees of these species occur within the botanical plots at each site.

Family	Genus	Species	# of trees/1.5 ha		Avg % Protein	
			TBS (N=140)	PPRA (N= 51)	TBS (*Avg = 9.08 SD = 2.29)	PPRA (Avg = 7.88) SD = 2.71)
1. Fabaceae	Pterocarpus	Rohrii	7	3	14.88	
2. Fabaceae	Lonchocarpus	seorsus cf.	1	1	11.73	
3. Fabaceae	Browneopsis	ucayalina	26	0	8.86	
4. Fabaceae	Parkia	multijunga	2	0	8.85	
5. Moraceae	Clarisa	Racemosa	1	1	8.43	
6. Sapotaceae	Diploon	sp.	0	0	8.17	
7. Moraceae	Sorocea	sp.	7	1	7.73	
8. Moraceae	Ficus	Piresiana	1	1	7.68	
9. Combretaceae	Terminalia	amazonia	0	0	7.58	
10. Dichapetal	Tapura	Juruana	1	4	6.93	
1. Sapotaceae	Pouteria	sp.	14	17		13.89
2. Mimosaceae	Inga	Yacoana	0	0		11.59
3. Sapindaceae	Paullinia	Bracteosa	0	0		8.43
4. Rubiaceae	Warszewiczia	Coccínea	0	2		8.43
5. Fabaceae	Tachigali	guianensis	0	0		7.75
6. Fabaceae	Browneopsis	sp.	26	0		6.09
7. Fabaceae	Brownea	grandiceps	30	14		6.05
8. Pabaceae	Marmaiotylum	Basijugim	0	0		5.55
9. Myristicaceae	Otoba	glycycoorpa	23	7		5.55
10. Fabaceae	Inga	thibaudiana	1	0		5.51

TABLE 4: Tree species density: phenolic content. Table shows the top four tree species at each site that have the lowest average phenolic content (TBS: #1-4; PPRA: #5-8) and how many individual trees of these species occur within the botanical plots at each site.

Family	**Genus**	**Species**	**# of trees/1.5 ha**		**Avg % Phenolics**	
			TBS **(N=127)**	**PPRA** **(N= 44)**	**TBS** **(Avg = 0.50 SD = 0.21)**	**PPRA** **(Avg = 0.49 SD = 0.11)**
1.Fabaceae	Inga	sp.	76	0	0.24	
2. Moraceae	Sorocea	Pubivena	1	20	0.43	
3. Moraceae	Ficus	“lija”	3	0	0.59	
4. Fabaceae	Browneopsis	Ucayalina	25	0	0.72	
1. Ulmaceae	Celtis	Iguanea	1	23		0.36
2. Bombacaceae	Matisia	Malacocalys	10	0		0.44
3. Bibnoniaceae	Memora	Cladotricha	0	1		0.51
4. Tiliaceae	Apeiba	membranacea	11	0		0.60

TABLE 5: Group demographic characteristics

Site	# of groups	Avg # Ad M	Avg # SAd M	Avg # Ad F	Avg # SAd F	Avg # Juv	Avg # Inf	Avg Total #
PPRA	3	1.00	0.67	2.67	0.33	1.00	0.67	6.33
TBS	10	1.11	0.50	1.78	0.63	0.89	0.75	5.44
Mann-Whitney U Test Values		U = 12.0 Z = -0.28 P = 0.78	U = 10.5 Z = 0.55 P = 0.78	U = 7.5 Z = 1.20 P = 0.23	U = 11.5 Z = -0.37 P = 0.71	U = 12.0 Z = 0.28 P = 0.78	U = 13.0 Z = 0.09 P = 0.93	U = 9.0 Z = 0.83 P = 0.41

TABLE 6: Summary of ecological and behavioral variables

*** Indicates a significant difference**	**PPRA (lower density)**	**TBS (higher density)**
Home range (MCP)	**Smaller** (23.6 ha)	**Larger** (27.4 ha)
Avg. daily path length	No difference	No difference
Avg. B/T patch distance*	**Longer** (99.6 m)	**Shorter** (74.4m)
Avg. patch residency time	No difference	No difference
Avg. # of feeding trees/day*	**Lower** (5.5)	**Higher** (9.3)
% Feeding*	**Lower** (14.7)	**Higher** (31.5)
% Moving	Higher (25.4)	Lower (14.1)
% Resting	No difference	No difference
% Socializing	No difference	No difference
Inter-group encounters observed	**Lower** (1)	**Higher** (5)
Relative long call vocalization frequency*	**Lower** (5.3)	**Higher** (97.9)
% Plant protein*	**Lower** (4.93)	**Higher** (6.78)
Protein:Fiber ratio in leaves*	**Lower** (0.07)	**Higher** (0.10)

TABLE 7: Summary of the ecological hypotheses found to be supported and their corresponding predictions. This table shows the three hypotheses that were supported by the ecological data and their corresponding predictive sets. Behavioral predictions that were supported have a check mark while those that were not supported have an X.

Hypotheses	**Predictions**				
H2 *A high protein-to-fiber ratio in leaves supports a high* Alouatta *density*	Higher % Rest ✗	Higher % Feed ✓			
H3 *A high density of resources low in phenolics supports a high* Alouatta *density*	Shorter % Rest ✗	Higher % Feed ✓	Shorter % Move ✓	Shorter BPD ✓	
H4 *A high density of resources with high protein to fiber ratios supports a high* Alouatta *density*	Higher % Rest ✗	Higher % Feed ✓	Shorter % Move ✓	Shorter BPD ✓	> # of Trees Fed on/Day ✓

TABLE 8: Average time spent resting by folivorous hind-gut fermenting primate species

Genus and Species	% Time Spent Resting	Study Length (Months)	Source
Alouatta belzebul	58.7	10	Pinto, 2002
A. belzebul	55.9	13	Bonvicino, 1989
A. caraya	61.6	12	Bicca-Marques, 1993
A. caraya	56.0	12	Prates and Bicca-Marques, 2008
A. guariba	71.8	13	Mendes 1989,
A. guariba	57.6	12	De Marques 1995, 1996
A. guariba	63.7	12	Chiarello, 1993
A. palliata	65.5	10	Milton, 1980
A. palliata	79.7	12	Estrada et al., 1999
A. palliata	72.5	49	Teaford and Glander, 1996
A. palliata	~56	15	Stoner 1996,
A. palliata	57.0	13	Williams-Guillén, 2003
A. pigra	61.9	14	Silver et al., 1998
A. seniculus	78.5	10	Gaulin and Gaulin, 1982
A. seniculus	53.7	7	Derby, this study
A. seniculus	59.4	3	Derby, this study
Gorilla. gorilla beringei	43.7	9	Yamagiwa, 1986
G. gorilla beringei	34.4	17	Watts, 1988
G. gorilla gorilla	37.3	11	Lodwick, unpublished data
Propithecus candidus	45.0	14.5	Santorelli et al., 2006

FIGURE 1: Map of the study sites

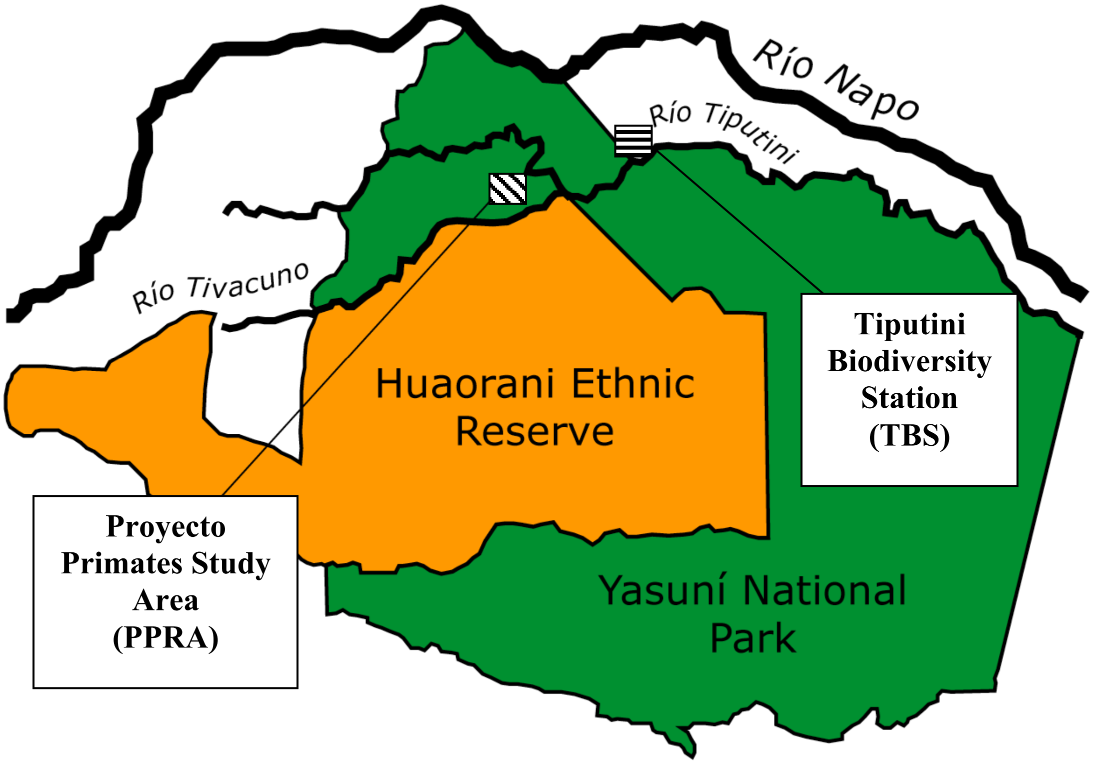


FIGURE 2a: Average number of howler long calls per day at TBS. The figures represent the monthly average of howler long calls at (a) TBS and (b) PPRA. The Y axis shows the average number of vocalizations per day and the X axis shows the months with the total number of vocalization events and the total number of days at the study site in parentheses.

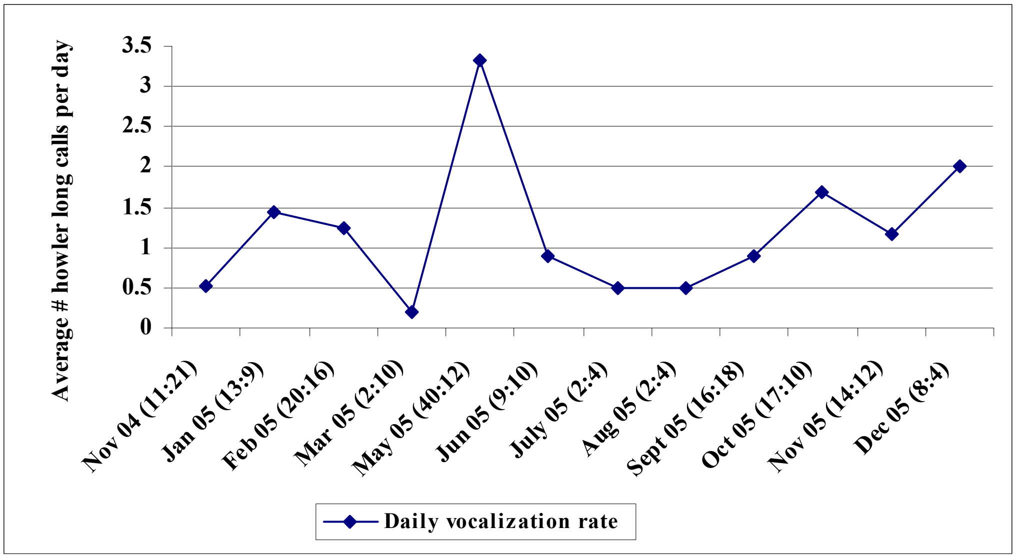


FIGURE 2b: Average number of howler long calls per day at PPRA

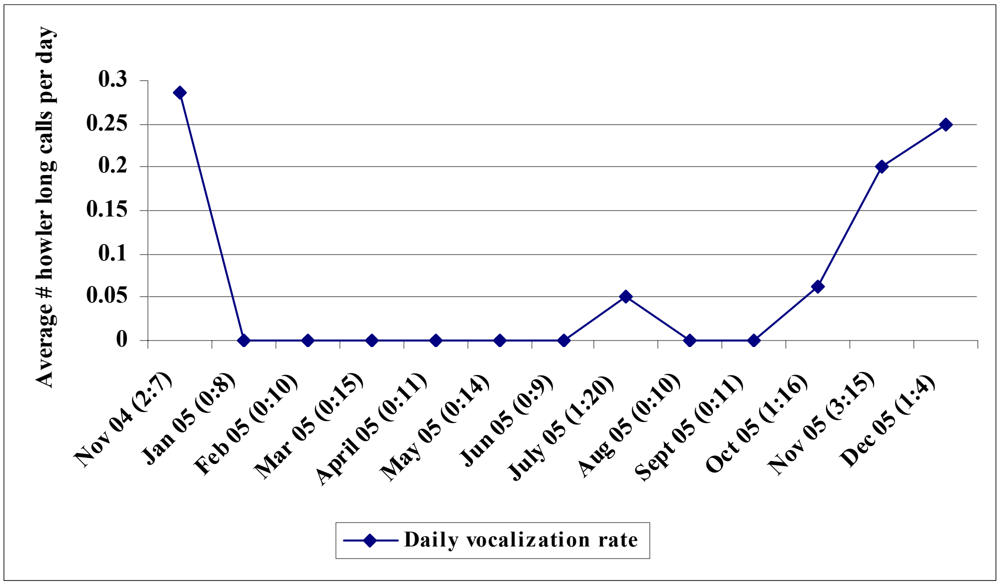


FIGURE 3: Average daily path length

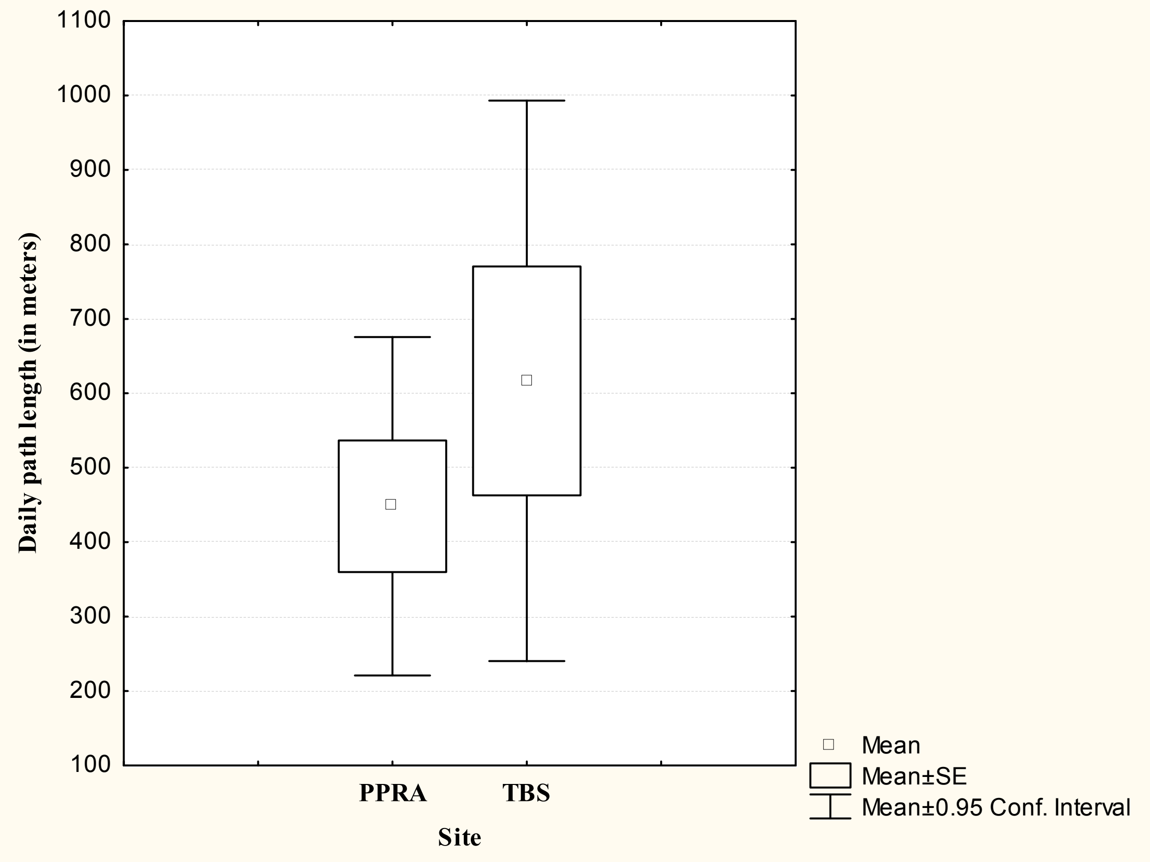


FIGURE 4: Average monthly activity budgets

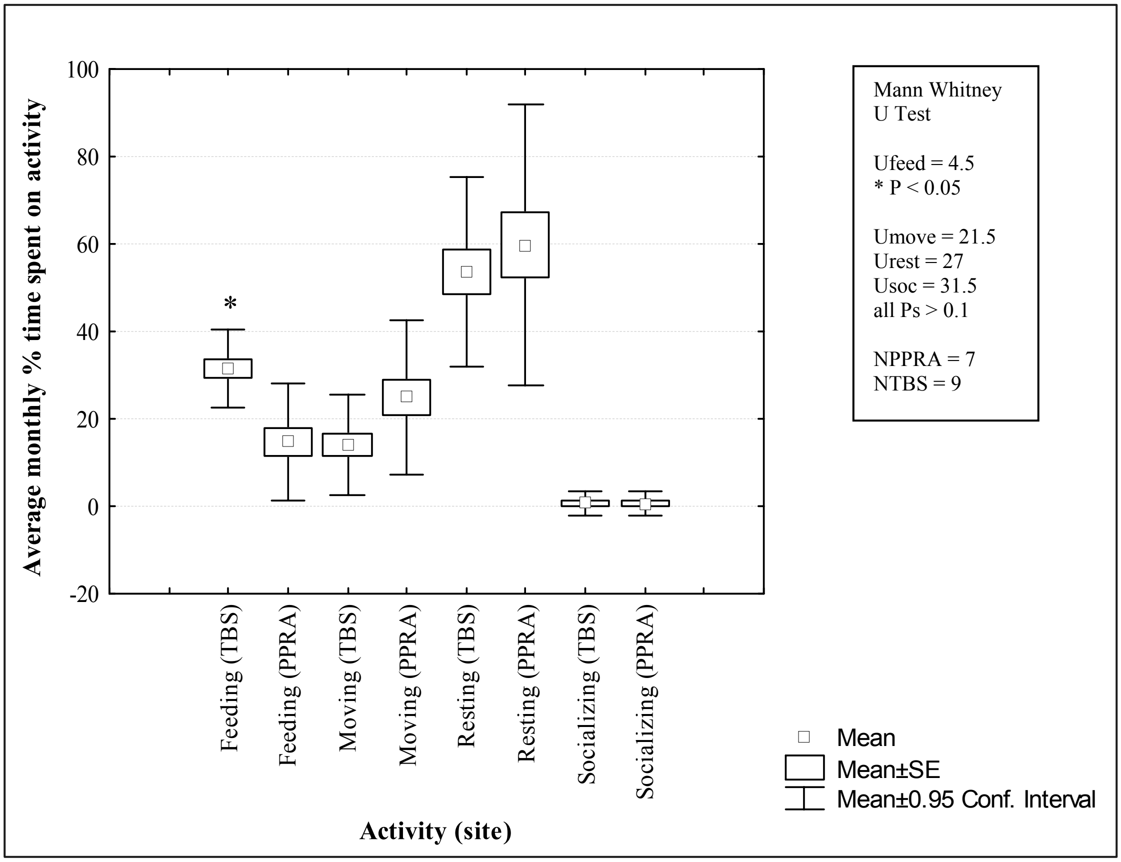


FIGURE 5: Monthly average percentage plant part in the diet

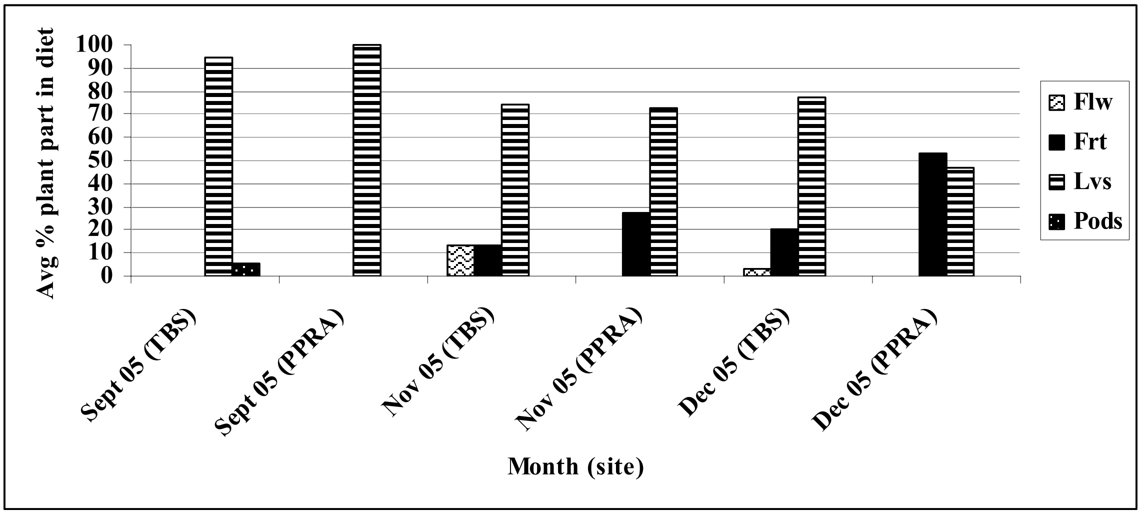


FIGURE 6: Average inter-patch distance

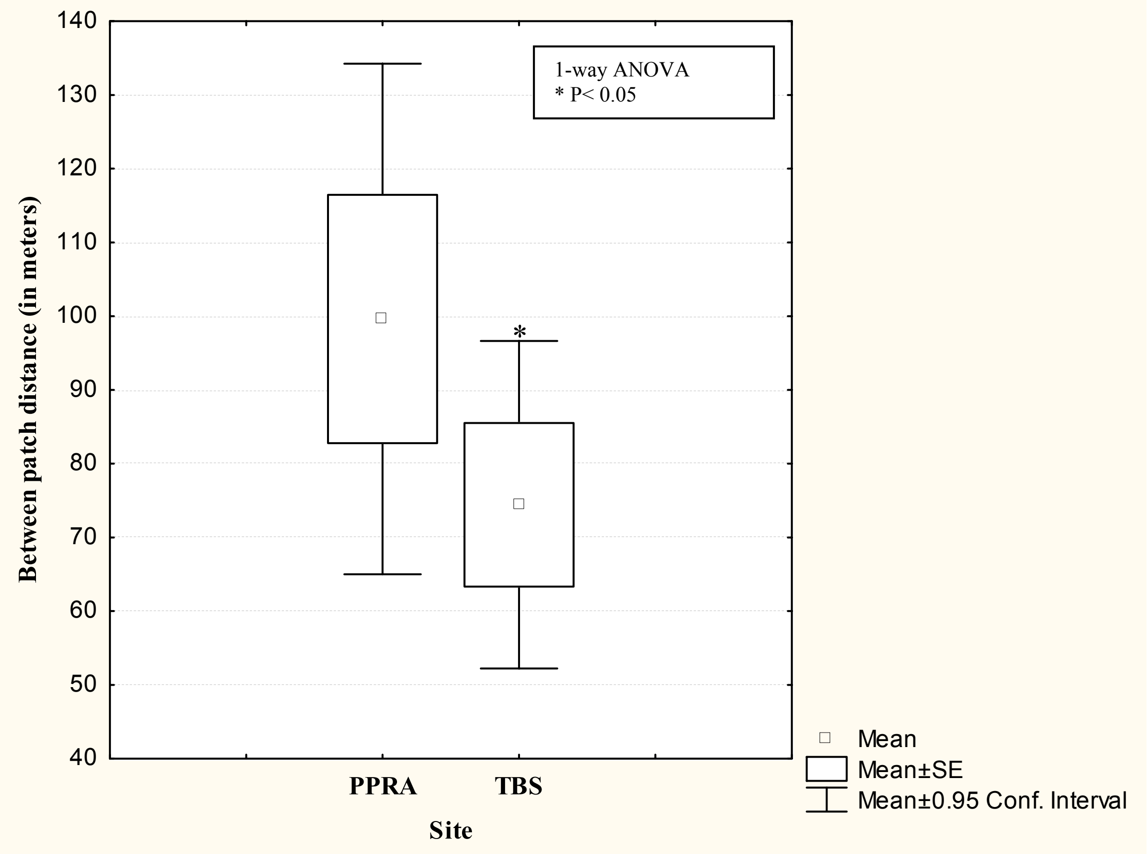


FIGURE 7: Average number of feeding trees used per day

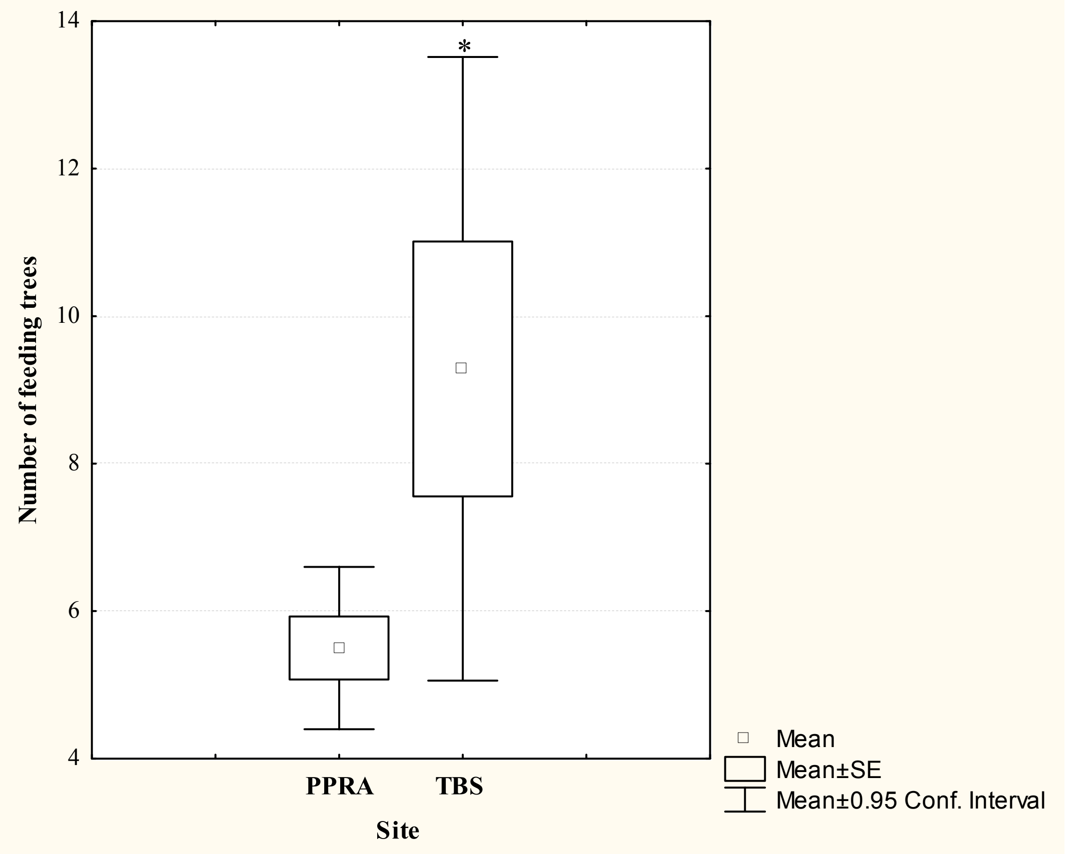
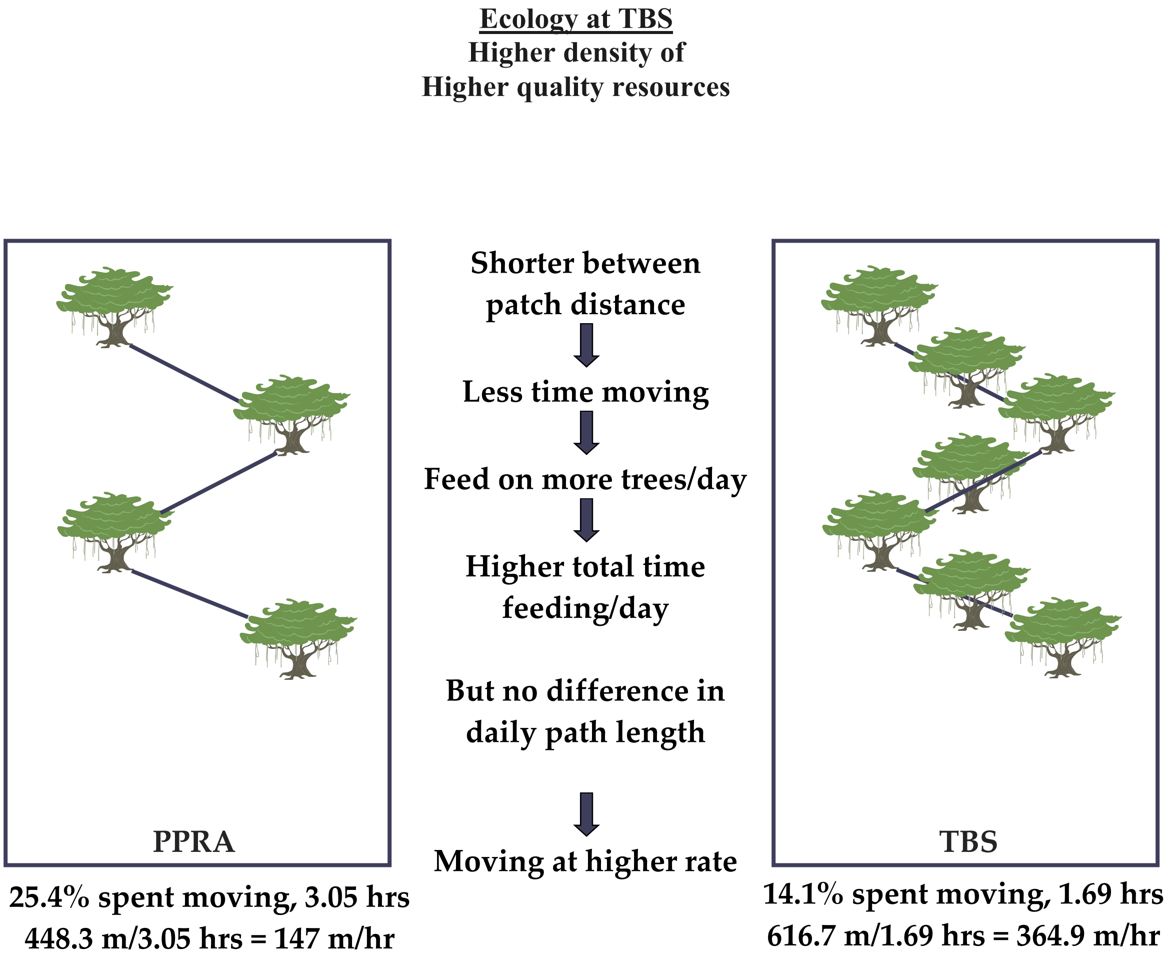


FIGURE 8: Ecological influences on howler monkey behavior at TBS. The diagram illustrates the connection between a higher density of higher quality food resources at TBS influencing the distance between patches to be shorter, enabling howlers to spend less time moving between patches, and allowing them to feed on a larger number of patches per day, ultimately resulting in a higher time spent feeding per day. The howlers are not moving further at TBS, but are moving at a faster rate reflected by the daily average path length divided by the average number of hours spent moving per 12 hour day.



CHAPTER 5

How Ecology Affects the Behavior and Demography of Red Howler Monkeys (*Aloutta seniculus*) in Western Amazonian: Synthesis and Conclusions

5.1 Introduction

The aim of this study was to examine the relationships between ecology, demography and behavior in order to address the question of which factors most influence folivore density in two populations of howler monkeys (*Alouatta seniculus*). The premise of this endeavor stemmed from previous work that illustrated there were numerous aspects of forest ecology which could potentially affect primate, and specifically folivore, population density (e.g., **food quality**: Waterman et al., 1988; Oates et al., 1990, Ganzhorn, 1992, Chapman et al., 2002, 2004; **seasonality:** Janzen, 1975; Davies, 1994; for a recent review see Brockman and van Schaik, 2005; **habitat heterogeneity:** Bourliere, 1985; Terborgh and van Schaik, 1987: **soil fertility**: Peres, 1997; **density and availability of food resources**: e.g., Terborgh and van Schaik, 1987; Davies, 1994). Additional factors such as hunting (Redford, 1992; Alvard, 1997, Peres, 2000) and forest fragmentation (DeGama-Blanchet and Fedigan, 2006) have also been shown to affect primate population density as well. Attempting to narrow down and tease apart many of the closely related biological factors thought to affect primate density is not only relevant because it may further our understanding of the process of behavioral adaptations (e.g., Oates et al., 1990; Davies, 1994), but also because it has become a critical component in contributing aid to conservation endeavors (e.g., Chapman et al., 2002; Struhsaker et al., 2004).

This research combined the cumulative work of various theoretical and field work studies that investigated 1) which ecological factors may influence primate, and specifically folivore, density, 2) how ecology may affect the demography of a population and 3) how ecology should affect the behavior of primates in a given habitat. I then synthesized and integrated this information into a multivariate design that tested which ecological variables best predicted the observed patterns of behaviors in a folivorous Neotropical primate (*Alouatta seniculus*), which has received relatively little attention on this issue compared to African and Asian taxa (but see Milton, 1980; Peres, 1997).

This design was carried out in the context of a comparative study of two populations of *Alouatta seniculus*, the red howler monkey, in Yasuni N.P. Ecuador, which were geographically close but occurred in different forest types and at different densities. A priori predictions were made as to how, all aspects being equal, each ecological component should affect primate behavior, yielding mutually exclusive predictive sets for each of the variables. The predictions were derived from examples provided in the literature which indicated differences in the activity budgets of folivorous primates in response to variation in food availability (e.g., Dasilva, 1992; Fashing et al., 2007; Korstjens and Dunbar, 2007).

There were three main goals of this study. The first was to evaluate which ecological variables, possibly affecting population density, differed between the sites (Table 1). The second was to identify whether high population density was linked to the following demographic characteristics as proposed for other primates: 1) The average number of males per group is **higher** (Crockett, 1996), 2) The average number of adult female howler monkey per group is **higher** (Crockett, 1996), but does **not exceed four** (Crockett, 1996; Crockett and Janson, 2000; Horwich et al., 2001), 3) The average group size is **larger** (Crockett, 1996) and 4) The ratio of infants and juveniles to adult females is **higher**, (Sadlier, 1969; Jorde and Spuhler, 1974). Lastly, in order to try and tease apart which aspects of forest ecology were contributing to howler monkey densities in Yasuni N.P., a comparison was done to test which ecological variable(s) had behavioral predictive sets that best matched the observed patterns of *Alouatta* behavior.

5.2 Summary of Ecological Testing

Eight ecological variables were tested in this study (Table 1), the first of which was hunting and was addressed in chapter two. There were two main questions addressed in this chapter, whether hunting pressure correlates with body size and whether it has a measurable effect on the population density. A comparative density ratio was first calculated to measure between site density differences by dividing species' density in the lightly hunted site (PPRA) by the non-hunted site (TBS). Additionally, in order to look at the relationship between harvest rate and body mass, which is likely confounded by the population density of these species, an index of hunting pressure was calculated separately for each species. This index was defined as the number of individuals harvested per year (harvest data taken from Franzen, 2006) divided by the raw population density, which was assumed to be the density from the non-hunted site. The index was used to represent the relative ratio of hunted to available individuals. It was expected that if hunting was mainly driving lower population density in the hunted site then species with the lowest comparative density should also have the highest hunting pressure index.

The population density data indicated that the majority of species in this study occurred at slightly lower densities at PPRA, where there had been a very low level of hunting over the past decade, versus TBS, where there had not been any hunting observed (total primate biomass at PPRA is 284.19 kg/km^2, with 33.3 kg/km^2 represented by howler monkeys, while at TBS it is 410.54kg/km^2 with howler monkeys comprising 76.26 kg/km^2). In addition, the data indicated that large bodied taxa (*Alouatta, Ateles,* and *Lagothrix*) had the highest annual harvest rates and occurred at significantly lower densities in the hunted site compared to that of small and medium sized taxa. Furthermore, two of the three large bodied primates show a relationship between a high hunting pressure and a low comparative density ratio (*Alouatta* and *Lagothrix*).

When all taxa were compared, there was not a significant relationship between the comparative density ratio in the hunted versus the non-hunted region and annual harvest rates, as would be expected if larger-bodied primates were differentially harvested to the point where that harvest had a measurable effect on the population. However this measure assumes that all populations should respond to hunting pressure in the same way, which may not necessarily be the case. A capuchin monkey, for example, may not respond in the same way as a saki monkey or a spider monkey would due to differences in behavior, social organization or life history patterns. That being said, all species were found to have larger group sizes at PPRA versus TBS, which could potentially be a predation avoidance response. This grouping pattern would likely only be beneficial if entire groups were not pursued and killed by hunters, which is a strategy used by the

Aché in Paraguay (Stanford and Wrangham, 1998). However, the culling of entire groups during hunting episodes has not been observed or recorded to occur by the Waorani. The extreme cryptic behavior of the howler monkeys at PPRA also seems to suggest they may be responding to hunting pressure by trying to reduce detection as much as possible. The fact that they had the lowest comparative densities but did not have the highest harvest rates may even indicate they are responding to past high hunting pressure, and are not harvested as much now because their densities are reduced and they are in fact harder to find. Although this hypothesis is reasonable, I suggest it may be unlikely in this study for three reasons: 1) howler monkey densities are reported to be generally much lower in *terra firme* habitats across Amazonia (Peres, 1997), 2) there has been little hunting in the site for the past ten years (Di Fiore, personal communication), and 3) *Alouatta* reproductive rates are higher in comparison to the other large bodied atelines (Di Fiore and Cambell, 2007). I suggest that these factors, together with the density and behavioral data collected on red howler monkeys during this study, suggest that hunting is likely affecting the howler monkey population to some degree, but that in addition, habitat ecology is also contributing to the difference in density observed between these two populations.

Next, chapter three evaluates ecological variables two, three and four. The hypothesis for variable two states that a habitat with a more heterogeneous forest and higher soil fertility should support a higher *Alouatta* population density. Forest heterogeneity, which has been shown to co-vary with soil fertility (Peres, 1997), was tested by using the Simpson's Diversity Index (D) to look at species diversity between sites. Additionally, soil was examined for macronutrients and pH levels. Contrary to the prediction, the study site characterized by *terra firme* habitat and lower howler population density (PPRA) had a significantly higher diversity index than the seasonally flooded habitat with higher howler density (TBS), although both sites were indicative of hyper-diverse and extremely heterogeneous environments. There were also no overall differences in soil fertility between sites. There were, however, significant differences between pre- and post flooding samples and between microhabitats within the sites. First, post flooding samples from both sites were found to have levels of Mn that were significantly higher and Al that were significantly lower than pre-flooding samples. Second, the post-flooding samples from riparian micro-habitats were found to be significantly higher in pH, Ca, and Mg than non-riparian at both sites. Furthermore, when the post-flooding samples from riparian transects at both sites were combined and compared to all non-riparian transects, these levels were significant. Thus, no significant differences were found between sites, but rather between the microhabitats within sites in that the flooded, or riparian transects, were found to be higher in several macronutrient and lower in pH. Due to the fact that TBS has a more extensive area of flooded forest, and thus a larger area characterized by higher soil fertility and more hospitable pH levels, this data was suggested to partially support variable two.

The hypothesis for variable three states that a habitat with less phenological seasonality should support a higher *Alouatta* population density. This hypothesis was not supported by the data. Although the temporal patterns of when the peak percentage of trees in each phase occurred were somewhat different between sites, the total percentage of trees scored in each phenophase per month did not differ significantly between sites. On the other hand, the hypothesis for variable four, which states that a habitat higher in phenological productivity should support a higher *Alouatta* population density, was supported. The total amount of new leaves, flower buds and mature flowers produced per month were significantly higher at TBS. It is has been proposed that higher phenological productivity may be related to high soil fertility and more hospitable soil pH levels (e.g., Woodward, 1996). The flooded transects, which were higher in soil nutrients and lower in pH, were in fact found to have a higher production of fruit compared to the non-flooded transects. Additionally, the flooded transects at TBS had a significantly higher production of fruit than did the flooded transect at PPRA.

The remaining ecological variables were examined in chapter four. Hypotheses five and six reflect solely plant quality (i.e., a lower level of phenolic content and a higher overall protein and/or higher ratio of protein-to-fiber in leaves, respectively, support a higher *Alouatta* population density) while seven and eight reflect the combined effects of both quality and density (i.e., a higher density of resources low in phenolics and a higher density of resources higher in overall protein and/or ratio of protein- to-fiber in leaves, respectively, support a higher *Alouatta* population density). While there was no difference in the phenolic content across species between sites, the resources at TBS were of higher quality, in the form of overall percent protein in all leaves and protein-to-fiber ratio in the mature leaves. There were no differences in fiber, however, suggesting that protein levels were likely driving this difference. Lastly, a greater density of stems lower in phenolics and higher in percent protein were found at TBS, suggesting that there was a greater availability of leaves at TBS that are higher in total energy and easier to digest. Thus, in sum, six of the eight hypotheses regarding forest ecology were shown to be relevant to test their predictive behavioral sets against the observed patterns of *Alouatta* behavior (Table 2).

5.3 Summary of Demographic Patterns

Given the higher abundance of high quality food at TBS, theory would suggest that the following trends in demography should be present: 1) The average number of males per group is **higher**, 2) The average number of adult female howler monkey per group is **higher**, but does **not exceed four**, 3) The average group size is **larger** and 4) The ratio of infants and juveniles to adult females is **higher**. Although the overall population density was higher at TBS, there were no significant differences found in the demographic characteristics of average group size or composition, however the ratio of immature to females in the population was slightly higher at TBS. The first two aspects are in large part due to the presence of newly formed groups, which were only observed at TBS. Furthermore, the average number of adult females per group and the percentage of adult females in the population were higher at PPRA instead of TBS. While these were not significantly different, it was contrary to the predicted demographic patterns for howlers occurring at higher population density.

One reason there were more females per group at PPRA may be that there was less female-female aggression at this site. It other *Alouatta seniculus* populations high rates of infanticide have been observed and groups with higher numbers of females are more at risk of a group takeover (Crockett, 1996; Crockett and Janson, 2000; Janson and van Schaik, 2000). At PPRA, however, the density may be so low that the threat of infanticide is less because there are fewer males that could take over groups. Under this circumstance female-female aggression may be relaxed and thus howler monkeys can afford to have larger groups, as long as feeding competition is not too high. A second reason for larger groups could be because distances between potential new groups were presumably greater due to the overall lower population and group density, potentially producing a higher cost of dispersal at PPRA. The longer the duration that individuals spend without a group, either searching to join or form a new one, the higher the risk of predation may be, especially at PPRA where there is occasional hunting in and around the study site. Hence, all else being equal, females should be less inclined to expel their daughters out of the group, resulting in larger groups

Also, there was no difference found between the percentage of infants and juveniles in the population, which suggests that the birth rates were similar between the two sites. Assuming the reasons for this are not due to differences in mortality, but rather to differences in food availability, it is expected that populations of different densities at equilibrium will be equally constrained reproductively (Mangel and Clarke, 1989). It is therefore possible that both of the populations are at carrying capacity, which is likely to be lower at PPRA and higher at TBS due to differences in food quality and density.

5.4 Summary of Ecological and Behavioral Predictions

The six significant associations between differences in forest ecology and the density of howler monkeys at the two sites, along with their corresponding behavioral predictions, are shown in Table 2. None of the predictive sets of behavioral correlates for any of the hypotheses are fully supported. The behavioral prediction that all of the fully supported ecology hypotheses failed to meet was a significant difference in resting time. Based on resting times reported for other populations of red howler monkeys and other *Alouatta* species, I suggest that the resting time may be at, or near, a minimal level required for digestion in both of these populations and thus making it less likely to detect differences between the two populations.

It is interesting to note that one hypothesis, soil fertility, did support the above prediction which all the others failed to. This is because there were no differences in behavior predicted for any of the behavioral categories between the sites for this variable, supporting the observed non-significant difference found in resting time. However, this hypothesis is only partially supported by the ecological data and thus may not be fully representative of the effect it had on howler behavior.

Only one prediction was met for H1, H2, H4 and H6. This suggests it is unlikely that hunting, soil fertility, phenological productivity or plant quality (in the form of higher protein-to-fiber ratios) are, on their own, influencing differences in density in a significant way. In contrast, the last two hypotheses, which combined leaf quality in the form of lower phenolic content (H7) and higher protein levels (H8) with the density of these resources, were most heavily supported by the data, suggesting these factors are likely playing the largest roles influencing the difference in howler population density between the sites.

5.5 Conclusions

The degree of hunting pressure can profoundly affect mammalian biomass, and this has been documented explicitly for howler monkeys (e.g., Peres, 1997, 2000). Peres (1997) showed that howler monkey populations subjected to varying degrees of harvest intensity occurred at significantly lower densities and biomass than those which had never been subject to hunting, or no longer hunted for more than fifteen years. However, while hunting pressure was found to be a good indicator of howler monkey population density, this was most evident in presumably high quality habitats such as deciduous, late-successional, floodplain and gallery forests, and had far less predictive power for evergreen forests or *terra firme* which housed "intrinsically low howler monkey densities even in the complete absence of hunting" (Peres, 1997). Peres (1997) also showed that hunting pressure alone only accounted for one-quarter of the variation exhibited in howler monkey densities and biomass across twenty-three Amazonian sites, and pointed to the necessity of considering the effects of site-specific indicators of habitat quality, in addition to hunting pressure, to explain the variation in howler monkey population density throughout the Amazonian region. It was shown that once differences in hunting pressure were controlled for, most of the variation in howler monkey densities was explained by indirect measures of habitat quality, specifically forest structure, seasonality, and geomorphic correlates of soil fertility (Peres, 1997). Other studies have also cited that hunting pressure can mask the effects of logging or forest type on other species as well (e.g., *Ateles paniscus* and *Cebus apella*; de Thoisy et al., 2005).

Additionally, the single best predictor of *Alouatta* densities in evergreen forests of central lowland Amazonia was found to be the distance to major white-water rivers, which co-varies with forest heterogeneity and soil fertility (Peres, 1997; Haugaasen and

Peres, 2005). It has therefore been suggested that higher soil fertility, in the form of higher levels of primary and secondary macronutrients, can in turn influence the abundance, quality, heterogeneity and associated phenological patterns of the resources that grow upon them (Janzen, 1975; Peres, 1997; Haugaasen and Peres, 2005). This study shows some support that food abundance is affected by soil fertility in relation to fruit production, and while it is possible that leaf quality may also be affected, this hypothesis could not be directly tested in this study.

I suggest that hunting is likely contributing to the difference in howler monkey density at PPRA versus TBS to some degree. However, I also suggest that the difference in density between the two populations is also likely being affected by a higher abundance of higher quality resources at TBS. By integrating these hypotheses with the full spectrum of behavioral data collected (Chapter 4), I suggest the following scenario to explain the observed behavioral patterns of howler monkeys at the high density site. Due to the higher density of higher quality food resources at TBS the distance between patches are shorter, enabling howlers to spend less time moving between patches and to feed on a larger number of patches per day, ultimately resulting in a longer time spent feeding per day. There was no difference in daily path length between the sites, however, so the howler monkeys at TBS are accomplishing this not by moving further each day but possibly by moving faster. This aspect can be examined indirectly by taking the average time spent moving per day and converting it to a 12 hour day, which is representative of a howler monkey daily activity cycle. For example, it was found that howler monkeys at PPRA spend on average 25.4% moving per day, if this converted to a 12 hour day they are spending 3.05 hours moving. When the average daily path length is now divided by this time it equates to a movement rate of 147 m/hr (448.3 m/3.05 hrs = 147 m/hr). Contrast this with the much lower time spent moving at TBS, only 14.1%, and divide it by the longer daily path length and the resulting movement rate is nearly 2.5 times faster (616.7m/1.69 hrs = 364.9 m/hr). The ability to move more quickly between patches may again tie back in to the overall higher amount of protein, and thus energy, available in the leaves and allow howler monkeys to be less energetically limited at TBS compared to PPRA. Although whether the rate of travel differs greatly enough between the animals at these sites to actually effect caloric expenditure is not known. Regardless, this behavior may well be indicative of greater inter- and perhaps intra-group scramble competition at this site due to higher howler group density.

Despite the fact that leaves are generally considered to be ubiquitous and evenly distributed, data from this study and others illustrates that folivore resources vary both in quality and abundance. Furthermore, there is behavioral evidence to support scramble competition occurring in folivorous primates (recently reviewed in Snaith and Chapman, 2007). For example, research on *Colobus angolensis,* a species that can reach group sizes up to 300 members, suggests that despite high habitat quality individuals may experience intense intra-group scramble competition reflected by their increased rate of movement and lower percentage of time spent resting compared to other species within the genus (Fashing, 2007). In addition, folivores do not simply forage continuously through the canopy but instead have been found to preferentially use certain trees that are not large enough for all group members to feed simultaneously (*Semnopithecus entellus*: Koenig et al., 1998, Koenig, 2000), to feed on selected food parts (*C. guereza*: Oates, 1977; Harris, 2006) and to travel directly from one source to another (*A. palliata*: Milton, 1980; *A.*

seniculus: this study). Thus, both Old and New World folivores appear to demonstrate patterns of food selectivity, indicating that scramble competition does occur in folivorous species and would likely be exacerbated in areas of high population density such as the TBS site in this study.

Results from this study also show support for several aspects of forest ecology that have been suggested to affect folivore primate density. First, previous studies on howler monkeys found population density in Central America to be positively correlated with resource abundance in regenerating forests, estimated using the average tree DBH (*A. palliata*: Sorensen and Fedigan, 2000), and forest fragments, calculated from the annual productivity of the most important food item in the howler monkey diet (*A. pigra*: Silver et al., 1998). Second, research on Old World folivorous primates have shown population density to be positively correlated with a high abundance of higher quality foods. For instance, a positive correlation was found between colobine biomass and the average protein-to-fiber ratio in mature leaves of the 20 most abundant species at sites in Kibale National Park, Uganda (Chapman et al., 2002). Data from this study illustrate that the ecological factors influencing Old World folivorous primate density may also hold true for folivorous Neotropical species, which are characterized by a different digestive morphology. Lastly, this data illustrates partial support for work showing that the single best predictor of *Alouatta* densities in central lowland Amazonia is the distance to major white-water rivers (Peres, 1997; Haugaasen and Peres, 2005).

As with all short term studies however, it is important to view the population density and demographic patterns within and between sites as part of a larger construct of animal life history patterns that change over time and space (Struhsaker, 2008). There is no doubt that the best strategy for acquiring this information on primate populations, and the most relevant for conservation management strategies, is certainly long-term population monitoring. However, because many primate populations are now vulnerable to local extinction due to increased human disturbance activities in and around tropical habitats (e.g., Alvard, 1997; Peres, 1997), there is an urgency to try and identify areas and populations that are at greatest risk. I suggest that short term studies, if approached from a multivariate and integrative viewpoint, may be helpful in identifying the factors that most greatly influence primate density and allow conservationists to target regions characterized by these parameters as high priority. In this way habitats that are capable of sustaining higher densities of primates will be conserved, which may foster the sustainability of vulnerable or at risk species or populations and provide the opportunity for long-term studies to take place.

5.6 Conservation Implications for Yasuní

The biodiversity of flora and fauna that occurs within the Yasuní region is among the highest in the world (Pitman, 2000). Amidst the incredible species richness, a precarious relationship between forest existence and human subsistence is faced with the pressure of a new dynamic- namely, the effects of increasing human colonization and oil development. Once a vast sea of tropical forest sparsely inhabited by indigenous Waorani, Yasuní is quickly becoming more like a patchwork of roads, bridges, permanent human settlements and farms. It is thus imperative that research and conservation efforts focus on this region in order to monitor the effects of increasing land use on both the plant and animal communities and to contribute to informed management planning to preserve particular areas within this rapidly changing ecosystem.

This study has shown that small scale variation in habitat ecology occurs within Yasuní, and that areas characterized with a higher abundance of high quality of resources, and possibly higher soil fertility, are underlying factors influencing differences in howler monkey density. This knowledge can be used to identify and target areas that may be capable of sustaining higher howler monkey populations throughout the region and to propose such areas to be concessioned as non-development sites in order to preserve their ecological integrity. Although the genus *Alouatta* is widely distributed from Mexico to Argentina and only one of the seven species is currently list by the IUCN as Endangered (*A. pigra*: Cuarón et al., 2003), populations are still at risk of local depletion due to habitat destruction (Horwich, 1998), habitat fragmentation (Mandujano and Escobedo-Morales, 2008) and hunting (Peres, 1997). Unlike some primates, howler monkeys are able to adapt to low and moderate levels of forest disturbance (or in some cases even do better) giving them the chance for survival, but only if hunting can be controlled (Horwich, 1998; Peres, 1999). Currently the low hunting levels in Yasuní appear to be to having some affect on howler monkeys and the primate community as a whole. This study showed that large bodied primates are experiencing higher harvest rates, a familiar pattern seen throughout the tropics, and this aspect should continue to be monitored in conjunction with the hunting practices of an increasing human population. Yasuní thus represents an ideal region not only for continued research and scientific discovery, but also for conservation endeavors that can contribute to long-term animal population monitoring and strategies for land use management.

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5.8 Tables

TABLE 1: Ecological variables examined and compared between the two study sites and their corresponding predictions of the patterns expected to occur at the high density site.

Ecological variable	Predictions for the ecological context expected to occur at the high density howler monkey site	References
(1) Hunting	*Lower* hunting	e.g., Peres, 1997, 1999
(2) Soil fertility/ Forest heterogeneity	*Higher* heterogeneity and *higher* soil fertility	Soil fertility: McKey, 1978; Peres, 1997; Hauggesen and Peres, 2005 Forest heterogeneity: Fleagle, 1999; Bourliere, 1985; Oates et al., 1990; Ganzhorn, 1993
(3) Phenological seasonality	*Less* phenological seasonality	Ripley, 1979; Terborgh, 1986; Gupta and Chivers, 1999
(4) Phenological productivity	*Higher* phenological productivity	Sadleir, 1969; Chapman and Chapman, 1999
(5) Resource quality: Phenolic content	*Lower* level of phenolics in leaves	Coley and Barone, 1996
(6) Resource quality: Ratio of protein-to-fiber	*Higher* ratio of protein-to-fiber in leaves	Milton, 1980; Chapman et al., 2002, 2004
(7) Resource density: Phenolic content	*Higher* density of plants low in phenolics	Chapman et al., 2002, 2004
(8) Resource density: Ratio of protein-to-fiber	*Higher* density of plants with high ratios of protein-to-fiber in leaves	Chapman et al., 2002, 2004

TABLE 2: Summary of supported ecological variables and corresponding behavioral predictions. Predictions were made based on how each variable should, all aspects remaining equal, affect howlers in a high versus a low density area.

	Behavioral Predictions				
Ecologically Supported Hypotheses	**% Time spent resting** **(Observed: *Same*)**	**% Time spent feeding** **(Observed: *Higher*)**	**% Time spent moving** **(Observed: *Lower*)**	**Between patch movement** **(Observed: *Lower*)**	**# of trees fed upon per day** **(Observed: *Higher*)**
H1 **Hunting** PARTIALLY	**Predicted:** *same* ✓	**Predicted:** *same* ✗	**Predicted:** *higher* ✗	**Predicted:** *same* ✗	**N/A**
H2 **Soil fertility:** PARTIALLY higher levels of Mg, Ca, and pH in riparian regions of both sites	**Predicted:** *same* ✓	**Predicted:** *same* ✗	**Predicted:** *same* ✗	**Predicted:** *same* ✗	**N/A**
H4 **Phenological productivity:** higher amount of leaves, fruit buds, fruits	**N/A**	**N/A**	**Predicted:** *higher* ✓	**Predicted:** *same* ✗	**N/A**
H6 **Resource quality:** higher protein in all leaves; protein:fiber ratio in mature leaves	**Predicted:** *higher* ✗	**Predicted:** *higher* ✓	**N/A**	**N/A**	**N/A**
H7 **Resource density:** higher density of plants low in phenolics	**Predicted:** *lower* ✗	**Predicted:** *higher* ✓	**Predicted:** *lower* ✓	**Predicted:** *lower* ✓	**N/A**
H8 **Resource density:** higher density of plants high in protein	**Predicted:** *higher* ✗	**Predicted:** *higher* ✓	**Predicted:** *lower* ✓	**Predicted:** *lower* ✓	**Predicted:** *higher* ✓

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