

THE BEHAVIORAL ECOLOGY OF MANTLED HOWLING MONKEYS
(*ALOUATTA PALLIATA*) LIVING IN A NICARAGUAN SHADE
COFFEE PLANTATION

by

Kimberly Williams-Guillén

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Clifford J. Jolly

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DEDICATION

This dissertation is dedicated to my parents, Roger Williams and Nomi Trapnell, for giving me all their love and support throughout graduate school, and to Colleen McCann and Fred Koontz, for their generosity in inviting me to join them in their research.

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ABSTRACT

I conducted a 14-month study of the foraging behavior, nutrient intake, energy budgets, ranging patterns, and social behavior of mantled howling monkeys (*Alouatta palliata*) living in Finca La Luz, a shade coffee plantation on Mombacho Volcano, Nicaragua. The shade coffee forest has relatively low tree density and diversity. Annual diets comprise 28.0% mature leaves, 27.7% young leaves, 34.8% fruits, 7.9% flowers, and 1.6% other plant parts. At least 57 tree species are used as food sources, with leaves and fruits of *Ficus costaricana* dominating the diet at 32% of total feeding time. The howlers spend 57.0% of daylight hours resting, 27.4% traveling, 13.6% feeding, 1.5% socializing, and 0.5% vocalizing. Abundant tree species were important food sources and provided relatively high-quality foliage. The consumption of seasonally-available foods shows only a weak relation to availability; however, on a species-by-species basis, consumption of preferred parts closely tracks abundance. Average diets contain 38.7% acid detergent fiber, 14.0% crude protein, 9.5% water-soluble carbohydrate, and 0.1% crude fat. Mean caloric intake was estimated at 440 kcal metabolizable energy/day. Estimates of average daily metabolic needs based on activity budgets suggest that pregnant and lactating females may frequently experience negative energy balance. Home ranges varied from 13 to 20 ha in size, and the howlers traveled an average of 617 m daily. Ranging variables increase with group size, providing indirect evidence of within-group scramble competition. Seasonal variation is seen in patterns of feeding, activity, and ranging, with foraging effort (i.e., time spent feeding and traveling, range area, and day journey length) increasing during the rainy season, when fruits and mature leaves are consumed more frequently. Contest competition

is relatively rare, and occurs at a rate of only 0.25 events per focal hour; females engage in agonistic behavior more frequently than males or immatures. The results suggest a less selective foraging strategy, which may be an adaptation to the high abundance of high-quality forage; contest competition for feeding and social resources may be reduced in this population, and shade coffee plantations may be more favorable habitats for howlers than initially hypothesized.

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CHAPTER 1

INTRODUCTION

Finding, processing, and consuming food is an animal's most fundamental activity; foraging strategy explains many aspects of an organism's basic behavioral ecology (Hughes, 1993; Oates, 1987; Pyke *et al.*, 1977). Given that the nutrients from foods fuel all bodily processes, that food resources are finite, and that increased foraging success increases the chances of surviving to reproduce, natural selection should favor optimal foraging strategies (Cody, 1974; Pyke, 1986). Attempts to explain the foraging patterns of animals through optimality models have revealed that simple rules of rate maximization often predict behavior (Stephens and Krebs, 1986). However, the variables used in such models (e.g., search and processing time, encounter rate, and energy content) do not describe the many constraints that affect herbivore food choice (Freeland and Janzen, 1974; Milton, 1979; Westoby, 1974). For herbivores, the problems of locating and processing food are outweighed by heterogeneity in the nutrients and feeding deterrents that plant foods contain (Freeland and Janzen, 1974; Westoby, 1974): foliage is highly inconsistent in nutrient content, with protein and feeding deterrents (fiber, secondary plant compounds) sometimes varying widely between selected and ignored resources. Determining the relative importance of factors influencing food choice, and how variance in food density and diversity affects these constraints, has remained problematic (Belovsky and Schmitz, 1991).

Primate studies have played an important role in investigations of food choice by generalist herbivores. *Alouatta palliata*, the Central American mantled howler, has been the subject of several long-term ecological studies (Chapman, 1987, 1988a, 1988b; Estrada, 1982, 1984; Glander, 1978b, 1981; Milton, 1978, 1980; Serio-Silva, 1993; Stoner, 1994, 1996). Information gathered on the mantled howler's feeding patterns has contributed to our understanding of the factors shaping herbivore food choice (e.g., Glander, 1978b; Milton, 1978, 1979). Howlers demonstrate a high degree of feeding selectivity, exploiting a diversity of seasonally-available food sources in order to maximize nutrient intake while minimizing search time, digestive energy input, and consumption of toxic compounds (Milton, 1978, 1979). Having a wide array of potential food sources may be an important component of the "optimal" howler monkey foraging strategy. However, howlers of all species are known to occupy disturbed areas characterized by lower levels of tree species density and diversity than are observed in primary habitats (e.g., Estrada and Coates-Estrada, 1996; Limeira, 1997).

Because howlers occupy primary and secondary habitats, comparative studies can be used to elucidate the effects of habitat richness on foraging strategy. Comparing conspecifics in contrasting environments is a useful method for exploring how environmental variables shape primate food choices, and ultimately, population and social organization (Dunbar, 1987). Disturbed, fragmented, and secondary habitats have distinctive plant communities and provide excellent opportunities to test hypotheses regarding how the resources a primate exploits shape feeding, ranging, activity, and grouping patterns. Nevertheless, there have been few long-term primatological studies in

intensively disturbed areas. The exceptions reveal that primates often change their behavior in predicted directions when living in these habitats (for example, by having lower-quality or less diverse diets, larger home ranges, smaller group sizes, and altered activity budgets; Clarke *et al.* 2002a; Decker, 1994; Johns, 1986; Limeira, 1997). Such studies may be particularly useful because in tropical habitats speciation possibly happens most frequently in marginal or fragmented habitats (Ogden and Thorpe, 2002; Schneider *et al.*, 1999; Smith *et al.*, 1997). Moderately disturbed habitats may approximate some natural changes in vegetation; therefore, studies of primates in these areas may demonstrate how and why some species have the adaptability and niche breadth to survive climatic fluctuations and landscape-level changes.

Forested agricultural habitats have lower tree density and less species diversity than non-cultivated forest habitats (Estrada and Coates-Estrada, 1996), making these ideal locales for understanding the relationship between foraging strategy and environmental richness. I therefore conducted a 14-month field study on mantled howling monkeys living in a Nicaraguan shade coffee plantation. In this dissertation, I document the feeding patterns, ranging behavior, nutritional ecology, and activity budgets of three groups of *A. palliata*, and relate these to tree diversity, density, and phenology. This information allows me to explore the effects of plant chemistry on howler food selection and to examine howler foraging strategies in a previously uninvestigated habitat type. I also relate the unique patterns of resource abundance and distribution found in the shade coffee plantation to levels of feeding competition and explore how these affect the social organization and behavioral patterns of howlers.

OPTIMALITY AND HERBIVORE DIETS

Animals relying on foliage generally must select food carefully, due to the considerable variation found in plant foods' content of nutrients, digestion inhibitors, and feeding deterrents (Freeland and Janzen, 1974; Westoby, 1974). Optimal foraging theory, in its most simplistic form, predicts that animals will forage to maximize energy intake or some similarly straightforward currency (Belovsky, 1984); however, as herbivores are limited more by digestive capacity (Westoby, 1974) and energetic costs of detoxification (Freeland and Janzen, 1974), optimal foraging strategy for a plant-eating mammal should incorporate aspects of nutrient mix, avoidance of toxin consumption, rate maximization, and reduction of energy expenditure. Experimental and field investigations have shown that mammalian herbivores demonstrate selectivity in choosing food sources, maximizing not net energy gain *per se*, but nutrient mix (e.g., Danell *et al.*, 1991; Lacher *et al.*, 1982; Murden and Risenhoover, 1993; Owen-Smith and Novielle, 1982; Parsons *et al.*, 1994) and minimizing secondary compound intake (e.g., Dearing, 1997; Schmidt *et al.*, 1998; Sinclair *et al.*, 1988).

Similarly, research on folivorous colobine and howling monkeys (e.g., Dasilva, 1994; Glander, 1978b, 1981; Milton, 1979, 1980; Oates *et al.*, 1977, 1980; Silver, 1997) has established that these primates also select food judiciously, demonstrating preferences for seasonally available resources with high levels of protein or digestible carbohydrates and low levels of indigestible cell wall material. The role of secondary compounds in primate food selection is less clear. Although some studies have suggested that phenolics or alkaloids influence primate food choice (Barton *et al.*, 1993; Glander, 1981; Oates *et al.*,

1977), other studies have failed to demonstrate a strongly negative relationship (Milton, 1979; Oates *et al.*, 1980; Silver, 1997). The complexity of the interactions between the many types of plant secondary metabolites and digestive processes in the animal gut makes understanding their effects on food selection difficult (Belovsky and Schmitz, 1991; Waterman and Kool, 1994).

Although no one factor consistently explains primate food selection (Silver *et al.*, 2000), it is expected the resources chosen will differ from other resources in having higher nutrient levels and/or lower levels of fiber and secondary plant metabolites (Lacher *et al.*, 1982; Milton, 1979; Murden and Risenhoover, 1993). However, such selectivity comes at the expense of greater time and energy expended in foraging, a loss in time available for other activities, and, potentially, higher levels of feeding competition between group members for relatively rare resources (Cuthill and Houston, 1997). A broader dietary strategy may be adopted under certain circumstances, for example when high-quality resources are extremely rare in the habitat making high selectivity too energetically expensive (Lacher *et al.*, 1982; Stephens and Krebs, 1986), when nutrient content in foliage is less heterogeneous (Westoby, 1974), or when abundant foliage is relatively high quality and therefore nutrient content is not limiting (Kool, 1992; Murden and Risenhoover, 1993). In habitats where the availability of preferred foods is not limiting, either due to overall high nutrient quality or pan-seasonal availability of preferred foods (e.g., Kool, 1992), food selection in relation to plant chemistry by folivorous primates should be relatively weak. In these situations, availability may interact more strongly with nutrient content to govern food choice.

FORAGING STRATEGY, ENERGY GAIN, AND COMPETITION

All animals must maintain a relatively even balance between caloric intake and energy expenditure to maintain body condition and support growth and reproductions (Coelho, 1986). However, competition for access to resources may affect individual ability to maintain energy balance, manifest as variation within and between social groups in net energy gain (Milinski and Parker, 1991). Feeding competition is considered to be a major factor constraining group size in primates, particularly frugivores (Janson and Goldsmith, 1995; Isbell, 1991; Sterck *et al.*, 1997; Terborgh and Janson, 1986); individuals in large groups, although better able to avoid predation (van Schaik, 1989) and defend resources from usurpation from other groups (Wrangham, 1980), may be subject to lower levels of net energy gain, and, by extension, reproductive success due to depletion of food resources by other group members (Terborgh and Janson, 1986; Sterck *et al.*, 1997).

Feeding competition can take different forms with consequently varying effects on primate social organization and structure. The variation observed among primate species in patterns of grouping and social interactions has been linked to specific characteristics of resource quality, abundance, and distribution (e.g., Wrangham, 1980; van Schaik, 1989). The numbers of males and females grouping together can result from a number of contrasting pressures, such as predation risk, resource monopolization within a supplying area, the need for protection from conspecifics, mate competition, and the type and intensity of feeding competition (Crockett and Janson, 2000; Nunn, 1999; Treves, 2001). Recent reviews have emphasized the broad predictive power of these ecological models in explaining primate social systems, although certain primates –

among them howlers – seem to defy some expectations (Sterck *et al.*, 1997). In general, results from field studies of primate ecology and social organization have supported the “ecological model,” which relates the strength of different types of feeding competition to variation in female social relationships (Sterck *et al.*, 1997; Koenig, 2002). Competition is assumed to be an all but inevitable cost of group living (Janson, 1988b), but one whose costs differ in response to resource characteristics.

Factors of predation risk and, to a lesser extent, the ability to communally defend resources, are thought to be the primary forces favoring group living in primates (van Schaik, 1993; Wrangham, 1980). However, the advantages conferred by group living are tempered by the costs of competition for resources (food, mates, resting sites, etc.) with other group members. All primates with limiting food resources are thought to experience some level of within-group scramble competition for food, in which individual net energy gain is reduced because other group members have already located and eaten food resources. Scramble is the dominant type of feeding competition when resources are of relatively low value or small and highly dispersed. Due to their largely folivorous diets, levels of scramble competition are expected to be relatively low in howlers, as they are for most folivorous primates (Janson and Goldsmith, 1995; Larose, 1996; Sterck *et al.*, 1997). The action of within-group scramble competition is frequently measured through investigation of ranging behavior, which serves as a proxy for foraging effort (Isbell, 1991; Janson and Goldsmith, 1995). While scramble competition may affect ranging behavior, it is expected to have few, if any, consequences for social behavior, because overt agonism over food resources will not result in access to more or better food; all

group members will suffer roughly equal effects of scramble competition (Koenig, 2002; Sterck *et al.*, 1997).

Within-group contest competition will occur when food patches are high value, clumped, of intermediate size in relation to group size, and when some individuals are able to systematically exclude others from feeding access while increasing their own food acquisition. Contest competition is measured via agonism in feeding contexts, and is thought to lead to the evolution of dominance systems within groups because the ability to monopolize a food patch or eject a group member should result in higher individual net energy gain; thus, contest competition reflects dominance effects, although its intensity may also change with group size (Sterck *et al.*, 1997). Between-group competition is much rarer, and apparently is affected by both population density and food patch distribution (Sterck *et al.*, 1997; Koenig, 2002). Variation in the strength of forces of competition (the competitive regime) should affect patterns of female residency and social behavior. Strong contest competition within or between groups should lead to female philopatry due to the advantages of forming long-term alliances with relatives in order to defend access to resources from other individuals or groups. The strength of within-group competition is thought to determine the patterning of agonistic between females within a group: if low, then there are few advantages to forming strong dominance relationships or long-term alliances, while if it is high, the ability to ally with kin or form short-term coalitions with other females in response to resource monopolization should result in decided female dominance hierarchies. Sterck *et al.* (1997) classify these competitive regimes as “Resident-Egalitarian” (strong between-group

contest competition), “Resident-Nepotistic” (strong within-group competition), and “Resident-Nepotistic-Tolerant” (both forms of contest competition strong).

It is expected that primates feeding largely on leaves (which are often abundant, found in large patches, and of low value) experience low levels of both scramble and contest competition. Folivores are therefore expected to demonstrate a “Dispersal-Egalitarian” social system: there are few advantages to long-term alliances with kin or short-term coalitions with non-kin, as contesting access to resources is not worthwhile given their relative abundance and/or low quality. Females therefore do not demonstrate clear dominance hierarchies. Given the low social costs of transfer (no vital alliances are lost), females are therefore free to disperse from groups in response to pressures such as feeding competition (Sterck *et al.*, 1997). Female philopatry and female dominance hierarchies are largely absent in these species. This pattern stands in contrast to that characterizing species which experience high levels of within-group contest competition. While howler social systems show some unexpected features (strong linear dominance hierarchies among females, female expulsion of same-sex group mates, and relationships between dominance and reproductive success: Glander, 1992; Jones, 1980), patterns of female transfer and low rates of contest competition generally fit with the model, and observed inconsistencies may result in part from high population densities and infanticide pressure (Sterck *et al.*, 1997; Crockett and Janson, 2000).

Nevertheless, although howlers’ food sources are generally more abundant than those of sympatric frugivorous/insectivorous primates, they are not living in a “salad bowl” of endlessly abundant foods (Milton, 1980), and it is expected that different

environments will present different patterns of resource abundance and distribution, and that these, in turn, will lead to variation in the incidence and intensity of both scramble and contest competition. Studies of howlers in unique environments should reveal differences in levels of competition and concomitant variation in ecological adaptations and social behavior.

BACKGROUND AND PREVIOUS INVESTIGATIONS

Overview of *Alouatta palliata* Behavioral Ecology

Members of the genus *Alouatta*, the howling monkeys, are widely distributed across Latin America from southernmost Mexico to northern Argentina (Wolfheim, 1983; Crockett and Eisenberg, 1987). The six species comprising the genus have broadly similar dietary niches as generalist herbivores that regularly consume foliage (Milton, 1998). Although sometimes regarded as analogous to the folivorous colobine monkeys of the Old World, howlers lack their highly specialized digestive systems and may not have the same capabilities to digest cellulose or detoxify food (Crockett and Eisenberg, 1987; Milton, 1998). The Central American mantled howler, *Alouatta palliata*, is the most extensively studied member of the genus (Kinzey, 1997) and has been the subject of numerous long-term ecological investigations. Found from southern Mexico through Panama and the western coasts of Columbia and Ecuador, the species has been studied in Mexico, Costa Rica, and Panama (Kinzey, 1997; Neville *et al.*, 1988); recently, studies have been initiated in Nicaragua and Honduras (Garber *et al.*, 1999; Snarr, personal communication). *Alouatta palliata* is smaller and less sexually dimorphic than its

congenerics (Kinzey, 1997). Mantled howlers are found in a wide variety of habitats, from high evergreen rainforest to highly disturbed secondary habitat. Like other howlers, *A. palliata* is a dedicated herbivore, feeding on a wide variety of foliage and fruit. In spite of similar diets (and, presumably, similar foraging strategies and competitive regimes), *A. palliata* has, on average, larger social groups, more females per group, a higher frequency of multi-male groups, and higher female to male ratios than do other howler species (Crockett and Eisenberg, 1987; Treves, 2001). Mantled howlers also demonstrate linear female dominance hierarchies, with dominant females having higher reproductive success (Glander, 1992; Jones, 1980). Infanticide associated with male immigration has been reported for mantled howlers (Clarke, 1983).

***Alouatta* Feeding Ecology and Activity Patterns**

Foliage is a vital component of the diet, and all howlers regularly consume leafy material (Milton, 1998). Leaves generally constitute 50% to 65% of the annual diet, and up to 80% of the diet of howlers in highly seasonal environments (Galetti *et al.*, 1987; Strier, 1992). Howlers prefer young leaves to mature foliage (Estrada, 1984; Gaulin and Gaulin, 1982; Glander, 1978b; Julliot and Sabatier, 1993; Silver *et al.*, 1998; Stoner, 1993). Young leaves generally have higher levels of protein and water and lower levels of indigestible cell wall material than mature leaves (Coley and Barone, 1996; Waterman, 1984). The consumption of young leaves frequently does not correlate with their abundance in the habitat, and it has been suggested that young leaves are used as alternatives to fruits when the latter are scarce (Milton, 1980; Silver *et al.*, 1998). Although

early studies (Carpenter, 1934; Freese, 1976) characterized howlers as fully folivorous, subsequent investigations indicate that many populations consume sometimes substantial amounts of fruit, typically between 25% and 50% of annual feeding records (Neville *et al.*, 1988). Fruit exploitation generally reflects its presence in the habitat, with consumption patterns roughly tracking seasonal availability (Glander, 1978b, 1981; Milton, 1980). Flowers may also be preferred food sources that are heavily exploited during their brief periods of availability.

Howlers generally eat a wide variety of plants; at some sites, study groups exploit over 100 food species (e.g., Milton, 1980; Stoner, 1993; Julliot and Sabatier, 1993). However, many of these foods are eaten only once over the course of the study; such sampling augments consumption of a limited number of “staple” species which comprise most of the diet (Neville *et al.*, 1988). It appears that behavioral strategies, such as opportunistic reliance upon seasonally-available fruits and careful selection of foliage, mediate folivory by howlers more strongly than does digestive morphology (Milton, 1978, 1998). Howlers are known to choose foods carefully, concentrating on the more digestible fruits, flowers, and young leaves of what are usually rare trees in the habitat. For example, at Barro Colorado Island and Finca La Pacifica, the top ten howler food species accounted for 65 to 70% of feeding time, but only about 11% of the available tree species. The apparent flexibility in the degree of frugivory exhibited by howlers may account for the ability of these animals to exist in a variety of primary and disturbed habitats (Silver *et al.*, 1998).

Patterns of activity and travel in *Alouatta* reflect their dietary strategies. Howlers have been characterized as “energy minimizers” (Milton, 1998), limiting energetic needs by reducing expensive activities such as travel and foraging: howlers generally spend 60% to 70% of the day resting, 15% to 25% of the day feeding, 10% to 20% of the day traveling, and less than 5% of the day in social activities (Crockett and Eisenberg, 1987; Neville *et al.*, 1988). This pattern of reduced energy expenditure has been explained as an adaptation to the high amounts of foliage included in their diets: given their relatively unspecialized digestive tracts, howlers rely on particularly slow passage rates to maximize fermentation of fibrous material (Milton, 1979, 1981). Energy extraction from foliage is therefore a particularly long process, best accomplished when the body is at rest (Smith, 1977; Gaulin and Gaulin, 1982). The large amounts of time howlers spend resting may comprise a vital aspect of their digestive physiology. Activity patterns of howlers vary seasonally, with resting at some sites decreasing as rainfall and fruit availability and consumption increase (e.g., Glander, 1981; Milton, 1980).

Descriptions of Primary Study Sites of *Alouatta palliata*

The conclusions drawn in this dissertation rely on comparisons with other studies of *Alouatta palliata*. Although mantled howlers occupy diverse habitats, the majority of the long-term studies have taken place in tropical dry deciduous or semi-deciduous forests subject to varying degrees of human disturbance. The two “classic” studies of *Alouatta palliata* foraging behavior were conducted by Milton (1978, 1980) at Barro Colorado Island (BCI), Panama, and Glander (1978b, 1981) at Finca La Pacifica, Costa

Rica. BCI, created by the construction of the Panama Canal, is composed mostly of mature evergreen moist forest (Milton, 1980); however, some areas of the island comprise later secondary growth, and one of Milton's study groups occupied these older regenerating forests. Finca La Pacifica was heavily deforested for agriculture, with the remaining fragments of semideciduous dry and riparian forest left to serve as windbreaks and prevent erosion (Glander, 1981); however, within these fragments, the forest is relatively intact (Clarke *et al.*, 2002b). A third site where continued studies of mantled howlers have been conducted is Santa Rosa National Park, Costa Rica. This area comprises highly fragmented semideciduous tropical dry forest; some areas were deforested prior to the park's incorporation, and the area currently comprises a mosaic of mixed deciduous, riparian, and early secondary forests (Fedigan *et al.*, 1998). Two other studies of mantled howlers to which I refer were conducted in tropical wet forest exhibiting various degrees of disturbance. Estrada (1984) studied mantled howlers at the northernmost area of their range in fragmented lowland tropical wet forest in Mexico, while Stoner (1996) studied Costa Rican howlers at La Selva, an area consisting primarily of mostly undisturbed lowland and premontane wet forest. Population densities are higher at BCI and La Pacifica than at the other sites (Chapman and Balcomb, 1998). In spite of varying degrees of disturbance, these sites apparently maintain relatively intact canopies with a full or mostly full complement of forest tree species.

Study Country and Conservation Issues

Nicaragua, Central America's largest country, contains diverse tropical habitats, from coniferous forests to coastal mangrove swamps (Dinerstein *et al.*, 1995). Based on distribution patterns and recent investigations, Nicaragua's primate fauna is thought to include three species: the mantled howling monkey (*Alouatta palliata*), the black-handed spider monkey (*Ateles geoffroyi*), and the white-faced capuchin (*Cebus capucinus*) (Wolfheim, 1983; Crockett *et al.*, 1997). Due to political instability, few researchers have conducted primatological studies in Nicaragua (Crockett *et al.*, 1997). Although brief studies have been conducted on howlers on Ometepe Island (Garber *et al.*, 1999), there have been no continuous field studies encompassing the full annual cycle on primates in Nicaragua (Rodriguez-Luna *et al.*, 1996). As is the case for many Central American countries, Nicaragua's forests have been subject to rapid deforestation: forested areas once covered 8 million hectares in Nicaragua, but have been reduced by 50% since 1950; dry forest on the Pacific coast and pine forest on the Atlantic coast have been subject to extensive destruction (Heckadon-Moreno, 1997). Nevertheless, from the point of view of forest conservation, the situation in Nicaragua is not as grim as for its neighbors: internal political unrest led to the suspension of many development projects during the 1980's, meaning that large areas of the country remain forested and relatively undisturbed. For example, the 2 million hectare BOSAWAS biosphere in northern Nicaragua represents the largest tract of intact rainforest north of the Amazon (Heckadon-Moreno, 1997). Due to its large size, central location, and diversity of habitats, Nicaragua plays a vital role in biodiversity conservation in Central America (McCann *et al.*, 2003).

Nicaragua's Pacific coast is heavily populated, and many of the remaining forested habitats are encompassed within human-use areas, such as agricultural fields, rangelands, and second-growth forests. Such semi-natural areas are capable of sustaining limited wildlife populations; as these lands dominate the landscape in many areas of the tropics, they could therefore play an important role in long-term biodiversity preservation (Vandermeer and Perfecto, 1997). Shade coffee plantations represent an anthropogenic habitat capable of supporting native flora and fauna. Traditionally, coffee has been grown beneath an understory of native forest trees, which protect the growing coffee plants from too much direct sunlight; this method stands in contrast to more recently developed systems in which coffee is grown as a monoculture without any shade cover. Shade coffee systems vary widely in their degree of "technification" (the most rustic forms resemble native forest with the understory replaced with coffee, the most technified comprising only a few tree species with heights less than 5 m and a discontinuous canopy; Toledo and Moguel, 1997). While only the more traditional (rustic) shade coffee plantations serve as wildlife refuge, these areas should not be ignored by conservationists, as they comprise a significant percentage of remaining tropical forest coverage in Latin America (Perfecto *et al.*, 1996). Although no shade coffee plantation can provide habitat to the native forest that it replaces (Rappole *et al.*, 2003), they have conservation value as reservoirs for biodiversity and as corridors between protected areas. For example, recent ornithological studies have documented the importance of shade coffee plantations in providing buffer zones and wintering habitats for both Old and New World tropical birds (Shahabuddin, 1997; Perfecto *et al.*, 1996). Such investigations

have led to public education campaigns linking the consumption of shade-grown coffee with bird conservation (Goldberg, 1997; Marks, 1997; Rappole *et al.*, 2003). The majority of studies of biodiversity in shade coffee plantations have focused on birds and arthropods, although they surely comprise habitat for native plants, non-arthropod invertebrates, reptiles, and mammals. Indeed, several primates, such as lemurs (Ganzhorn and Abraham, 1991), howling monkeys (Estrada and Coates-Estrada, 1996), and lion tamarins (Kleiman and Mallinson, 1998) exploit agricultural habitats, including coffee plantations. Nevertheless, few primate conservation efforts have focused on plantations.

This project was initiated in response to this lack of data. From a conservation standpoint, the goal of this research is to determine how howlers are surviving in these agroforests, what resources and habitat characteristics are crucial for their survival, and to integrate this information into a management plan for primates in shade coffee plantations in southwestern Nicaragua. Researchers from Wildlife Conservation Society have been working with Fundación Cocibolca, a Nicaraguan NGO, to preserve wildlife in and around Mombacho Volcano Nature Reserve in southwestern Nicaragua; data from this project will be used to create a management plan for howlers living in shade coffee plantations around the reserve. Several populations of mantled howlers persist in Nicaragua (Crockett *et al.*, 1997; Garber *et al.*, 1999), but their current conservation status is uncertain. Howlers in Nicaragua are known to exist in coffee plantations, where they cause no crop damage. Additionally, shade coffee encompasses a large portion of the remaining forest cover on Nicaragua's Pacific coast, encompassing some of the last

remaining fragments of (heavily disturbed) tropical dry forest in Central America. Conservation in these areas is therefore vital to maintaining populations of howlers and other primates in western Nicaragua (McCann *et al.*, 2003).

CONTENT AND ORGANIZATION OF THE DISSERTATION

Although this research was initiated in response to conservation goals, data collection was designed to allow me to address questions regarding the relationships between habitat structure, food abundance and distribution, and foraging, ranging, activity, and social patterns. The order in which I present the data and results roughly follows the hypothesized causal chain from resource base to social system: I begin with a description of resource abundance and distribution, describe how howler foraging strategies map on to these, examine the nutritional consequences of foraging behavior, examine ranging behavior as a measure of resultant scramble competition, and then inspect directly observed contest competition in relation to group composition and dominance. Below, I present general predictions, which are presented in more detail in the relevant chapters.

In Chapter 2, I describe general methodologies common to all aspects of the data and analyses presented in this dissertation. The same methods of behavioral data collection are used for all analyses, and I therefore present these in Chapter 2; methods specific to subsequent analyses are detailed in the chapters in which they appear. Because a detailed understanding of forest community composition and phenology is critical to interpreting data presented in later chapters, I also present in this chapter an analysis of

the structural and phenological characteristics of the trees comprising the shade in the coffee plantation. An understanding of species richness and diversity, as well as of the temporal patterns of phenophase production, provides a base for the analyses presented in the following chapters. Given that the shade coffee plantation is subject to human disturbance, I predicted that the tree community in the shade coffee plantation would comprise fewer individuals per hectare and be less species rich than in other habitats where mantled howlers have been studied.

Chapter 3 provides a detailed account of the foraging (i.e., diets and activity patterns) of the three study groups, with diet compositions presented in terms of the contribution of different phenophases and species to the diet. Differences between groups and seasons in dietary composition and activity budgets are considered. Patterns of foraging at La Luz are contrasted with those observed for congenetics at other sites and differences are related to habitat characteristics. I predict that the reduced tree density and diversity seen at La Luz, coupled with the relatively high forage quality (Chapter 4), will result in a less selective foraging pattern in which common tree species are important food sources and relationships between consumption and abundance of plant parts are not as strong as at other seasonal sites.

In Chapter 4, I further explore diet and activity in relation to nutritional intake and energy budgets. I present data on the macro- and micronutrient content of major food items and use data from focal follows to estimate ingestion rates of food and energy. I also describe differences between age-sex classes in activity patterns and estimate individual energy expenditures. Finally, I consider estimated energy budgets in relation to

group size, season, and age-sex class, and discuss whether differences provide evidence for effects of feeding competition on net energy gain. Data on the annual diet of howlers in La Luz demonstrate that a fair number of fruits and flowers are eaten, and I predict that the diets at La Luz will be of comparable nutrient quality to those described at other sites. I also predict that energy budgets will vary with group size, reflecting higher levels of feeding competition in larger groups.

I focus on ranging behavior in Chapter 5, where I present data on home range sizes, day journey lengths, and patterns of range use for the three study groups. I consider seasonal variation in ranging patterns in relation to changes in food abundance and dietary patterns, and consider indirect evidence for scramble competition provided by the ranging data. Given the low density of trees in the shade coffee plantation, it is expected that howlers at La Luz will have larger home ranges and longer day journey lengths than groups of comparable size in less disturbed habitats, that larger groups at La Luz will have larger ranges and average day journey lengths, and that ranging patterns will change in response to fluctuations in resource availability.

Chapter 6 presents a more detailed discussion of group compositions, patterns of intergroup transfer, and social interactions in the three study groups. Contest competition for food in relation to resource type, seasonality, group size, and age-sex class is described. I also relate instances of between-group agonism and circumstantial evidence for infanticide in relation to male takeovers of groups. I expect more contest competition in rare fruit trees with limited numbers of feeding spaces. I also predict

differences in social behavior related to variation in food density and distribution, as well as to low population densities and rapid population growth at La Luz.

In Chapter 7 I discuss the overall picture that emerges of the relationships between habitat structure, seasonality, foraging strategy, and feeding competition. I describe the results from each chapter in relation to broader theoretical contexts of foraging strategy and primate socioecology. I review the support provided for the predictions above and discuss differences between the overall patterns of behavioral ecology of howlers at La Luz to that of conspecifics at other sites. I also return to the original question of conservation that led to the initiation of this research, discussing the implications for the long-term management of this population presented by my data.

CHAPTER 2

STUDY SITE, METHODS, AND TREE COMMUNITY CHARACTERISTICS

This chapter provides a context for information presented in later sections on the feeding ecology, ranging and activity patterns, and social behavior of howling monkeys living in the coffee plantation of Finca La Luz, Mombacho Volcano, Nicaragua. I describe the study site, methodologies of data collection and analysis common to all sections of the dissertation, and present data on tree community composition and phenological patterns that are referred to throughout the dissertation.

STUDY AREA

Mombacho Volcano

I carried out this study in Finca La Luz, a shade coffee plantation on the southwestern side of Mombacho Volcano, Nicaragua (Figure 2.1). Mombacho Volcano, located in southwestern Nicaragua, lies on the country's heavily populated Pacific coast north of the city of Granada at 11°50'N latitude and 85°59'W longitude. Mombacho is a large, quiescent volcano with elevations ranging from about 300 m to 1,345 m at its highest peak (Atwood, 1984). All areas of the volcano experience a dry season from December to April and a rainy season from May through November; however, climate varies with elevation, the summit being cooler, moister, and less seasonal than the surrounding flanks (Atwood, 1984). This area comprises the northernmost extent of



Figure 2.1. Location of Mombacho Volcano, Nicaragua.

Costa Rican seasonal moist forests (Dinerstein *et al.*, 1995), although forest type shows a strong elevation gradient. The lower slopes of Mombacho support highly disturbed “tropical dry” forest and become increasingly wet with elevation.

The Reserva Natural Volcán Mombacho (RNVM), a 650 ha area, consists of the volcano’s summit above the 850-meter elevation mark. Fundación Cocibolca, a Nicaraguan environmental NGO, manages the reserve. RNVM comprises tall evergreens in its lower portions and elfin cloud forest above 900 m (Atwood, 1984). The majority of the lower moist forest, of which little remains undisturbed, falls within a belt of coffee plantations in the 300-800 m elevation zone surrounding the reserve. Most of these plantations grow “shade” coffee, using large native trees to shield the growing coffee bushes from direct sunlight (Perfecto *et al.*, 1996). A second agricultural zone at elevation 100-300 m contains cattle ranches and patches of highly disturbed deciduous broadleaf forest. Together, the two agricultural areas form an unofficial buffer zone around the nature reserve. Beyond these areas are more densely populated farmlands and areas of heavy deforestation; primates are found in these areas in only small, isolated populations. A census of the Mombacho’s primate community (McCann *et al.*, 2003) revealed that in spite of high human population density and extensive disturbance, Mombacho is home to a population of nearly 1,000 mantled howling monkeys (*Alouatta palliata*), as well as to lesser numbers of white-faced capuchins (*Cebus capucinus*); a few spider monkeys (*Alouatta palliata*) may also live in the reserve (Otterstrom, personal communication).

Approximately 97 troops of howlers with an average group size of 9.9 ± 6.2 individuals

were located, yielding a population estimate of 960 howlers for the census area (approximately 8 km²). The majority of these troops were located not in the reserve itself, but in the approximately 25 shade coffee plantations surrounding RNVM (Figure 2.2). Although highly disturbed, the seasonal broadleaf forest that comprises the shade cover in Mombacho's coffee plantations apparently provides a more favorable habitat for the howlers than the cool, windy elfin forest within the reserve. The low primate density (~13 howlers/km², whereas values for other *A. palliata* typically range from 15 to 90 per km²; Stoner, 1996) is thought to result not from habitat characteristics, but from a population bottleneck 20 to 30 years ago caused by intensive hunting and a possible epidemic of yellow fever amongst the howler population (McCann *et al.*, 2003).

Finca La Luz

La Luz is one of several shade coffee plantations surrounding RNVM. At 125 hectares in size, it is one of the larger properties in Mombacho, and comprises areas of pasture, active shade coffee cultivation, abandoned coffee, young regeneration, and older secondary forest (Figure 2.3). Areas of active coffee cultivation are defined as those parts of the property where coffee predominates in the understory and where it is regularly maintained (bushes are pruned, organic fertilizer is applied, the amount of shade is regulated, and the ground is cleared of competing understory plants). In abandoned coffee, coffee bushes still comprise the most important element of the understory, but other undergrowth occurs, the coffee bushes are not pruned and become so large that

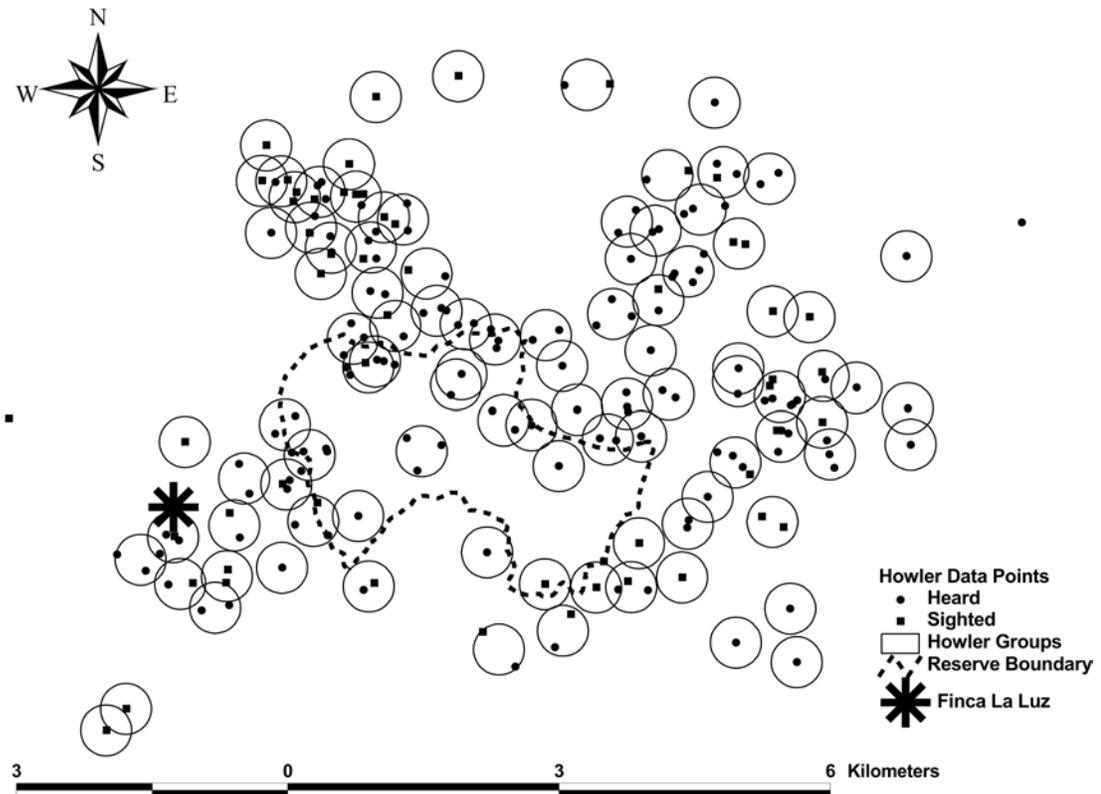


Figure 2.2. Howling monkey troop locations in Mombacho Volcano (from McCann *et al.*, 2003); points represent individual observations of howlers, circles represent estimated group ranges based on point locations. Far outliers are not included.

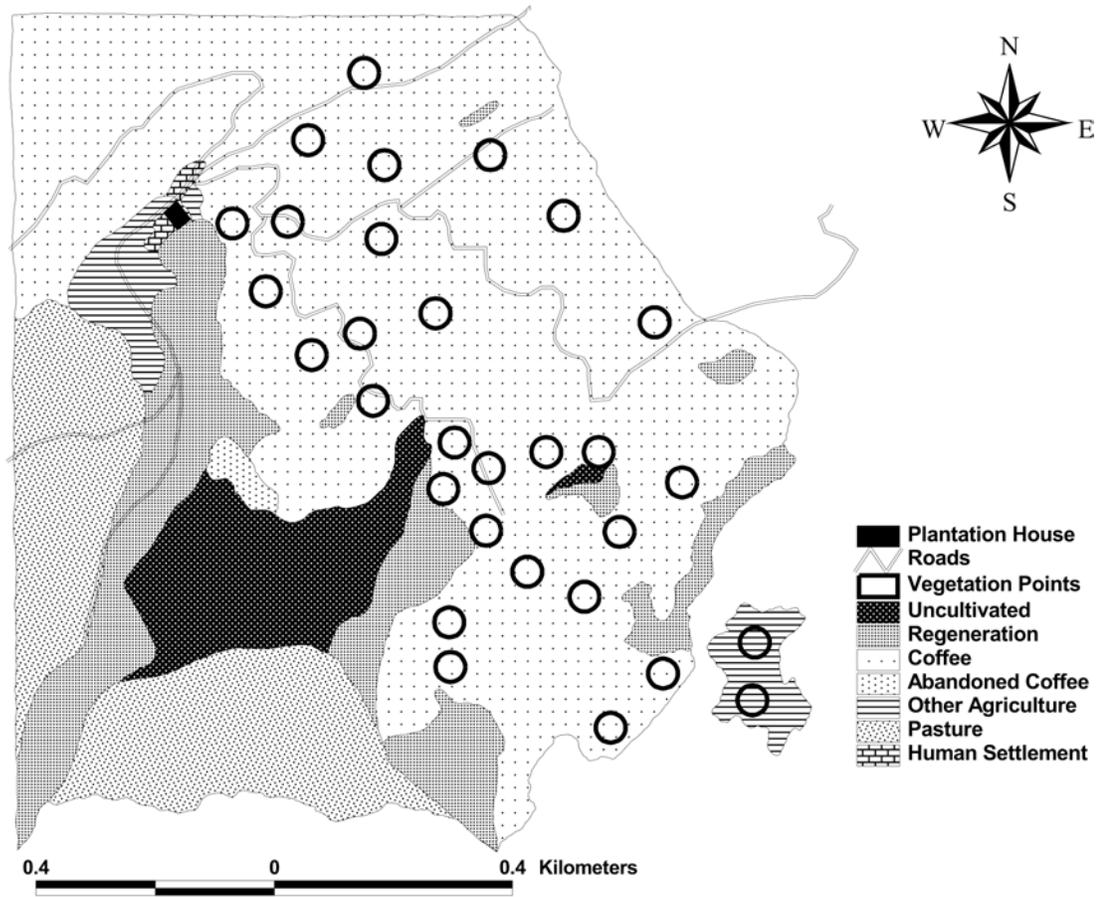


Figure 2.3. Habitat composition and location of vegetation enumeration plots at Finca La Luz (based on data collected by author).

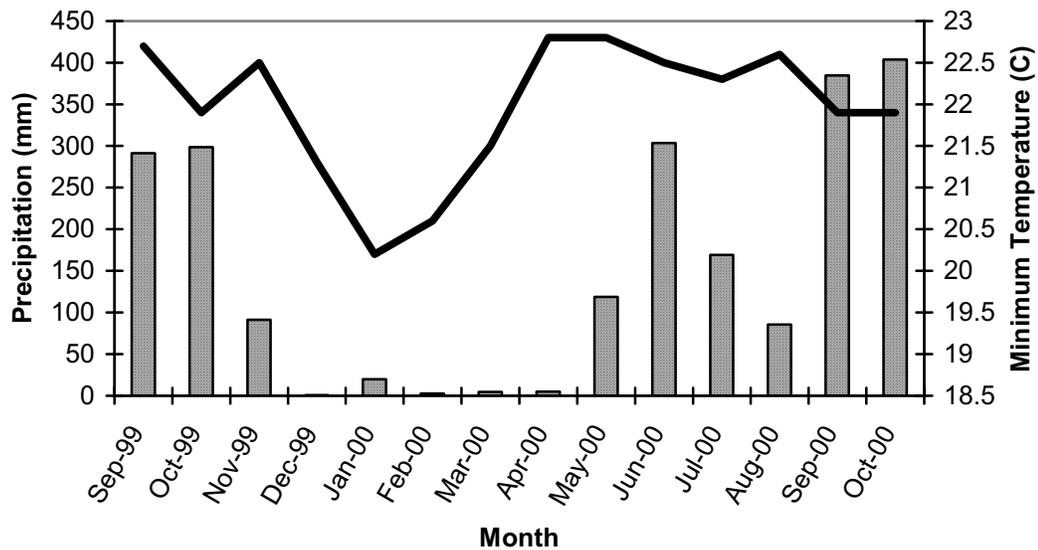


Figure 2.4. Total monthly precipitation (bars) and mean monthly minimum temperature (solid line).

they start to fall over, and there is more evidence of forest regeneration (e.g., more saplings mixed in with the coffee). Areas of young regeneration have a thick understory of *Piper* and vines, impenetrable without a machete; the canopy in such areas may be quite broken, and *Cecropia* trees are dominant members of the tree community. Older secondary forest comprises areas that have not been cleared in over 50 years (based on information from interviews), with a relatively sparse understory, trees with boles typically 40 cm wide or larger, and with a different tree community composition than seen in the shade coffee plantation (predominance of *Bursera simaruba*, *Cordia alliodora*, *Lysiloma aurita*, and *Guazuma ulmifolia*). La Luz has been a coffee plantation for over 100 years, making it

a locally stable environment. The plantation house lies at 500 m elevation, although elevations in the property range from about 350 to 650 m. Many long, steep-walled ravines cross the property from northwest to southeast; during the rainy season, these are flooded with ephemeral, fast-flowing rivers.

La Luz lies near the transition from semi-deciduous seasonal to evergreen moist forest. Because La Luz is located on the southwestern side of Mombacho, it receives less precipitation than the northern flanks due to a rain shadow (Atwood, 1984). Rainfall and temperature were noted each day in the morning before the commencement of data collection and were recorded from a thermometer mounted in a shaded area at the plantation house. Annual rainfall at the site was approximately 1490 mm (Figure 2.4). As is typical for the Pacific slope of southern Central America, there is a pronounced dry season from December through April (Figure 2.4; see also Atwood, 1984). The rainy season occurs between May and November, with rainfall peaking in September and October. For the purposes of the analyses in the following chapters, the rainy season is defined as May through November (Months 1, 2, and 8 to 12 of data collection) and the dry season as December through April (Months 3 to 7 of sampling). Minimum monthly temperatures are relatively constant (20 to 23° C), peaking during the late dry season. During the dry season, many of the trees in La Luz drop some or all of their leaves, subsequently producing a flush of flowers and young leaves.

Although howlers are common in the area, other fruit-eating primates are absent, reducing competition for fruit resources. Nor is there much competition from other large-bodied mammalian frugivores: kinkajous are relatively rare (seen fewer than 10

Table 2.1. Group compositions (based on averages of monthly counts) and sampling time of the three study groups.

	Group Compositions					Sampling Time	
	Males	Females	Juveniles ¹	Infants	Total	# Hours	# Days
Group 1	2.0	11.1	9.4	3.3	25.9	396	38
Group 2	1.3	7.5	2.9	3.6	15.3	451	44
Group 3	2.3	7.2	9.6	1.1	20.2	461	45
Total						1308	127

¹ Includes subadults that could not be confidently sexed.

times over 16 months in the plantation), and coatis are absent in plantation. The degree to which howlers and bats in the area may overlap in fruit resources is unknown.

Howlers may experience some competition for fruit from the abundant populations of small parrots (genus *Amazona*) and toucans, both of which were observed to feed on *Ficus costaricana* fruits, a primary resource for the howlers (Chapter 3).

BEHAVIORAL DATA

Study Groups

La Luz has a population of 65 to 70 howlers, the majority of which belong to three permanent groups ranging in size from 15 to 26 individuals (Table 2.1; see Chapter 6 for further discussion of group compositions at this site). Due to the large group sizes and the fact that many individuals could not be recognized, it is difficult to document

Table 2.2. Behavioral categories recorded during focal and scan sampling.

Category	Description	Additional Information Recorded During Focal Sampling
Rest	Subject is stationary, reclining or sitting, without being engaged in any other activity (e.g., feeding, socializing, etc.).	Contact with other individuals.
Feed	Subject is harvesting, chewing, or ingesting food.	Individual feeding tree, species, plant part, feeding rate.
Move	Subject moves at least 2 body lengths between feeding/resting positions within a tree or between tree crowns.	Travel in context of feeding (foraging) versus travel between feeding/resting locations (traveling).
Socialize	Subject engages in interaction with other individuals.	Agonistic or affiliative; behavior (e.g., groom, chase, displace, etc.); other individuals involved; context of interaction (feeding or non-feeding).
Vocalize	Subject produces loud, energy-demanding vocalizations.	Type of vocalization; context.
Other	Subject engages in behavior that cannot be easily characterized by the above categories.	Description of behavior (e.g., scent marking)
Unknown	Subject is out of sight or lost.	

exact changes in group composition. Group 1, the largest group, had 26 individuals at the beginning and end of the study (minimum count 24, maximum 28); during this period, at least 1 female left the group, and 3 infants were born, one of which subsequently disappeared. Group 2 had 12 individuals at the beginning of the study and 14 at the end, although group size varied from 12 to 17 animals. During the study, the resident male was displaced by 2 adult males, 1 female left the group with her juvenile, and 2 other juveniles left the group; 5 infants were born during this time. Group 3 had 18 individuals at the beginning of the study and 21 at the end (minimum count 17, maximum 24), with several subadult males entering the group partway through the study. At least 1 subadult female emigrated from group 3, and 3 infants were born (one of which disappeared after the entry of the males). These three groups were the focus of the study, and over 1,300 hours of data were collected on their behavior during the course of the study period. Several solitary animals, usually males, were also observed regularly in La Luz in areas not occupied by the study groups.

Data Collection

Behavioral data on the three groups were collected between 0530 and 1800 hours. Ideally, data on each group was collected for four full-day follows every 4 to 5 weeks. This data collection schedule deviates somewhat from the norm of timing data collection periods to coincide with calendar months, and was necessary due to scheduling conflicts and periodic travel; however, it is probably that primate behavior and ecological factors are not tied to calendar dates *per se*, and as data were collected at regular intervals

throughout the year with all calendar months represented, I believe that the data properly capture seasonal variation in behavior and resource availability. In this dissertation, I will refer to these data collection periods as cycles; there were 12 data collection cycles between October 1999 and October 2000.

Due to difficulties in finding groups, during some cycles the first day was dedicated to locating the animals. Eleven follows were completed for Group 1, and 12 for Groups 2 and 3; these cycles of data collection roughly coincided with calendar months. I collected data using a mixed strategy of scan and continuous focal animal sampling augmented by *ad libitum* sampling of rare events (Altmann, 1974). A field assistant collected fifteen-minute scan samples of visible group members throughout the day (approximately 40 to 60 per day) to provide data on the group's ranging and activities as a whole. I conducted concurrent daylong focal sampling of recognizable individuals (adult and immature) to provide detailed information on individual strategies of food choice, social interactions, and activity patterns. Focal animals were recognized by naturally occurring features such as scars, patches of light fur, and unpigmented areas of skin on the hands and feet. The order of focal animal sampling was determined at random before the start of each month's 4-day follow. Focal animals were recorded as performing one of several mutually exclusive behaviors (resting, feeding, traveling, vocalizing, and social; Table 2.2); states lasting less than 3 seconds were not recorded. Behavior duration was also recorded. The activity states of scanned animals were recorded using the same criteria. When the focal animal was observed feeding, plant part, phenophase, and species eaten were recorded. The length of feeding bouts for each plant

species and part was also noted so that accurate feeding profiles (by part and species) may be established. Whenever possible (i.e., when visibility allowed), the feeding rate was recorded as units of food (e.g., individual leaves or fruits, whole compound leaves, raches-worth of leaflets, etc.) consumed per minute. All accessible feeding trees were marked with forester's tape, and later identified, measured, and mapped with a GPS unit.

Statistical Analyses

Data were analyzed using SPSS (SPSS Inc., 2001) statistical software; all tests are two-tailed unless noted otherwise. Parametric tests are used whenever possible. Analysis of variance (ANOVA) is used to test for differences between groups (Sokal and Rohlf, 1995), and, in cases of two independent variables, are equivalent to Student's T-test. All ANOVAs are unbalanced one-way unless otherwise noted. All data were tested for homogeneity of variance using Levene's test and for normality with the Kolmogorov-Smirnov test. Non-normal data were log transformed for analysis. If assumptions of homoscedasticity were violated or data highly skewed, non-parametric Kruskal-Wallis ANOVAs were performed (equivalent to Mann-Whitney U tests in cases of two factors). Because these tests are relatively conservative, I considered *P*-values of 0.05 significant. *Post hoc* pair-wise comparisons were then examined using a sequential Bonferroni adjustment (for ANOVAs) or repeated pair-wise comparisons (for Kruskal-Wallis ANOVAs) to determine the sources of significant overall differences. Wilcoxon signed-rank tests were used in the case of matched samples. Spearman rank correlations are

used to test for relationships between sets of variables, and chi-square tests to determine if observed distributions of behaviors differed from expected.

TREE COMMUNITY COMPOSITION AND PHENOLOGY

Methods

To characterize the composition of the vegetation community, I conducted a census of the trees in the shade coffee plantation. Enumerations were conducted in 30 points in areas of shade coffee cultivation (Figure 2.3). A map of the coffee plantation was divided into a grid of 100 m by 100 m; grid cells in areas of active coffee cultivation were selected at random and the center of each plot was placed as close to the center as possible. Within a 25-m radius circle, I numbered, counted, and identified all stems ≥ 20 cm in diameter at breast height. A minimum value of 20 cm was chosen because howlers rarely feed from smaller trees (Milton, 1980) and because the majority of shade trees fell above this threshold, meaning that the majority of trees in each plot were included in the enumeration. Identifications were made with the assistance of Diego Osorno, a principal field assistant trained in botanical identification; vouchers were collected and identifications made in the field using guidebooks or at the herbarium associated with the Universidad Centroamericana, Managua. The diameter at breast height was measured, and tree height and canopy connectivity were estimated. Tree heights were estimated visually and selected estimates were checked by measuring tree height with a clinometer. Canopy connectivity was estimated by noting the approximate percent circumference of

the tree crown touching other trees. The same measurements were taken for all trees in which the howlers fed in order to facilitate comparisons between feeding trees and available trees. All trees used by the study subjects for feeding were tagged and circumference at breast height was measured and used to calculate the basal area, an estimator of fruit (Leighton and Leighton, 1982) and foliage biomass (Kool, 1992; Gillespie and Chapman, 2001). Each feeding tree was mapped using differential GPS. The Shannon index of diversity (H) is used to provide an estimate of both species richness and relative abundances (Krebs, 198):

$$H = \sum_{i=1}^s p_i \ln p_i$$

where H is Shannon's index of diversity, s is the total number of species in the community (richness), and p_i is the proportion of s made up by the i th species.

To characterize phenological patterns, I visited each of the 492 trees marked in the 5.89 hectares of vegetation enumeration points monthly to record the production of leaves, fruits, and flowers. I followed the method of Dasilva (1994) to calculate an *index of abundance* for the different phenophases. Through visual inspection with binoculars, I estimated the amount of leaves, fruits, and flowers present as a percentage of the maximum possible for the tree's crown size and structure. Vegetative (young and mature leaves) and reproductive (fruits and flowers) parts were considered on separate scales, each having a maximum value of 100%. Determinations of leaf maturity were generally done visually; leaves were considered immature if they exhibited at least two of the following characteristics: a different color, shape, or size than obviously mature leaves.

Because maxima are more difficult to establish for reproductive parts, as they are not borne in all parts of the crown and vary from species to species in size, the fruit and flower indices are less reliable than the foliage indices (Dasilva, 1994). Although I attempted to differentiate between mature and young fruits, many species (for example, *Ficus obtusifolia*, *Cedrela odorata*) have fruits whose maturity is difficult to determine based on visual inspection alone. I therefore pooled all data for fruits in presentation of results. The contribution of each species to forest production is estimated by weighting the phenological scores with a measure of the species' basal area, using an equation based on that presented by Dasilva (1994):

$$W_i = \sum (A_i B_i)$$

where W_i is the weighted abundance of the phenophase for tree i , A_i is the estimate of abundance for the part for each individual tree i , and B_i is the proportion of total basal area of each individual tree i . To facilitate understanding of temporal patterns of forest production, and to make more comparable comparisons with phenological data from other studies, I also calculate an *index of production* for each phenophase, which is calculated as the percentage of trees sampled bearing a given phenophase per month. Finally, I calculate a standardized Morisita's index of dispersion, I_p , to characterize the spatial distribution of the tree species (see Krebs, 1989 for a complete review of calculations, which are involved); because these are basically comparisons of mean to variance, indices are calculated only for species with 3 or more individuals represented in the enumeration plots. Indices of dispersion are normalized to an absolute scale from -1

to 1, with 95% confidence limits at 0.5 and -0.5; an I_p of zero indicates a random distribution, positive values indicate clumped distributions, and negative values uniform distributions.

Tree Community Composition and Structure

A total of 492 trees with a diameter at breast height of 20 cm or more were found in the 5.89 hectares of enumeration points. The average density of trees was 83.5 individuals per hectare. The trees in the enumeration represent 48 species. However, there were a few rare species that were not represented in the enumeration, and I estimate that there are 60 to 65 tree species present in the plantation. This is in contrast to other, less disturbed sites where *Alouatta palliata* has been studied, where there are generally over 100 species available as food sources for howlers (for example, Glander, 1981; Milton, 1978). The Shannon index of diversity is 2.88 for the site (versus 3.8 to 3.9 for BCI).

The tree community is dominated by a few common species, several of which belong to the superfamily Leguminosae (Fabaceae in recent taxonomic revisions; Appendix I). When considered by number of individuals, the most common species are *Gliricidia sepium*, *Cecropia peltata*, and *Cedrela odorata*. The 10 most common trees comprise more than 75% of individual stems in the enumerations. Many of the most common trees are typically smaller, meaning that percentages of stems may not accurately reflect their contributions to the total canopy area available to the howlers. I therefore considered tree species composition as a proportion of total basal area (Appendix I). *Gliricidia sepium* is still the most common component of the canopy. However, other tree

species, such as *Enterolobium cyclocarpum* and *Ficus costaricana* (both significant sources of food for the howlers; Chapter 3) contribute more to canopy area than stem counts alone would suggest. Leguminous trees dominate the tree community, whether considered by number of individuals or by basal area. Coffee plantation owners favor them as shade trees due to their ability to fix nitrogen. I did not observe trees being planted; however, the plantation manager reported that *Gliricidia sepium* and *Spondias mombin* are sometimes planted as fence rows, while *Inga* trees may be planted as shade cover.

Of the enumerated trees, the mean diameter at breast height was 55.3 cm, although the majority of trees are smaller (Figure 2.5). Several species, such as *Enterolobium cyclocarpum*, generally reach diameters of 200 cm or more. Tree heights range from 5 to 25 m tall. 62% of trees reach heights of 12 or more meters; only 9% of trees in the enumeration reach heights of 18 m or higher. Although the density of trees is lower than in undisturbed habitat, it is high enough to provide a relatively closed canopy through which the monkeys can travel. On average, tree crowns touch those of other trees along approximately 70% of their circumference. Indices of dispersion ranged from -0.19 (slightly uniform) to 1.0 (highly clumped) at a scale of 0.2 ha (the approximate area of each enumeration point). Several of the most common tree species (*Gliricidia sepium*, *Cedrela odorata*, *Cecropia peltata*, etc.) have indices of 0.5 or higher, indicating significantly clumped distributions. *Gliricidia* and, in particular, *Cecropia* are small and occur in stands, thereby forming “super patches” of several individuals. *Enterolobium cyclocarpum* and *Ficus costaricana* trees (important food sources for the howlers; Chapter 3) have only slightly positive indices, indicating distributions that do not deviate significantly from

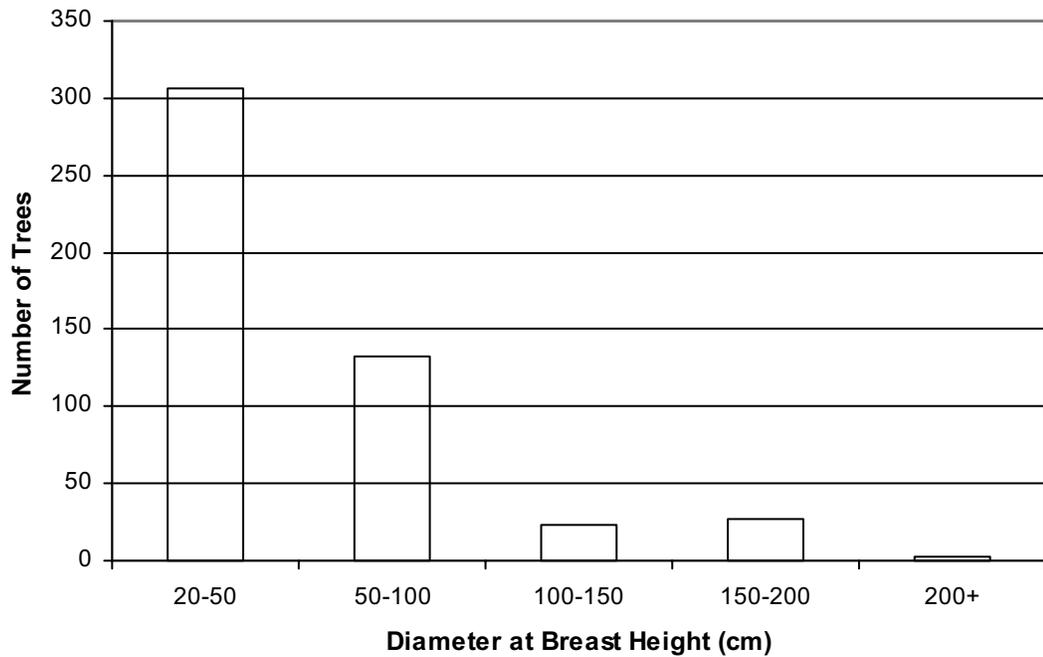


Figure 2.5. Histogram of the diameters at breast height of trees measured in the enumeration points.

randomness.

Although I did not collect data on sapling presence or recruitment, I did observe saplings in areas of shade coffee cultivation. These small trees were relatively rare as actual shade trees, but they were common on in the very small patches of regenerating secondary forest found throughout the shade coffee. Occasionally, parts of the coffee plantation are temporarily “abandoned,” particularly in areas where the coffee trees are older. These may be left to lie fallow for several years before being rehabilitated through clearing of the understory and replanting of coffee bushes. Saplings and small trees were

observed in these areas, which may serve as reservoirs of regeneration within the shade coffee. Finally, forest regeneration is clearly underway in larger patches of older secondary growth, where many more trees with boles of 5 to 15 cm were observed. Regardless, as there are many trees in the coffee plantation with diameters at breast height of less than 50 cm, it seems that tree growth and forest regeneration has been possible in the recent past, and I did not observe any management practices that would rule out the regeneration *per se* of any tree species.

Phenological Patterns

The two indices (production and abundance) correlate closely with one another (mature leaves: $r_s = 0.881$; young leaves: $r_s = 0.902$; fruits: $r_s = 0.951$; flowers: $r_s = 0.937$; $P < 0.001$, $N = 12$ for all tests). Indices of production indicate that mature leaves are present in the canopy throughout the year, although the number of trees bearing this phenophase is lower during the dry season (Figure 2.6). The dry season coincides with peak production of seasonal plant parts. At the beginning of the dry season, many tree species produce flowers, especially *Gliricidia sepium*. This peak is mirrored by increased production of fruits, particularly by leguminous species, and young leaves. Fruit production remains relatively high through the wet season, when trees such as *Spondias mombin* produce sweet, fleshy fruits. Although the production of various phenophases generally peaks in or is confined to one season, there are no statistically significant relationships between the monthly abundance of any phenophase and monthly rainfall. There is a negative relation between the production of mature leaves and all other

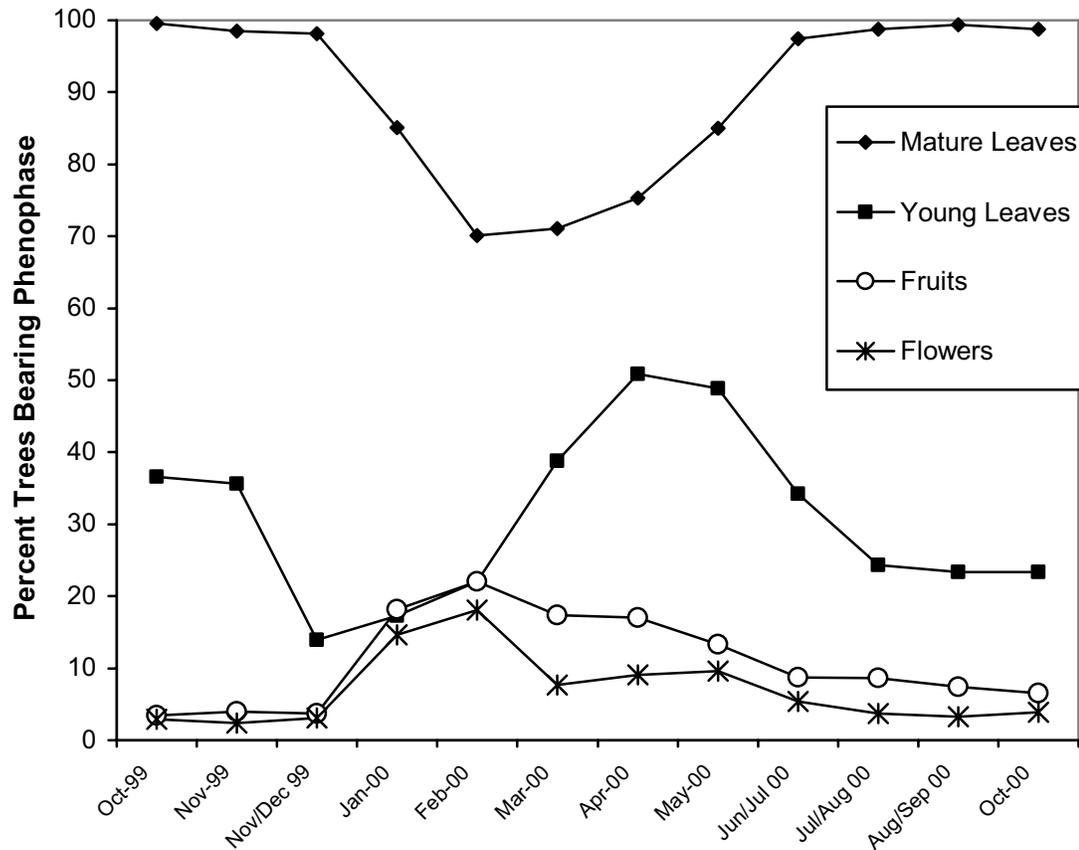


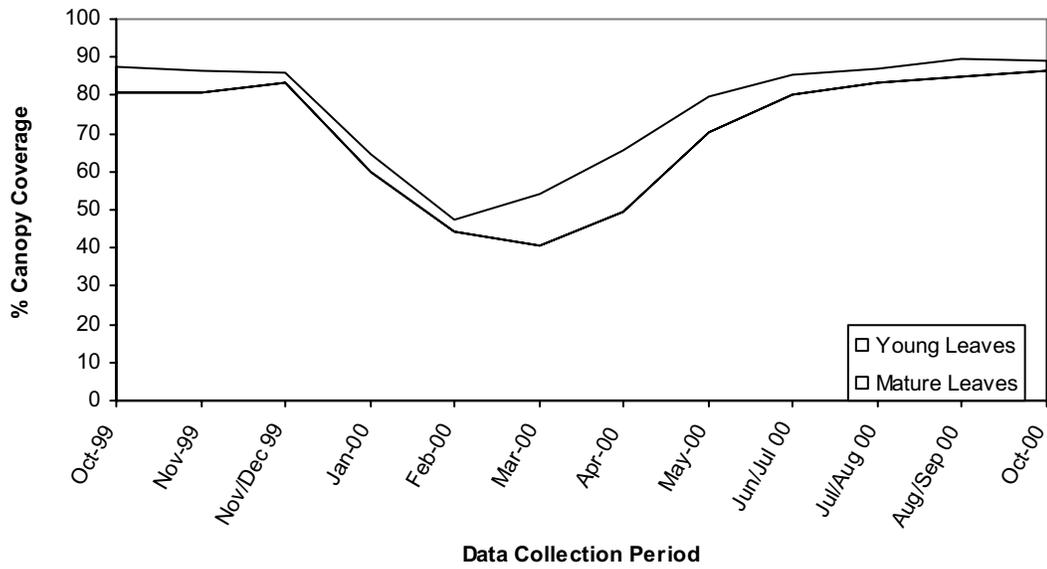
Figure 2.6. Indices of phenophase production.

seasonal phenophases (Spearman rank correlation, $N = 12$ for all: $r_s = -0.175$, $P = 0.587$ for young leaves; $r_s = -0.839$, $P = 0.001$ for fruit; $r_s = -0.790$, $P = 0.002$ for flowers).

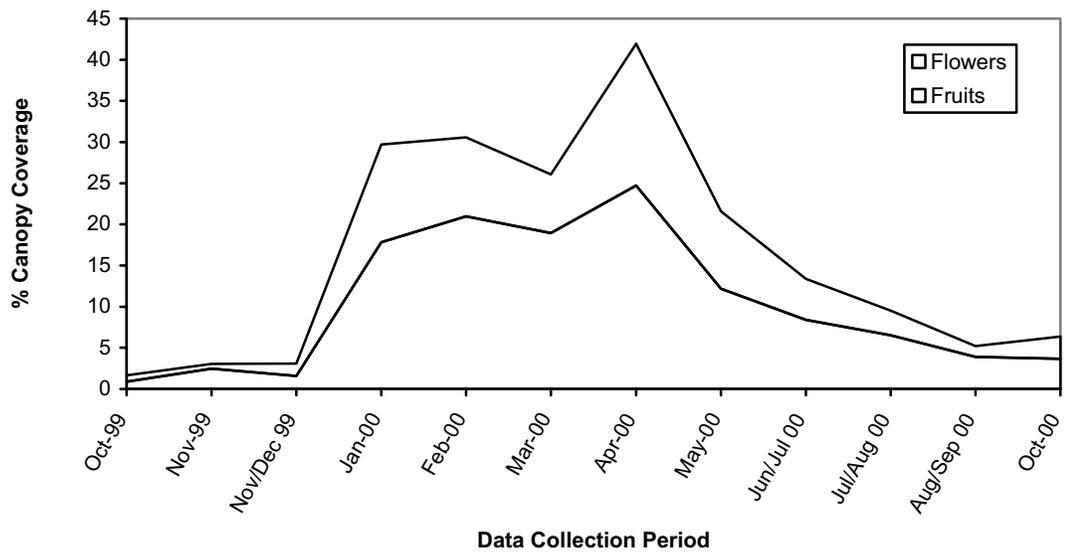
Young leaf production shows no correlation with fruit production ($r_s = 0.049$, $P = 880$) or flower production ($r_s = 0.021$, $P = 0.948$). Flower production has a significantly positive relationship with fruit production ($r_s = 0.930$, $P < 0.001$), reflecting the flowering and fruiting of the leguminous tree species during the dry season.

Figure 2.7. Abundance of (a) vegetative and (b) reproductive parts in the forest canopy.

(a) Young and mature leaves



(b) Flowers and fruits



The indices of abundance for various phenophases also differed between seasons. Mature leaves are always more abundant than young leaves (Figure 2.7a), although abundance drops significantly during the dry season, as the abundance of young leaves increases; the negative relationship between mature and young leaf abundance approaches significance ($r_s = -0.545$, $P = 0.067$, $N = 12$). The abundance of reproductive parts never reaches more than 45% of the canopy (Figure 2.7b). There are two peaks in the abundance of fruits and flowers, one early in the dry season, when many leguminous trees flower and produce hard, dehiscent fruits, and one at the transition from the dry to wet season, when trees such as *Spondias mombin* and *Manilkara chicle* produce succulent fruits; *Spondias mombin*, an important fruit source for the howlers (Chapter 3) begins fruiting in the early wet season and continues fruiting throughout the wet season. Most species, especially leguminous trees, had synchronous phenological patterns. Notable exceptions were *Ficus costaricana* and *Cecropia peltata*, both of which were frequently used as food sources; individuals of these species varied in the timing of the production of leaves, fruits, and flowers.

DISCUSSION

Finca La Luz differs from other study sites where *Alouatta palliata* has been studied in the structure and composition of its tree community (Table 2.3). Although the differences in tree density could result in part from differences in methodology (some studies include a larger total enumeration area, which could result in recording more species, while the smaller trees measured in some studies could result in higher reported

Table 2.3. Tree community characteristics at selected sites where the behavioral ecology of *Alouatta palliata* has been studied.

Study Site	Enumeration Area (ha)	DBH Measured	Species in Enumeration	Stems/ha	Source
Barro Colorado Island, Panama	6.0	19 cm	135	169.5	Milton (1979)
Santa Rosa, Costa Rica	2.0	20 cm	45	251.0	Larose (1996)
Hacienda La Pacifica, Costa Rica	9.9	“all trees”	96	171.9	Glander (1978)
La Suerte, Costa Rica	0.35	10 cm	--	474.3	Stoner (1993)
Los Tuxtlas, Mexico	3.0	Unknown	> 150	--	Estrada (1984)
La Luz, Nicaragua	5.9	20 cm	48	83.5	Current study

tree densities. However, La Luz has low species richness in comparison to other, less disturbed sites with similar or lower enumeration areas (e.g., Milton, 1979; Estrada, 1984), and the density of trees is very low, even in comparison to sites where similar tree sizes were measured (e.g., Milton, 1979; Larose, 1996). Overall, the structure and species composition of the trees at La Luz most closely resembles that at Finca La Pacifica, located on the Pacific coast of Costa Rica. La Pacifica is also quite disturbed, although in a different way: the forest is highly fragmented (Glander, 1978b, 1981) but is not intensively managed as at La Luz, where certain species are sometimes planted and trees may have branches cut to regulate the amount of shade the coffee bushes receive. As at many other howler study sites, there is marked seasonality in rainfall, and the production of seasonal items varies greatly throughout the year. Phenological patterns at La Luz closely resemble those described for La Pacifica (Glander, 1978b, 1981) with young leaf and flower production peaking in the dry season.

Changes in resource abundance and availability have fundamental effects on the behavior and ecology of primates (Dunbar, 1988). Howlers are known to favor seasonally available resources such as young leaves, flowers, and fruits (Glander, 1978b; Milton, 1980). Given that La Luz is highly seasonal in both the production and abundance of these resources, and that howlers shift their feeding, ranging, and activity in response to fluctuating resource availability, seasonal changes are expected to affect many aspects of howler behavioral ecology at this site. The low density of trees at La Luz means that howlers will have to travel more and farther in order to visit the same number of trees. Low diversity suggests that the howlers will have a much less varied diet than at

other sites, demonstrating heavy reliance on those few species that make suitable food resources. If these key food species are rare, the howlers should demonstrate more intense scramble (and contest, depending on resource distribution) competition than conspecifics at other sites. Determination of the effects of the habitat structure at La Luz on primate behavioral ecology relies upon a close analysis of basic foraging patterns, which should, in turn, affect nutrition, ranging behavior, and the incidence of contest competition; the next chapter closely examines the foraging strategy of howlers in La Luz.

CHAPTER 3

FORAGING BEHAVIOR AND ACTIVITY PATTERNS

INTRODUCTION

In Chapter 2, I described the structural characteristics and community composition of the shade coffee forest and La Luz. The agroforest of the shade coffee plantation has lower tree density and species richness than the habitats where mantled howlers have been intensively studied. This environment therefore provides an opportunity to investigate the relationship between foraging strategy and environmental richness. Patterns of howler feeding behavior are closely tied to the availability of habitat-specific resources (Milton, 1980), suggesting that feeding patterns of *A. palliata* in coffee plantations will differ from those recorded in primary or non-cultivated habitats. Based on current theory describing the foraging strategy of generalist herbivores and on information from previous studies of howler monkeys at other sites, it is expected that the diets of howlers in such disturbed habitats will differ in species diversity and plant part composition, and that these differences will reflect the influences of reduced tree species diversity and abundance. I predict that howlers in these human-managed forests will rely heavily on just a few staple species, use species that are avoided at other sites, and include more foliage in their diets.

Additionally, if potential food sources are less abundant than in less-disturbed habitat, it is expected that howlers in shade coffee plantations will exploit those food patches that *are* acceptable more heavily and for longer periods of time than do

conspecifics at other sites. Reduced food tree density may result in increased travel time due to increased distance between food sources. If more foliage is included in the diet, then time spent resting may also be high as a necessary consequence of digestion. Increased travel and resting time will come at the expense of feeding and social time. In this chapter, I describe the annual diet composition of diets by food type and species, temporal variation in food consumption and its relation to the abundance of food items, and the concentration of feeding time on certain trees in relation to patch size and quality. I also describe activity patterns, considering overall characteristics and temporal variation. These data allow me to explore the basic feeding ecology and activity budgets of the population, to contrast these with foraging strategies of conspecifics studied at other sites, and to discuss the role of food abundance and forest structure in determining the foraging strategy of folivorous primates.

METHODS

Feeding Behavior

Data on feeding behavior were collected during focal animal sampling of recognizable individuals (see Chapter 2 for a detailed description of data collection methods and schedules). For the purposes of this analysis, *feeding bouts* are defined as periods of processing or consumption of a single food type within a single feeding tree uninterrupted by other behavior states lasting more than 3 seconds, the minimum amount of time in which I could accurately record the details of a behavioral state and its duration. During the course of the study, I observed 5,037 feeding bouts totaling 162.8

hours in duration. For each feeding bout, I noted the individual tree fed from, food species, plant part (young and mature leaves, fruits, flowers, etc.), duration of the bout, and, whenever visibility allowed, feeding rate (number of units of food eaten per minute). All accessible food trees were numbered and mapped, the diameter at breast height was measured, and tree height and crown connectivity were estimated; no attempt was made to mark or measure vines or epiphytes that were food sources. Approximately 75 feeding trees accounting for 4% of total feeding time could not be marked or mapped because they were located in inaccessible areas. Most of these were in Group 1's home range; with the exception of a few *Lysiloma aurita* trees, which were heavily exploited for flowers, none of these were major feeding trees.

Due to differences in topography and habitat types used, the amount of data collected for the three study groups varied; Group 1, which was the most difficult group to follow and observe because it ranged in very steep, uncultivated areas, accounts for fewer feeding records than the other two groups. Additionally, it was more difficult to collect feeding data during the rainy season, when the production of mature leaves reduced visibility and flash floods prevented data collection. In order to correct for these discrepancies, in presenting results on each group's monthly and annual diets the raw data on total feeding time for each species and part are summed on a monthly basis and then calculated as a percentage contribution to the monthly diet. Monthly diets for all groups are the averages of the monthly values for the 3 groups. Annual diets for each group are calculated as an average of the monthly values, and overall annual diets are derived by taking the mean of the annual diets of the three groups.

Feeding bouts as defined above are not independent of one another. Frequently, several sequential bouts represent feeding by the same individual in the same tree interrupted by brief periods of other behavior, such as movement or social behavior. Additionally, a focal animal may feed in a tree during the morning, travel to additional trees throughout the day, and return for further feeding during the evening. This interdependence presents problems in analyzing the relationships between the amount of time spent feeding in a tree and the type of food eaten, especially as brief movements within feeding trees are more common when resources are clumped within a tree crown (e.g., fruits and some young leaves). To better characterize the intensity of tree use, I calculate the *daily patch feeding time* as the sum of total feeding seconds per phenophase per individual food tree per day. It is likely that these data still demonstrate some autocorrelation, and statistical analyses applied in this presentation are, at this time, suboptimal. To characterize the intensity of food selection, I use a ratio of food species selection (Glander, 1981), in which monthly feeding time per species is divided by the percent contribution of the species to total basal area, as measured in the vegetation enumeration; values near 1 suggest that a species is eaten roughly in proportion to its abundance, values above 1 suggest selection, and values below 1 consumption below abundance. Phenological methods are as described in Chapter 2. Additionally, I use the methods described in Chapter 2 to calculate indices of production for species eaten in order to provide a more accurate description of the timing of phenophase production by key food species.

Activity Budgets

General activity budgets were determined on a group-by-group basis through scan sampling. Every 15 minutes, the activity state of all visible group members was recorded (Chapter 2). The percent contribution of the various activity states to each scan was calculated; the daily activity budget was calculated by averaging the values from all scans within a day. Data are included only from “complete” days, i.e., the group was in view and data were collected for 10 to 12 hours. Monthly activity budgets were computed by averaging daily values within each 4-day follow. Annual activity budgets for each group represent a grand mean of the monthly budgets. Activity budgets are generally reported based on scan samples, and because of their comparability, these are used to contrast activity patterns at La Luz with those of conspecifics at other sites.

RESULTS

Annual Diets

Composition by Food Type. Table 3.1 shows the composition of the average annual diet by food type. In general, the howlers focus on seasonally-produced food sources (young leaves, fruits, and flowers), which together comprise 71.4% of their annual diet. Leaves comprise over half of the annual diet of all groups (2,515 feeding bouts totaling 48.8 hours). Of the leaves and leaf parts consumed, 48.5% were of mature leaves and 49.8% were of young leaves; the remaining 1.7% of leaf consumption was of leaves of unknown maturity. Leguminous species, such as *Enterolobium cyclocarpum* and *Inga* spp., were the most important sources of mature leaves and leaflets; *Bursera simaruba*,

Table 3.1. Composition of the annual diet of all study groups by food type.

Food Type		% Diet	
Leaves	Mature Leaves	<i>Mature whole leaves</i>	8.1
		<i>Mature leaflets</i>	15.5
		<i>Mature leaf petioles</i>	2.6
		<i>Mature leaf pulvini</i>	0.7
		Total Mature Leaves	27.0
	Young Leaves	<i>Leaf buds</i>	11.4
		<i>Young whole leaves</i>	12.4
		<i>Young leaflets</i>	2.3
		<i>Young leaf petioles</i>	0.7
		<i>Young leaf pulvini</i>	0.1
		<i>Other young leaf</i>	0.9
		Total Young Leaves	27.8
		Leaves of indeterminate maturity	0.9
	Total Leaves	55.8	
Fruits	Mature fruit	26.6	
	Immature fruit	5.8	
	Fruit of indeterminate maturity	2.4	
	Total Fruits	34.8	
Flowers	Open flowers	7.4	
	Flower buds	0.5	
	Total Flowers	7.9	
Other	Stems	0.1	
	Twigs	0.2	
	Undetermined plant parts	1.3	
	Total Other Plant Parts	1.6	
TOTAL ANNUAL DIET		100.0	

Astronium graveolens, and various unidentified vines also account for much of the mature leaf component of the diet. Nearly half of the young leaves eaten were of *Ficus costaricana*.

Reproductive plant parts also comprise a significant portion of the diet (2,404 feeding bouts). Fruits comprise 34.8% of the overall diet, with 76.4% of these being mature fruits, mostly of *Ficus costaricana*, *Spondias mombin*, and *Cecropia peltata*. Most of the immature fruit eaten came from *Ficus costaricana* (fruits of this species can be characterized by maturity due to color changes upon ripening). Flowers comprise 7.9% of the diet; most flowers eaten come from leguminous trees, such as *Dyphisa robinoides*, *Enterolobium cyclocarpum*, and *Gliricidia sepium*. Other plant parts, such as stems and twigs, were eaten rarely (118 feeding bouts) and account for only 1.3% of the overall diet. The howlers were never observed ingesting animal matter or fungi, nor were they observed drinking water, as they do at La Pacifica (Glander 1978a).

Figure 3.1 shows the composition by food type of the annual diets of the three study groups. There are notable differences between the groups in dietary profiles, especially in the ratio of mature to young leaves consumed. The composition of vegetative (50 to 60% of the diet) versus reproductive parts (40 to 50% of the diet) was broadly similar for the annual diets of the three groups. However, the groups vary in terms of the proportions of food types within these categories, probably as a result of differences in the species compositions of their diets (see below). Group 1 ate more mature leaves and flowers than the other groups. Group 3 ate more young leaves than the other groups, while Group 2 had the highest proportion of fruit in their diet. Based on one-way ANOVAs comparing their monthly diets, differences between the 3 study

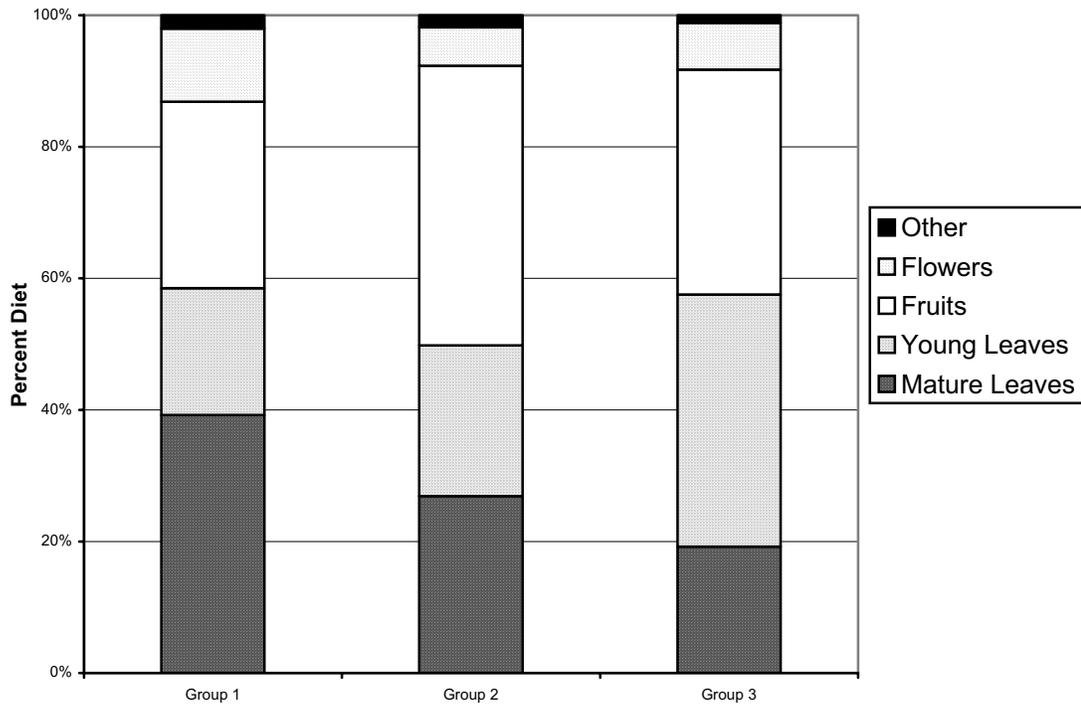


Figure 3.1. Annual diets by food type of the three study groups.

groups in the average consumption of mature and young leaves were significant for mature leaves ($F_{[2,32]} = 4.275, P = 0.023$) and young leaves ($F_{[2,32]} = 3.875, P = 0.031$) but not for fruits ($F_{[2,32]} = 2.25, P = 0.122$) or flowers ($F_{[2,32]} = 0.366, P = 0.697$). *Post hoc* comparisons demonstrate that Group 1 spent significantly more time eating mature leaves and less time eating young leaves than did Group 3.

Table 3.2. Species representing at least 1% of the overall annual diet, ranked in order of percent contribution.

Rank	Species	Family	Percent Annual Diet	Cumulative Selection Percent	Selection Ratio ¹
1	<i>Ficus costaricana</i>	Moraceae	32.02	32.02	3.72
2	<i>Enterolobium cyclocarpum</i>	Fabaceae	9.97	41.99	0.66
3	<i>Spondias mombin</i>	Anacardiaceae	7.01	49.00	5.61
4	<i>Cecropia peltata</i>	Cecropiaceae	6.56	55.57	0.51
5	<i>Bursera simaruba</i>	Burseraceae	6.17	61.74	High ²
6	<i>Albizia guachapele</i>	Fabaceae	3.41	65.15	2.33
7	<i>Inga</i> spp.	Fabaceae	3.34	68.49	1.06
8	<i>Lysiloma aurita</i>	Fabaceae	3.20	71.69	5.00
9	Unidentified epiphytes	Unknown	2.44	74.13	—
10	<i>Ficus obtusifolia</i>	Moraceae	2.22	76.35	0.92
11	<i>Diphysa robinoides</i>	Fabaceae	2.11	78.45	7.87
12	<i>Astronium graviolens</i>	Anacardiaceae	1.90	80.36	2.34
13	<i>Pithecellobium saman</i>	Fabaceae	1.85	82.21	0.70
14	<i>Ficus benjamina</i>	Moraceae	1.70	83.90	High
15	<i>Manilkara chicle</i>	Sapotaceae	1.53	85.43	0.58
16	<i>Mastichodendron capiri</i>	Sapotaceae	1.39	86.82	0.09
17	<i>Gliricidia sepium</i>	Fabaceae	1.22	88.05	0.06
18	“S-660”	Sapindaceae	1.10	89.14	High

¹ Selection ratio based on Glander (1981), in which the proportion contribution of the species to the diet is divided by the proportion contribution to the basal area of stems in the vegetation enumeration; values near 1 indicate that a species was used roughly in proportion to its availability. Because the vegetation enumeration did not include the areas of secondary forest that comprise the majority of Group 1’s home range, the ratios are calculated using the contribution of each species to Group 2 and 3’s diets only.

² “High” indicates species that were eaten but were not represented in the 5.8 ha of vegetation enumeration; “—” indicates epiphytes, whose abundances were not estimated.

Table 3.3. Composition of each group's annual diet by species.

Family	Species	Percent Annual Diet ¹				Parts Eaten ²
		Group 1	Group 2	Group 3	Mean	
Anacardiaceae	<i>Astronium graviolens</i>	2.40	2.85	0.67	1.90	ML, YL
	<i>Spondias mombin</i>	9.53	3.95	8.16	7.01	FR, YL, ML, FL
	<i>Spondias purpurea</i>	1.02	0.00 ^a	0.54	0.49	FR, YL
Annonaceae	<i>Annona purpurea</i>	0.00 ^a	0.00	0.09	0.03	FR
Bombacaceae	<i>Bombacopsis quinata</i>	0.00 ^a	0.00 ^a	0.12	0.04	YL, ML
	<i>Ceiba pentandra</i>	0.15	0.12	1.63	0.63	YL
Boraginaceae	<i>Cordia alliodora</i>	0.00	0.02	0.02	0.01	ML
Burseraceae	<i>Bursera simaruba</i>	14.65	2.16	2.93	6.17	ML, YL, FL, FR
Caricaceae	<i>Carica papaya</i>	0.07	0.10	0.00	0.06	ML, FR
Cecropiaceae	<i>Cecropia peltata</i>	7.94	5.79	6.24	6.56	FR, YL, FL, ML
Combretaceae	<i>Terminalia oblonga</i>	1.17	0.71	0.04	0.63	YL, ML
Ebenaceae	<i>Diospyros nicaraguensis</i>	1.24	0.00 ^a	0.00 ^a	0.38	MF
Euphorbiaceae	<i>Sapium macrocarpum</i>	0.20	0.00	0.13	0.11	ML, YL
Fabaceae	<i>Albizia guachapele</i>	1.84	5.49	2.75	3.41	ML, YL, FL
	<i>Diphysa robinoides</i>	1.21	0.45	4.74	2.11	FL, YL, ML
	<i>Enterolobium cyclocarpum</i>	10.40	10.45	9.76	9.97	ML, FL, OT, YL
	<i>Erythrina fusca</i>	0.00	2.16	0.00	0.77	ML, YL
	"Fabaceae sp. 1"	0.67	0.12	0.73	0.49	YL
	"Fabaceae sp. 2"	0.00 ^a	0.00 ^a	0.31	0.10	FL
	<i>Gliricidia sepium</i>	1.46	0.89	1.29	1.22	FL, ML, YL
	<i>Hymenaea courbaril</i>	0.11	0.00 ^a	0.00 ^a	0.03	ML
	<i>Inga vera</i>	1.99	6.61	0.97	0.31	ML, YL, FL
	Other <i>Inga</i> (2-3 species)	0.81	0.03	0.13	3.34	ML, YL
	<i>Leucaena leucocephala</i>	0.00 ^a	0.05	0.00	0.02	YL
	<i>Lonchocarpus</i> sp.	0.56	0.09	0.07	0.24	YL, ML
	<i>Lysiloma aurita</i>	8.93	0.50	0.90	3.20	FL, ML, YL
	<i>Pithecellobium saman</i>	2.38	0.15	3.15	1.85	ML, YL, FL
	<i>Schizolobium parahybum</i>	0.04	0.00 ^a	0.00 ^a	0.01	FL
Unknown	0.63	0.00 ^a	0.00 ^a	0.19	FL	
Moraceae	<i>Castilla elastica</i>	0.03	0.61	0.08	0.24	ML, YL, FL, FR

Family	Species	Percent Annual Diet ¹				Parts Eaten ²
		Group 1	Group 2	Group 3	Mean	
	<i>Ficus benjamina</i>	0.00 ^a	0.00 ^a	5.07	1.70	YL, FR
	<i>Ficus bullenei</i>	0.00 ^a	0.29	0.00 ^a	0.10	YL, FR
	<i>Ficus costaricana</i>	11.98	38.92	41.18	32.02	FR, YL, ML
	<i>Ficus obtusifolia</i>	1.00	4.24	1.46	2.22	YL, FR, ML
	<i>Ficus pertusa</i>	2.47	0.00 ^a	0.00 ^a	0.75	FR, YL
	<i>Ficus trigonata</i>	0.00 ^a	0.02	0.00	0.58	FR
	Other <i>Ficus</i> (2-3 species)	0.04	1.65	0.00 ^a	0.01	YL, FR, ML
Myrtaceae	<i>Eugenia salamensis</i>	0.68	0.00 ^a	0.00 ^a	0.21	FR
	“Cafecillo”	0.16	0.09	0.15	0.13	FR
Nyctaginaceae	<i>Bougainvillea</i> sp.	0.14	0.00 ^a	0.00 ^a	0.04	FL
Rubiaceae	<i>Calycophyllum candidissimum</i>	0.09	0.00	0.00	0.03	ML
Sapindaceae	<i>Melicoccus bijugatus</i>	0.76	0.00 ^a	0.00 ^a	0.23	FR
	“S-660”	0.08	2.58	0.00 ^a	1.10	YL, ML
Sapotaceae	<i>Manilkara chicle</i>	1.79	1.75	1.05	1.53	FR, FL, YL
	<i>Mastichodendron capiri</i>	2.80	0.99	0.46	1.39	ML, FL, YL
Simaroubaceae	<i>Simarouba glauca</i>	0.65	0.00 ^a	0.00 ^a	0.20	FR
Sterculiaceae	<i>Guazuma ulmifolia</i>	0.17	0.01	0.08	0.08	ML, YL
Tiliaceae	<i>Luebea candida</i>	0.62	0.00 ^a	0.00	0.19	ML
	<i>Luebea speciosa</i>	0.38	0.76	0.06	0.39	YL, ML, FL
Verbenaceae	<i>Vitex guameri</i>	0.00 ^a	0.02	0.00	0.01	ML
Unidentified	“Manzano negro”	0.00 ^a	0.92	0.00 ^a	0.31	FR
	“Araliaceae?”	0.00	0.00 ^a	0.43	0.14	FR
	Epiphytes (7+ species)	5.17	4.04	4.41	4.42	ML, YL, FR
	Shrubs (1 species)	0.00 ^a	0.05	0.00 ^a	0.02	FL
	Trees (4+ species)	1.61	0.36	0.19	0.69	ML, YL, FL

¹ Percentages based on averages of monthly feeding time for each group; “0.00^a” denotes no consumption of species because the species was absent in the group’s home range.

² ML = mature leaves, YL = young leaves, FR = fruit, FL = flowers; OT = Other.

Composition by Species and Family. During the course of the study, the howlers were observed feeding from at least 65 species of plants (57 tree species) belonging to at least 40 genera of at least 23 different families (Tables 3.2 and 3.3); the Shannon index of diversity (Chapter 2) for the overall annual diet is 2.78. Members of Group 1 were observed feeding on at least 50 species, Group 2 on 43 species, and Group 3 on 45 species; Group 1 had a more diverse diet than did the other study groups (Shannon index of 2.97 for Group 1 versus 2.43 and 2.33 for Groups 2 and 3). Although all groups used a wide variety of species, a few food items account for the majority of the diets. Four species from 4 different families comprise over half of the overall diet, and the top 10 food species make up 76% of feeding time. Only 18 species individually comprise more than 1% of the overall annual diet. *Ficus costaricana* dominates the overall diet at 32% of feeding time. Two families, the Moraceae and Fabaceae, comprise the majority of the diet and account for 60% of feeding time.

Although all three groups used roughly the same resources, they differ somewhat in the contribution of various species to the overall diet (Table 3.4). There is a good deal of dietary overlap, with groups sharing half of their top ten food species. Differences between groups in the utilization of certain food species likely reflect variation in the availability of these species in their respective home ranges. For example, while *Ficus costaricana* is the most important food resource for Groups 2 and 3, Group 1 concentrated its feeding most heavily on the mature leaves of *Bursera simaruba*. This tree is rare in the coffee plantation, but common in the secondary forests that comprise the majority of Group 1's home range (Chapter 5). Although Group 1 fed extensively from *Ficus* when it

Table 3.4. Species contributing at least 1% of the total diet of each study group.

Rank ¹	GROUP 1				GROUP 2				GROUP 3			
	Species ²	% Diet	G2 ³	G3 ³	Species	% Diet	G1 ³	G3 ³	Species	% Diet	G1 ³	G2 ³
1	<i>Bursera simaruba</i>	14.7	10	8	<i>Ficus costaricana</i>	38.9	2	1	<i>Ficus costaricana</i>	41.2	1	1
2	<i>Ficus costaricana</i>	12.0	1	1	<i>E. cyclocarpum</i>	10.4	3	2	<i>E. cyclocarpum</i>	9.8	3	2
3	<i>E. cyclocarpum</i>	10.4	2	2	<i>Inga vera</i>	6.6	12	15	<i>Spondias mombin</i>	8.2	4	7
4	<i>Spondias mombin</i>	9.5	7	3	<i>Cecropia peltata</i>	5.8	6	4	<i>Cecropia peltata</i>	6.2	6	4
5	<i>Lysiloma aurita</i>	8.9	22	16	<i>Albizia guachapele</i>	5.5	13	9	<i>Ficus benjamina</i>	5.1	--	--
6	<i>Cecropia peltata</i>	7.9	4	4	<i>Ficus obtusifolia</i>	4.2	21	12	<i>Diphysa robinoides</i>	4.7	18	23
7	Epiphytes	3.6	15	10	<i>Spondias mombin</i>	4.0	4	3	<i>Pithecellobium saman</i>	3.2	11	29
8	<i>Mastichodendron capiri</i>	2.8	16	23	<i>Astronium graviolens</i>	2.8	10	19	<i>Bursera simaruba</i>	2.9	1	10
9	<i>Ficus pertusa</i>	2.5	--	--	"S-660"	2.6	43	--	<i>Albizia guachapele</i>	2.8	13	5
10	<i>Astronium graviolens</i>	2.4	8	19	<i>Bursera simaruba</i>	2.2	1	8	Epiphytes	2.6	7	15
11	<i>Pithecellobium saman</i>	2.4	29	7	<i>Erythrina fusca</i>	2.2	--	--	<i>Ceiba pentandra</i>	1.6	39	31
12	<i>Inga vera</i>	2.0	3	15	Epiphyte #1	1.9	34	25	<i>Ficus obtusifolia</i>	1.5	21	6
13	<i>Albizia guachapele</i>	1.8	5	9	<i>Manilkara chicle</i>	1.7	14	14	<i>Gliricidia sepium</i>	1.3	15	18
14	<i>Manilkara chicle</i>	1.8	13	14	<i>Ficus</i> spp.	1.7	--	--	<i>Manilkara chicle</i>	1.0	14	13
15	Other unknown trees	1.5	18	13	Epiphytes	1.4	7	10	<i>Inga vera</i>	1.0	12	3
16	<i>Gliricidia sepium</i>	1.4	25	27	<i>Mastichodendron capiri</i>	1.0	8	21				
17	<i>Diospyros nicaraguensis</i>	1.2	--	--								
18	<i>Diphysa robinoides</i>	1.2	23	6								
19	<i>Terminalia oblonga</i>	1.2	20	--								
20	<i>Spondias purpurea</i>	1.0	--	20								
21	<i>Ficus obtusifolia</i>	1.0	6	12								

¹ Ranks within each group relative to total feeding time.² **Species names in bold** indicate species that comprise at least 1% of feeding time for all three groups.³ Rank of given species within diet of the other group indicated; "--" denotes that the species was not eaten by the other group.

was located, this genus is much less common in the areas of secondary growth, and only two or three large *Ficus* trees were found in the home range of Group 1 outside of areas of coffee cultivation. However, *Ficus costaricana* is much more common in the home ranges of Groups 2 and 3. Accordingly, there are significant differences between groups' monthly diets in time spent feeding on *Ficus costaricana* ($F_{[2,32]} = 9.853, P < 0.001$; Group 1 significantly feeds less than Groups 2 and 3) and *Bursera simaruba* (Kruskal-Wallis: $H = 6.912, P = 0.032, df = 2, N = 35$; Group 1 feeds significantly more than Groups 2 and 3).

Although the howlers at La Luz focus the majority of their feeding on only a few species, these are often relatively common in the coffee plantation. Based on the number of top food species represented in the enumeration, there is a slightly positive, but not significant, relationship between the amount of time spent feeding on a species and its contribution to the number of stems (Spearman rank correlation: $r_s = 0.227, P = 0.436, N = 14$) and basal area ($r_s = 0.138, P = 0.6369, N = 14$). The selection ratios (column 6, Table 3.2) demonstrate that many of these species are eaten roughly in proportion to their abundance in the canopy. Certain staple food species, such as *Enterolobium cyclocarpum* and *Cecropia peltata*, are actually eaten less frequently than they are encountered. This stands in contrast to the feeding behavior of conspecifics at other sites (e.g., Milton, 1980; Glander, 1981), which show far more reliance on uncommon trees.

Temporal Patterning of Feeding Behavior

Monthly Variation in Food Type. Leaves comprise at least half of the annual diets of the howlers. However, on a month-to-month basis there is extensive variation in

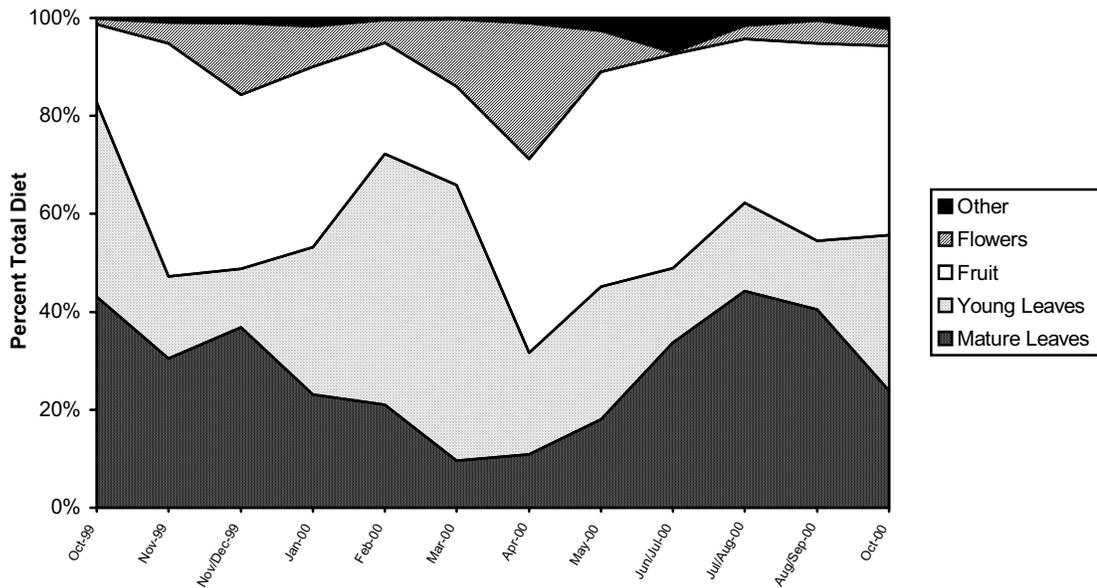


Figure 3.2. Combined monthly diets of all study groups.

the contribution of different food types to diets (Figure 3.2). Feeding on mature leaves peaked at 44.2% of the diet in Month 10 (wet season, July/August 2000) and was at its lowest at 9.6% during Month 6 (dry season, March 2000). Young leaf consumption varied from a high of 56.3% during Month 6 to a low of 11.9% during Month 3 (wet to dry transition, November/December 1999). The proportion of fruit in the diet reached a high of 47.6% of the diet in Month 2 (wet season, November 1999), although it was at a low of 15.9% the month before. Finally, flower consumption varied as well, peaking in Month 7 (dry season, April 2000) at 27.7% of the diet and reaching a low of 0.4% of the diet in Month 9 (wet season, June/July 2000). However, there are no significant differences in the average consumption of each food type between the wet (May through

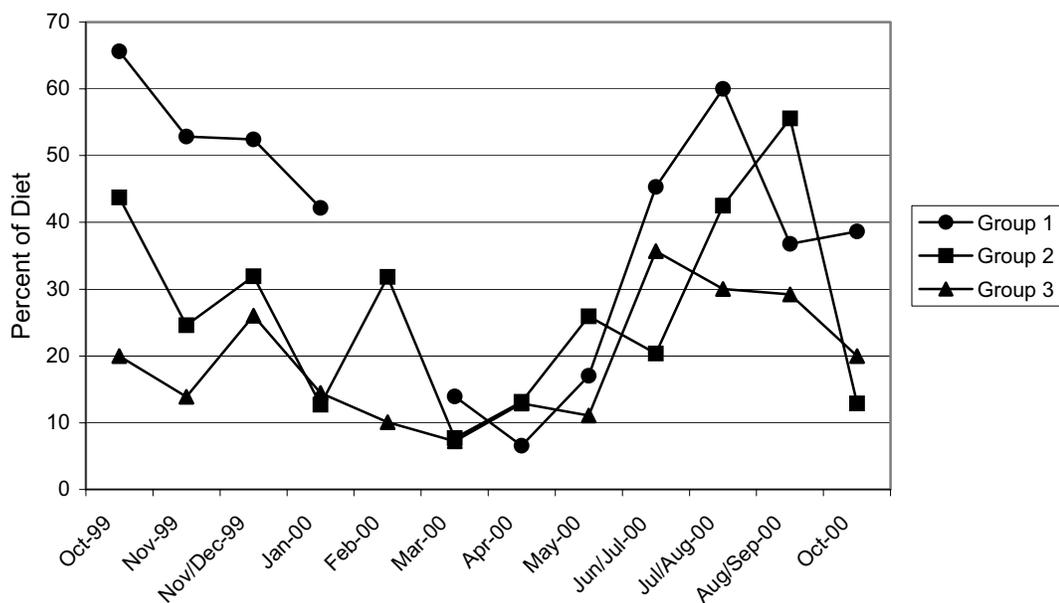
October) and dry (December through April), although the differences for mature leaf consumption approach significance ($F_{[1,10]} = 4.654, P = 0.056$).

Spearman rank correlations (based on raw seconds pooled from all groups) demonstrate that across months, the consumption of mature leaves decreases as the consumption of young leaves and flowers increases, although these relationships are not significant. There is a non-significant negative correlation between the consumption of fruits and young leaves, and a significantly positive correlation between the consumption of fruits and flowers ($r_s = 0.650, P = 0.022, N = 12$). However, there is no relationship between the consumption of mature leaves and of fruits. These patterns, although weak, are consistent with foraging strategies exhibited by howlers at other sites, in which seasonal resources are favored as food sources, with mature leaves serving as a perennially available fallback resource. The howlers apparently alternate between fruits and young leaves as major seasonal food sources.

The three study groups differ in the overall proportions of different foods in their diets, although there are times when consumption of certain food types increases for all groups (Figure 3.3). Mature leaf consumption increases for all groups between Months 9 and 11 (late June to early September 2000), during the wet season, while all three groups demonstrate high levels of young leaf consumption during Months 5 and 6, the middle of the dry season (February and March 2000). Fruit consumption is highly asynchronous between groups, although all groups show an increase in fruit consumption between Months 7 (end of the dry season, April 2000) and 9 (the early wet season, late June/early

Figure 3.3. Proportions of (a) mature leaves, (b) young leaves, (c) fruits, and (d) flowers in the monthly diets of the three study groups.

(a) Mature Leaves



(b) Young Leaves

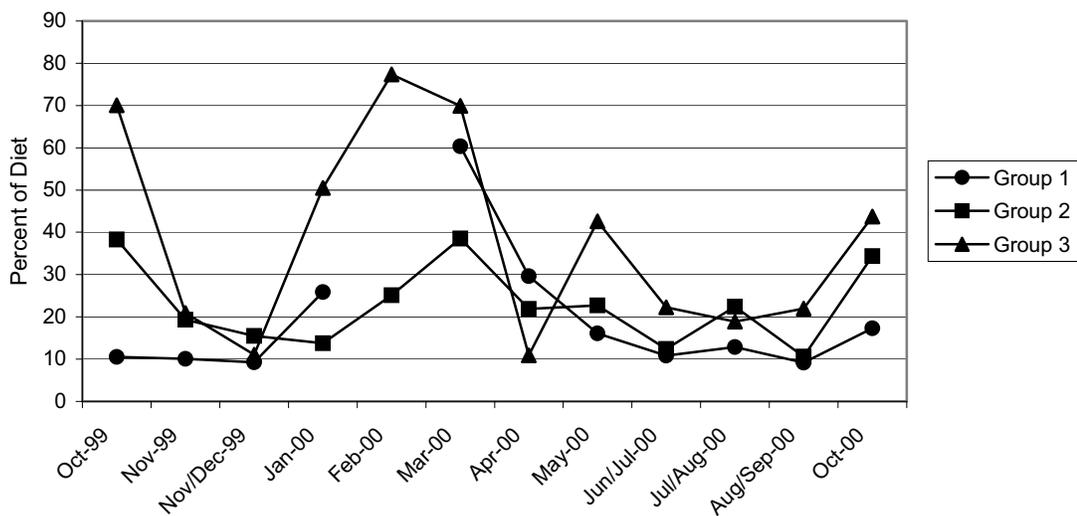
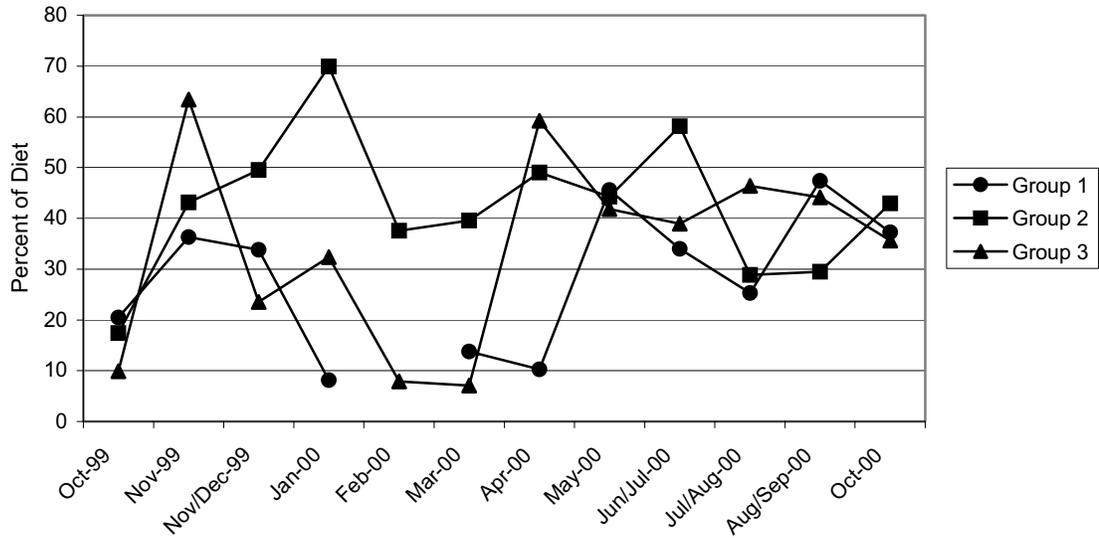


Figure 3.3 (continued)

(c) Fruit



(d) Flowers

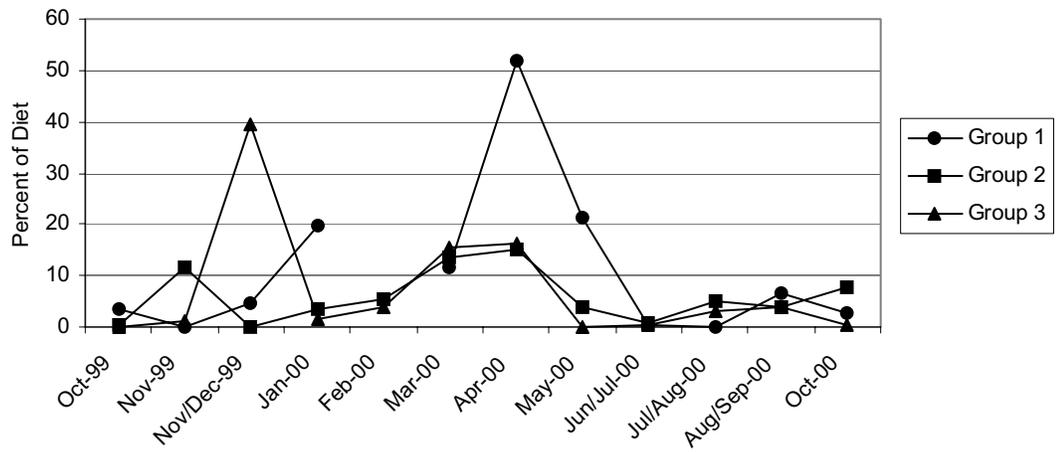


Table 3.5. Spearman rank correlation coefficients and associated P-values between groups in the percentage composition of monthly diets by food type.¹

Food Type	Pairwise Comparison		
	Group 1 vs. 2	Group 1 vs. 3	Group 2 vs. 3
Mature Leaves	0.44545	0.50000	0.36364
	0.1697	0.1173	0.2716
Young Leaves	0.39091	0.19091	0.46364
	0.2345	0.5739	0.1509
Fruits	-0.37273	0.10000	0.16364
	0.2589	0.7699	0.6307
Flowers	-0.0273	0.24201	0.18679
	0.9364	0.4734	0.5824

¹ N = 11 for all cells; all tests are 2-tailed.

July 2000). Although peak consumption of flowers is seen at different points of the year for the three groups, all groups show increased feeding on flowers during Month 7. The proportions of each food type in monthly diets show positive correlations across nearly all groups, although the relationship does not reach significance for any of the major food types (Table 3.5). Nevertheless, taken together these results suggest that seasonal changes in the diets of the study groups are related and may reflect habitat-wide changes in the abundance and availability of foods.

Monthly Variation in Species Eaten. Although the top 5 species in the overall annual diet comprise over 60% of feeding time, this does not mean that the howlers can

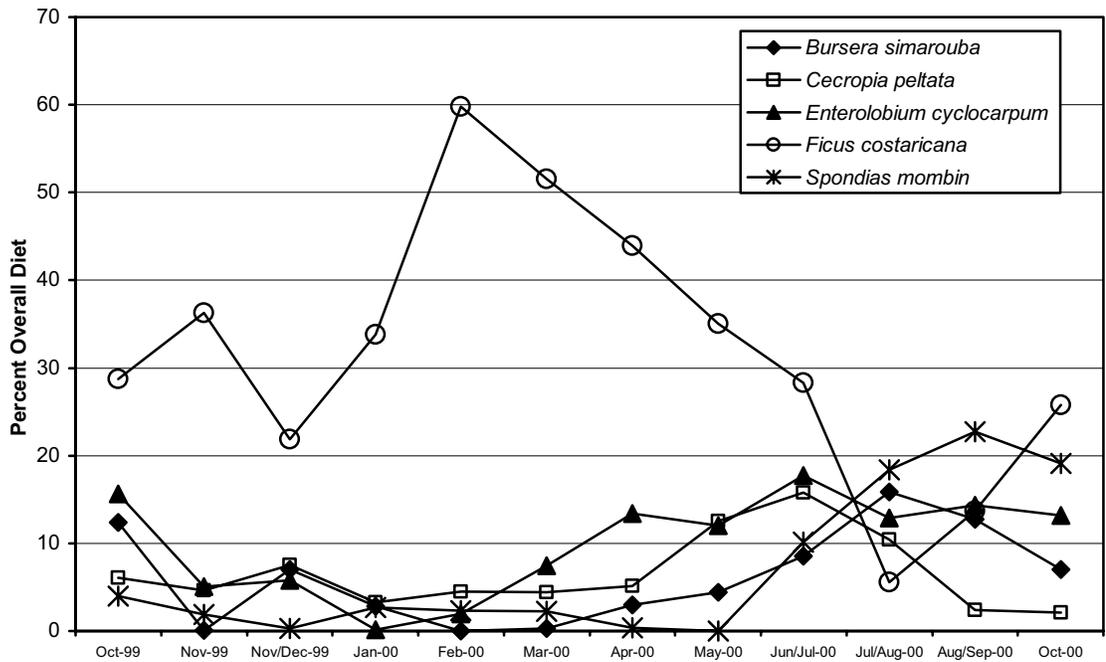
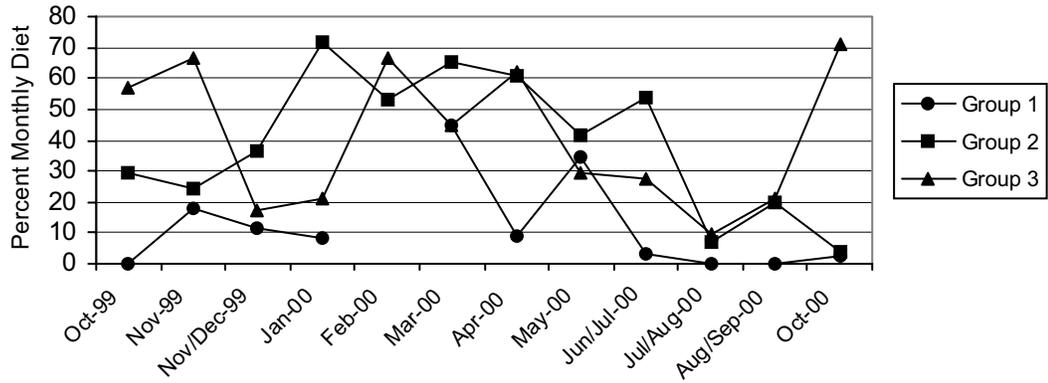


Figure 3.4. Temporal patterning in the consumption of the five most important food species.

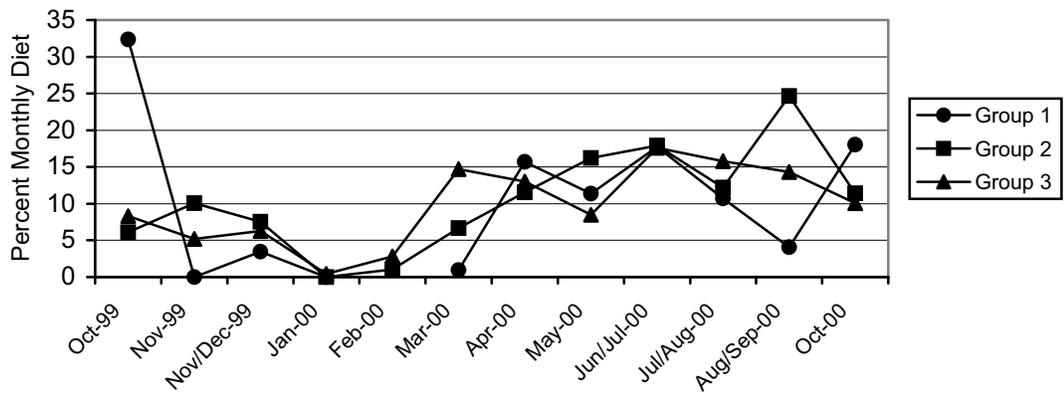
substist on these species alone, as they may not consistently provide edible plant parts throughout the year. Indeed, their inclusion in the diet on a month-by-month basis is highly variable (Figure 3.4). Only *Ficus costaricana* and *Cecropia peltata* are eaten during every month of the study. These are among the few tree species which not only produce several different palatable phenophases (e.g., young leaves, mature fruits, and flowers), but which also have asynchronous phenological schedules (individuals usually bear only one seasonal phenophase at a time, but the timing of production differs between individuals: *Ficus*) or which bear different seasonal phenophases throughout the year

Figure 3.5. Proportions of (a) *Ficus costaricana*, (b) *Enterolobium cyclocarpum*, (c) *Spondias mombin*, (d) *Cecropia peltata*, and (e) *Bursera simaruba* in the monthly diets of the three study groups.

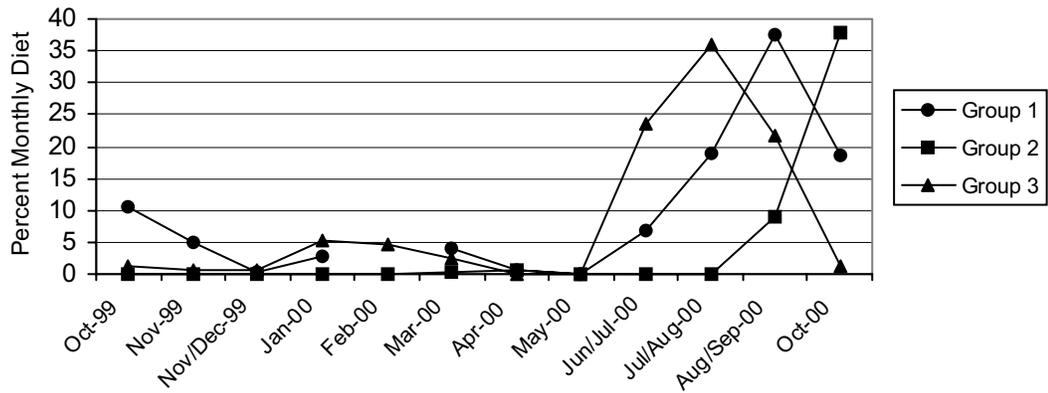
(a) *Ficus costaricana*



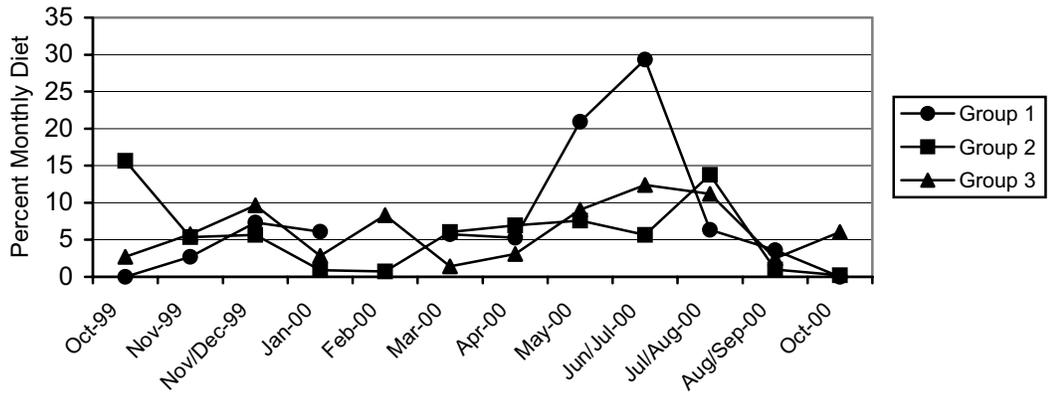
(b) *Enterolobium cyclocarpum*



(c) *Spondias mombin*



(d) *Cecropia peltata*



(e) *Bursera simaruba*

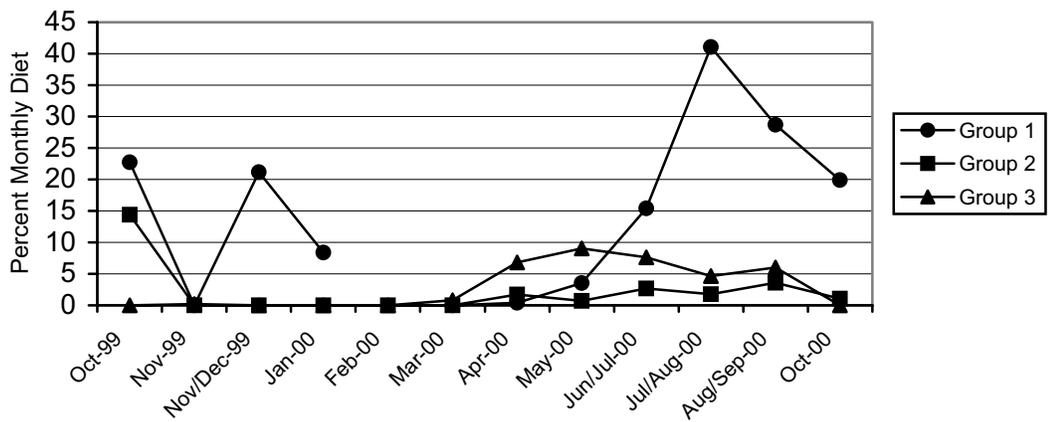


Table 3.6. Spearman rank correlation coefficients between groups in the percentage composition of monthly diets by species.¹

Food Species	Pairwise Comparison		
	Group 1 vs. 2	Group 1 vs. 3	Group 2 vs. 3
<i>Bursera simaruba</i>	0.63417*	-0.07167	0.35620
<i>Cecropia peltata</i>	0.04556	0.62415*	0.10909
<i>Enterolobium cyclocarpum</i>	0.36447	0.61048*	0.87273***
<i>Ficus costaricana</i>	0.55966 ^T	0.24772	-0.04545
<i>Spondias mombin</i>	0.21634	0.61872*	-0.02111

¹N = 11 for all cells; all tests are 2-tailed. ^T Trend (P < 0.10); * P < 0.05; *** P < 0.001.

(most individuals have a few young leaves, fruits, and/or flowers throughout the year: *Cecropia*). When considering variation in the contribution of each of the top 5 species to each group's diet, the three groups generally focus on the same species at the same time (Figure 3.5). Nearly all pair-wise comparisons between groups in the proportions of these food species in monthly diets are positive; in some cases they are highly significant (Table 3.6); the exception, *Ficus costaricana*, has an asynchronous phenological pattern, suggesting that palatable phenophases are available to different groups at different times. The positive relationships between the consumption of key food species suggest that the intensity with which the three groups feed on these species relates to habitat-wide

changes in the production of edible phenophases. Although there are differences in the number of species eaten per month, one-way ANOVAs demonstrate no significant differences between groups, seasons, or months in the number of species used or in the Shannon index of dietary diversity (number of species used: $F_{[2,32]} = 0.06$, $P = 0.938$ between groups, $F_{[1,33]} = 3.05$, $P = 0.090$ between seasons, $F_{[11,23]} = 1.60$, $P = 0.165$ between months; Shannon index: $F_{[2,32]} = 2.01$, $P = 0.151$ between groups, $F_{[1,33]} = 0.27$, $P = 0.606$ between seasons, $F_{[11,23]} = 0.75$, $P = 0.685$ between months).

Relationships between Feeding Patterns and Food Availability

Young and mature leaves together comprise most of the annual diet, and consumption generally follows a similar pattern as availability. To explore the strength of the relationship between consumption and abundance, I performed bivariate correlations between percent monthly feeding time and monthly indices of phenophase production (i.e., the percentage of trees bearing seasonal phenophases; Chapter 2); because the phenophase plots were located primarily in shade grown coffee, for the purposes of this analysis only, I use feeding data from only Groups 2 and 3, whose ranges comprise primarily areas of shade coffee cultivation (Chapter 5). The monthly proportion of mature leaves in the diet was positively correlated with its availability in the habitat (see Table 3.7). Similarly, there is a positive relationship between the consumption and availability of all seasonal food sources combined (i.e., the percentage of individual tree or percentage total crown volume bearing young leaves, fruits, or flowers; Spearman rank correlation: $r_s = 0.748$, $P = 0.005$, $N = 12$, for the index of production; $r_s = 0.755$, $P =$

Table 3.7. Spearman rank correlation coefficients between measures of phenophase production and diet composition.¹

		% Mature Leaves in Diet	% Young Leaves in Diet	% Fruits in Diet	% Flowers in Diet
Phenology of All Trees	Production Mature Leaves	0.650*	-0.196	-0.140	-0.385
	Abundance Mature Leaves	0.629*	-0.399	-0.084	-0.147
	Production Young Leaves	-0.196	0.023	0.154	-0.161
	Abundance Young Leaves	-0.413	0.196	0.266	-0.112
	Production Fruits	-0.545 ^T	0.273	0.11	0.077
	Abundance Fruits	-0.594*	0.168	0.259	0.196
	Production Flowers	-0.545 ^T	0.168	0.259	0.196
	Abundance Flowers	-0.608*	0.140	0.287	0.105
Phenology of Main Food Trees Only ²	Production Mature Leaves	0.585*	-0.287	-0.127	-0.245
	Abundance Mature Leaves	0.594*	-0.483	0.072	-0.455
	Production Young Leaves	-0.063	0.411	-0.266	-0.203
	Abundance Young Leaves	-0.741***	0.566 ^T	0.147	-0.333
	Production Fruits	-0.028	0.084	0.098	-0.231
	Abundance Fruits	-0.510 ^T	0.042	0.441	-0.683*
	Production Flowers	-0.622*	0.462	-0.042	-0.042
	Abundance Flowers	-0.608*	0.063	0.309	0.249

¹ N = 12 for all cells; all tests are 2-tailed. ^T Trend (P < 0.10); * P < 0.05; *** P < 0.001.

² ML = *Enterolobium cyclocarpum*, *Inga vera*, *Astronium graveolens*, *Albizia guachapele*, *Ficus costaricana*, *Pithecellobium saman*. YL = *F. costaricana*, *A. guachapele*, *Ficus obtusifolia*, *Cecropia peltata*, *I. vera*. FR = *F. costaricana*, *Spondias mombin*, *C. peltata*. FL = *Diphysa robinoides*, *E. cyclocarpum*, *Lysiloma aurita*, *Gliricidia sepium*, *C. peltata*, *A. guachapele*.

0.0045, $N = 12$ for abundance). However, although there are generally positive correlations between the consumption of young leaves, fruits, or flowers and measures of the availability of each respective part, none of these is significant (Table 3.7). Mature leaf consumption, however, does show a significantly negative relationship with the availability of fruits and flowers and a trend towards a negative relationship with fruit abundance. A reanalysis using phenological indices derived from the primary food species for each category does not reveal a strikingly different pattern: again, mature leaf consumption correlates with its production and abundance, and shows a negative relationship with flower availability and young leaf abundance. There is a negative relationship between flower consumption and the abundance of fruits and flowers (Table 3.7). Young leaf consumption peaks in the dry season, during the initial production of new leaves; however, peak new leaf production occurs earlier. Fruit consumption is high throughout the wet season, in spite of variable fruit production during this time, and the highest fruit consumption occurs during November (Cycle 2 of data collection), a period of generally low fruit production. Flower feeding generally follows production, although there is an anomalous peak during December (Cycle 3), due to extensive feeding on flowers of *Diphyssa robinoides* by Group 3. Mature leaf consumption shows negative relationships with the measures of availability of all other plant parts. This result may indicate that mature leaves are eaten when the availability of all other phenophases is low.

Given that the production of seasonal (young leaves, fruits, flowers) and perennial (mature leaves) plant parts show inverse relationships (Chapter 2), if the consumption of these phenophases tracks their availability, we should expect a positive relationship

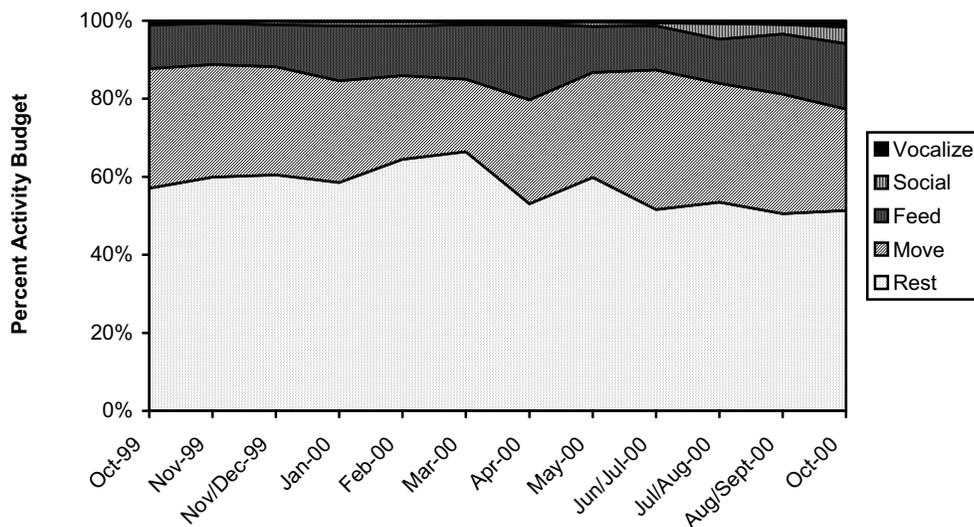
between both the consumption of seasonal parts and their availability, and between the consumption and availability of mature leaves. However, the pattern of consumption of each individual seasonally produced phenophase does not closely follow patterns of production. These disparities are explained in part by heavy reliance on certain species during certain months of the year. Peak feeding on young leaves occurs in Months 5 and 6, earlier than peak production; this increase is a result of increased consumption of the young leaves of *Ficus costaricana*. If the consumption of *Ficus costaricana* young leaves is compared to their abundance in the canopy, there is a significantly positive relationship (Spearman rank correlation: $r_s = 0.685$, $P = 0.014$, $N = 12$). Similarly, the peak in fruit consumption during Month 2 is due to high consumption of *Ficus costaricana* fruits; again, consumption appears to track abundance ($r_s = 0.566$, $P = 0.055$, $N = 12$). Peak flower feeding during Month 3 relates to heavy consumption of *Dyphisa robinoides* by Group 3 during its limited period of flower production; although this species was not well-enough represented in the vegetation enumeration to relate consumption of its flowers to abundance, peak feeding did occur while these trees were flowering *en masse* during December 1999, well before the florescence of the superabundant *Gliricidia sepium*. There were, however, some young leaves, fruits, and flowers that they never ate. Fibrous fruits from leguminous trees were consistently ignored, and the howlers were never seen feeding on *any* phenophase from *Cedrela odorata* or *Trichilia* sp., even though these are fairly common in some areas of their home ranges.

Table 3.8. Annual activity budgets of the three study groups as percent of daylight hours spent in each activity.

Group	N ¹	Rest	Move	Feed	Affiliative	Agonistic	Vocalize
Group 1	27	55.8	30.8	11.1	1.4	0.2	0.7
<i>SD</i>		<i>10.9</i>	<i>9.1</i>	<i>5.3</i>	<i>2.1</i>	<i>0.4</i>	<i>0.8</i>
Group 2	33	57.6	26.8	13.5	1.2	0.3	0.5
<i>SD</i>		<i>8.7</i>	<i>5.9</i>	<i>5.8</i>	<i>2.0</i>	<i>0.4</i>	<i>0.6</i>
Group 3	37	57.2	25.4	15.4	1.3	0.1	0.6
<i>SD</i>		<i>7.9</i>	<i>7.5</i>	<i>4.1</i>	<i>1.7</i>	<i>0.2</i>	<i>0.8</i>

¹The number of complete days (10-12 hours of uninterrupted data collection).

Figure 3.6. Monthly activity budgets of all groups pooled.



Variation Among Groups and Seasons in Activity Budgets

Based on pooled data from scans, the overall activity budget for all groups is dominated by resting. 57.0% of daylight hours are spent resting, 27.4% traveling, 13.6% feeding, 1.5% in social interaction (1.3% affiliative, 0.2% agonistic), and 0.6% vocalizing. The annual activity budgets are similar for the three groups (Table 3.8); one-way ANOVAs demonstrate significant differences between groups only in the percentage time spent feeding, with Group 3 spending more time feeding than Group 1 (Kruskal-Wallis test: $H = 12.339$, $P = 0.002$).

Although there were few differences between groups in activity budgets, there were monthly and seasonal differences (Figure 3.6). The proportion of daylight time spent resting ranged from 50.5% during the late wet season (August 2000) to 66.5% in the dry season (March 2000). March also saw the lowest amount of time spent moving, 18.6%, whereas moving peaked at 35.8% in the middle of the wet season (June 2000). Time spent feeding also varies, at its lowest in the late wet season (November 1999, 11.0%) and peaking in the late dry season (April 2000, 19.3%). Activity budgets considered on a seasonal basis show similar patterns (Table 3.9). Time spent resting is significantly higher during the dry season, while time spent moving, in affiliative social behavior, and vocalizing is higher during the wet season. Seasonal differences in activity patterns mirror those of differences in ranging patterns (Chapter 5), with more movement and greater distances traveled during the wet season, when fruit comprises a larger portion of the diet. Greater travel during periods of fruit consumption may reflect the more scattered distribution and faster depletion of fruit patches (see Chapter 5).

Table 3.9. Seasonal activity budgets.¹

Season	N	Rest	Move	Feed	Affiliative	Agonistic	Vocalize
Wet	56	54.43	29.98	12.80	1.81	0.21	0.76
<i>SD</i>		<i>8.39</i>	<i>7.01</i>	<i>5.28</i>	<i>2.32</i>	<i>0.38</i>	<i>0.87</i>
Dry	41	60.41	23.86	14.59	0.60	0.15	0.39
<i>SD</i>		<i>8.83</i>	<i>7.38</i>	<i>5.23</i>	<i>0.68</i>	<i>0.31</i>	<i>0.46</i>
ANOVA (F)		11.520***	17.246***	2.566	--	0.008	--
Kruskal-Wallis (H)		--	--	--	4.140*	--	3.826*

¹ANOVAs are either parametric (one-way unbalanced, F statistic) or non-parametric (Kruskal-Wallis test, H statistic) when transformed data do not fit parametric assumptions. For both the F and H statistics, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Seasonal variation in activity patterns can be related to environmental and dietary variables. Table 3.10 presents Spearman rank correlation coefficients between time spent in various activities, environmental measures, phenology, and diet. Rainfall and temperature could potentially affect the howlers' activity patterns, presumably due to needs of thermoregulation or the prevention of certain activities by heavy rains. However, rainfall shows a significantly negative relationship with resting; although howlers generally are inactive during heavy rain, they spend more time overall moving and feeding during the wet season. Howling, however, does increase with rainfall; heavy rains and thunder frequently stimulate howling bouts by males. The production of edible fruits shows no strong relationship to time spent in any one activity, even though it does correlate with distance traveled (see Chapter 5). The production of mature leaves,

Table 3.10. Spearman rank correlations between activity budget, environmental variables, measures of food availability (indices of production, from feeding trees only), and diet (% time spent eating various food types).

Variable	% Rest	% Move	% Feed	% Social	% Howl
Environmental					
Rainfall	-0.650*	0.462	-0.049	0.217	0.662*
Temperature	-0.499	0.471	0.114	-0.158	0.421
Phenological					
Mature Leaves	-0.179	0.599*	-0.579*	-0.042	0.077
Young Leaves	-0.098	0.049	0.032	-0.182	0.508
Fruits	-0.077	-0.007	0.207	0.378	0.112
Flowers	0.266	-0.650*	0.564	-0.063	-0.109
Dietary					
% Mature Leaves	-0.413	0.776**	-0.490	0.245	0.266
% Young Leaves	0.378	-0.699*	0.301	-0.042	0.095
% Fruits	-0.357	0.336	0.007	0.014	-0.028
% Flowers	0.385	-0.517	0.350	-0.224	-0.368

N = 12 for all cells; all tests are 2-tailed. * $P < 0.05$, ** $P < 0.01$.

however, does correlate positively with time spent moving and negatively with time spent feeding because during this time preferred seasonal foods are less abundant, necessitating greater foraging effort to locate these resources. There is also a negative relationship between movement and flower abundance. These general patterns are mirrored in the relationships between feeding and activity patterns. Movement shows a significantly positive relationship with the percent of mature leaves included in the diet, while it shows a significantly negative relationship with young leaf feeding. Although fruit and flower consumption correlate positively and negatively with movement, respectively, these relationships are not significant. However, when all of these high-quality seasonal resources are considered as a whole, time spent traveling shows an inverse relationship with consumption of these foods. Since mature leaves are a “fallback food” for howlers, increased foraging effort during periods of mature leaf consumption

Patch Size, Food Type, and Feeding Time

Optimal foraging theory, as applied to animals feeding on plants, predicts that generalist herbivores will select a diet that maximizes nutrient quality while minimizing the consumption of indigestible cell wall components and feeding deterrents (Freeland and Janzen, 1974; Westoby, 1974; Milton, 1979). It also predicts that feeding will be of longer duration in larger patches simply because they support more resources, increasing the time until the rate of food intake drops to the average rate for the habitat (Charnov, 1976; Pyke *et al.*, 1977). Similarly, feeding time should be longer in sources of preferred

Table 3.11. Daily patch feeding time and patch sizes for different food types.

Food Type	Time Feeding Versus Food Type					Tree Size versus Food Type				
	Mean Patch Residency (s)	SD	Min	Max	N	Mean DBH (cm)	SD	Min	Max	N
Mature Leaves	270	342	4	2214	477	83.7	63.7	7.1	325	310
Young Leaves	390	527	5	3628	428	85.0	74.0	17.1	484	276
Fruit	470	703	4	5059	424	80.3	66.9	14.2	350	246
Flowers	342	482	7	3535	144	76.5	53.0	20.9	275	117
Other Parts	98	164	9	130	60	107.2	77.8	15.0	300	55

food items because benefits are higher in relation to the costs (i.e., returns diminish relatively less rapidly; Charnov, 1976; Stephens and Krebs, 1986).

Although the howlers used several hundred trees for feeding (210 marked trees for Group 1, 248 marked trees for group 2, and 264 marked trees for Group 3), they all relied heavily on a few individual trees (Group 1: 19 trees account for 32.8% of total feeding time; Group 2, 25 trees for 51.2% of feeding time; Group 3, 22 trees for 50.8% of feeding time). Considering the 3 most important trees of each group, nearly all of these trees are *Ficus costaricana* (the third most important tree for Group 1 was a *Bursera simaruba*; the most important tree for Group 3 was of *Ficus benjamina*, an ornamental non-native species found only in their home range).

The average daily patch feeding time for all food types is 359 seconds (range 4 to 5059, SD \pm 531). Table 3.11 presents the daily patch feeding times for different food

types in the diet. Fruits and young leaves, the most important seasonal resources in the howlers' diets, have the longest average feeding times of the various food types. An ANOVA demonstrates significant differences between food types in the amount of time spent feeding per day per food type ($F_{[4,1363]} = 11.83, P < 0.001$); however, given the interdependence of data points, it is difficult to determine if this result represents a "real" difference. A qualitative examination of the data (Table 3.11) does suggest that patch residency times are longer in fruiting trees. A *post-hoc* analysis of the ANOVA results indicates that the howlers fed for longer periods when feeding on young leaves than mature leaves, on fruits versus mature leaves, and on flowers versus mature leaves, and for longer when eating fruit than when eating young leaves. While the howlers will feed heavily from trees bearing seasonal phenophases, their strategies when feeding on leaves vary. Mature leaves from many tree species are frequently only "sampled," that is, a few leaves are eaten and the howler leaves the tree.

The average feeding tree diameter at breast height for all food types is 77.9 cm (range 7.1 to 484 cm, $SD \pm 65.0$ cm), versus 55.3 cm for all trees marked in the enumeration. Table 3.11 presents the diameters of feeding trees by food type. There are no obvious differences between food types in the average size of the feeding patches, and an ANOVA does not demonstrate any significant differences between categories in patch size ($F_{[4,1363]} = 3.11, P = 0.0773$). There is a positive relationship between patch feeding time and diameter at breast height ($r_s = 0.292, P < 0.001, N = 1368$), although the inflated sample size makes the significance of the result questionable. If the relationship between patch residency time and patch size is considered for each food type separately,

there is a strong relationship between feeding time and patch size for fruit sources ($r_s = 0.429$, $P < 0.001$, $N = 424$), weaker relationships for flowers ($r_s = 0.191$, $P = 0.022$, $N = 143$) and young leaves ($r_s = 0.292$, $P < 0.001$, $N = 424$), and no relationship for mature leaves ($r_s = 0.062$, $P = 0.176$, $N = 476$). However, the large sample sizes again make the significance of these results questionable; future reanalyses using bootstrap sampling will be used to address these issues.

Summary of Howler Foraging at La Luz

Based on the data presented in this chapter, a picture of howler foraging ecology emerges that resembles that of conspecifics studied at other sites. The howlers at La Luz show a mixed foraging strategy, feeding on both vegetative and reproductive plant parts. The howlers prefer seasonal foods (young leaves, fruits, and flowers), which comprise over 70% of their annual diet. Foliage and fruits are included in the diet throughout the year, although the relative contribution of each varies greatly from month to month and shows some relationship to the availability of various seasonal food sources in the habitat. However, the consumption of specific favored resources (for example, *Spondias* fruits or *Ficus* young leaves) closely tracks availability, suggesting that the howlers thoroughly exploit key foods when they are available. The annual diet is relatively diverse in comparison to the number of species available in the habitat, though many of these species were consumed only once or twice during the course of the study. Although the howlers were not observed feeding extensively from some of the most abundant tree species in the coffee plantation (for example, *Gliricidia sepium*, *Guazuma ulmifolia*, and

Cedrela odorata), their most important food species were fairly common in the environment, and in some cases were eaten less frequently than encountered. Activity patterns are dominated by resting, as might be expected for *Alouatta*, although time spent moving is high. Energy spent in foraging (i.e., movement + feeding) apparently increases during the wet season, when mature leaves and fruits comprise the majority of the diet.

DISCUSSION

Contrasts with Dietary Adaptations of other *Alouatta*

The diets of howlers at La Luz show a foraging strategy that is in line with predictions based on foraging theory and show strong similarities to those of congenics. Although the proportions of different food types included in the annual diets of howlers vary between sites (Table 3.12), for the most part, foliage comprises one half to three quarters of the annual diet, with young leaves being favored. The La Luz howlers demonstrate a similar pattern, with vegetative parts comprising 57% of the diet. Clarke *et al* (2002a) observed that in deforested areas, *A. palliata* has a lower-quality diet, increasing its consumption of leaves and spending more time feeding and traveling. It might be expected that a similar pattern would be observed in the disturbed forest of the shade coffee plantation. However, reduced tree diversity and density in the coffee plantation apparently does not result in a reduced availability of high-quality, seasonal food items: the howlers in La Luz are therefore able to maintain a diet of presumably similar quality.

Table 3.12. Dietary profiles from long-term (10+ months), multi-seasonal studies of howling monkeys.

Species/Location	Habitat ¹	No. Avail. Species	No. Food Species	% Diet ²						Reference
				ML	YL	MF	YF	FL	OT	
<i>A. palliata</i>										
Mexico	MF, 1	--	27	10	39	42	9	0	0	Estrada (1984)
Mexico	MF, 2	63+	39		39		40	0	17 ¹	Serio-Silva (1993), Serio-Silva & Bello-Gutiérrez (1999)
Costa Rica	GF/DC, 2	96	61	19	50	13	0	18	0	Glander (1978, 1981)
Costa Rica	DC/SD, 2	--	11	28	21		29	22	0	Chapman (1987)
Costa Rica	MF, 1/2	--	111	4	64	23	0	9	1	Stoner (1996)
Panama	MF, 1/2	135	105	10	38	42	0	10	0	Milton (1978, 1980)
Nicaragua	SD, 2	> 65	57	27	28	27	6	8	1	Current Study
<i>A. pigra</i>										
Belize	GF, 1/2	> 60	74	8	37		41	11	3	Silver <i>et al.</i> (1998)
<i>A. seniculus</i>										
Columbia	HAF, 1	--	34	28	14	8	44	5	0	Gaulin & Gaulin (1982)
Fr. Guiana	MF, 1	400	195	22	4	3	54	13	5	Julliot & Sabatier (1993)
<i>A. fusca</i>										
Brazil	2	--	30		80		10	10		Galetti <i>et al.</i> (1987)
Brazil	SD, 2	186	68		73		5	12	3	Chiarello (1994)
Brazil	?	--	?		74		12	9	6	Gaspar (1997)
Brazil	SD, 2	--	37		72		12	10	8	Limeira (1997)
<i>A. caraya</i>										
Argentina	SD, 2	--	30		71 ²		29	--	--	Rumiz <i>et al.</i> (1986)
Brazil	2	--	29		60-65		25-30	~ 5	5-8	Bicca-Marques & Calegario-Marques (1994)

¹ Habitat types: MF, moist evergreen forest; SD, semi-deciduous forest; DC, deciduous forest; GF, gallery forest; HAF, high altitude forest; 1, primary forest; 2, secondary, disturbed, or degraded; TL, translocated animals.

² Dietary categories: ML, mature leaves; YL, young leaves; FL, flowers; OT, other (bark, stems, unknown). "--" indicates data not available. ¹ Includes leaves and fruits of vines. ² Fruit and flowers combined.

In spite of the relatively low number of plant species available, the La Luz howlers also maintained a relatively diverse diet, using at least 57 tree species. While howlers at other sites may feed on over 100 species (e.g., Milton, 1980; Stoner, 1993), the dietary breadth demonstrated by the howlers at La Luz falls well within the range of variation for the genus (Table 3.12). Howlers generally feed from many different species on a daily basis, possibly in order to minimize the intake of any one secondary plant metabolite (Glander, 1978b); species richness may therefore play an important role in the long-term survival of howlers in a given habitat.

Given the low diversity at La Luz, it may be expected that few species in the plantation will be suitable for regular, repeated consumption, and that the La Luz howlers will therefore demonstrate a higher reliance on a limited number of species than conspecifics. While the La Luz howlers do heavily exploit their primary food species, *Ficus costaricana*, howlers in Mexican primary rainforest rely as strongly on a few key species (Figure 3.7). There does, however, appear to be heavier exploitation of staple food species at La Luz than at most other sites where *A. palliata* has been studied, with the top 10 food species accounting for a larger proportion of the diet (76% at La Luz versus 68% at Finca La Pacifica or 64% at Barro Colorado Island; Glander, 1981; Milton, 1980).

Like conspecifics at other seasonal sites, the howlers at La Luz demonstrate a high degree of temporal variation in feeding behavior. The seasonal changes in the use of phenophases and their proportional contribution to the diet observed at La Luz resemble those observed by Glander (1981), the most similar site

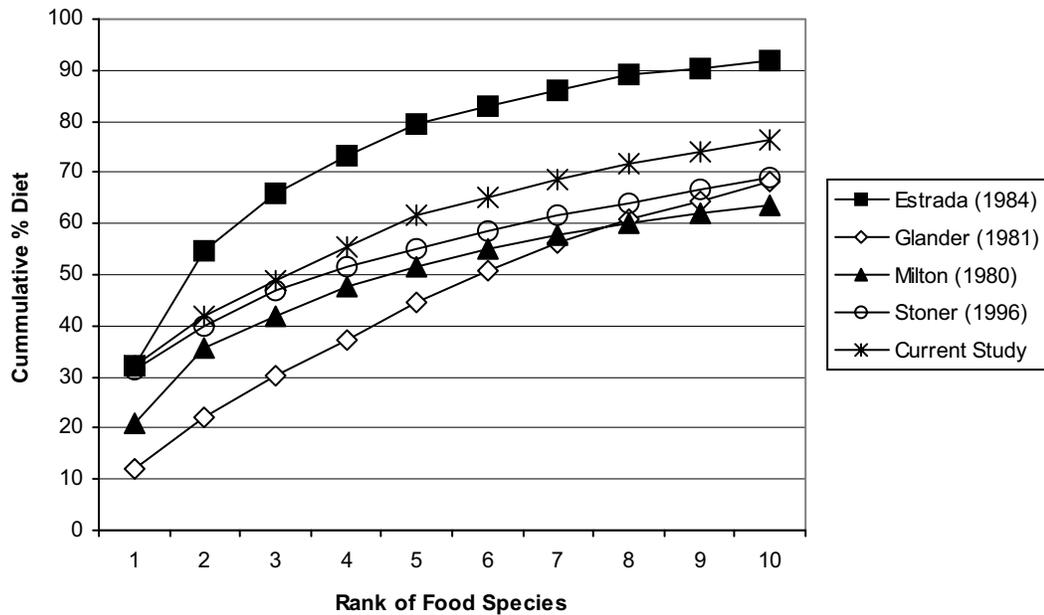


Figure 3.7. Cumulative contribution of the top 10 feeding species to the annual diet of mantled howlers at several sites where they have been studied over multiple seasons.

where continuous, multi-season data on howler feeding ecology have been collected.

However, at La Luz the relationships between the consumption and availability of seasonal resources are not as pronounced. Milton (1980) and Glander (1981) observed positive correlations between the consumption of both fruits and flowers with their availability in the habitat; no such relationships are observed at La Luz. Indeed, the relationship between the availability and consumption of vegetative parts is stronger.

However, the close relationship between the consumption of phenophases *by species* indicates that certain key resources are heavily exploited when they become available. As

observed by Glander (1978b, 1981) and Milton (1978, 1980), there was a negative relationship between the consumption of foliage and reproductive parts, consistent with suggestions that howlers balance the consumption of fruits and flowers (sources of nonstructural carbohydrates) with feeding on foliage (the primary source of protein), favoring less-fibrous young leaves and leaf buds (Chapter 4).

The howlers at La Luz differ from conspecifics at other sites in their lower levels of selectivity of food resources: the species that comprise the majority of their diet are fairly common, and the howlers frequently feed on species ignored elsewhere. For example, the selection ratio for the top ten foods eaten at La Luz (Table 3.2) averages approximately 2.5, indicating that feeding trees were used somewhat more frequently than encountered. However, at comparable sites, the selection ratio for the top 10 species averages 9.3 (Milton, 1980) and 11.3 (Glander, 1981), indicating more frequent use of rarer trees as food sources. This difference probably results both from the more diverse nature of the forest in less-disturbed sites and the selection of primary food sources at La Luz that are largely ignored at other sites. Many of the staple foods eaten by howlers at La Luz are eaten in much lower quantities at Barro Colorado Island and Finca La Pacifica. For example, at BCI, *Ficus costaricana* comprised only 2% of the annual diet, while the howlers at La Pacifica spent little time feeding on *Enterolobium cyclocarpum*, *Spondias mombin*, and *Cecropia peltata*. These species are much more abundant in the coffee plantation (due to a broken canopy that favors the growth of pioneer species such as *Cecropia* and selection for leguminous species like *Enterolobium*), and apparently of sufficient nutritional quality to sustain the population. Perhaps more importantly, as

many of the relatively common trees are acceptable to the howlers as food sources, high-quality food patches are separated by a matrix of moderate-quality foods. Therefore, the effort needed to maintain the high levels of selectivity observed at other sites may not provide the same benefits in terms of nutrient content and digestibility of foods.

Activity Patterns

The activity budgets derived from group scans generally resemble those of howlers studied at other sites (Table 3.13). However, time spent resting is relatively low and time spent traveling high in comparison to other studies of *Alouatta*. More time spent traveling may reflect the overall low density of trees in the coffee plantation, as the encounter rate with potential food sources may be lower than in less-disturbed habitat (see below). Activity budgets most closely resemble those reported for juvenile *A. caraya* in a highly seasonal secondary forest fragment in which foliage comprised a greater portion of the diet (Bicca-Marques and Calegaro-Marques, 1994). Data collected during scan sampling made no distinction between travel within a tree between feeding sites (foraging) and travel between feeding trees. However, this distinction frequently is not made in other analyses of howler activity patterns, and there is no *a priori* reason to believe that the howlers at La Luz are moving around more within feeding tree crowns.

I had initially predicted that diets in La Luz would be energy-poor in comparison to diets of howlers in less-disturbed habitats due to reduced food diversity and quality (Chapter 2), resulting in increased time spent resting in order to minimize energy

Table 3.13. Annual activity budgets at La Luz and other sites where howlers have been studied.

Species/Location	% Rest	% Feed	% Travel	% Other	Reference
<i>A. palliata</i>					
Mexico	66	22	12	0	Serio-Silva (1993)
Costa Rica	56	25	15	4	Stoner (1993)
Panama	66	16	10	8	Milton (1980)
Nicaragua	57	14	27	2	Current Study
<i>A. pigra</i>					
Belize	62	24	10	4	Silver <i>et al.</i> (1998)
<i>A. seniculus</i>					
Columbia	76	13	6	5	Gaulin and Gaulin (1982)
Venezuela	75	8	13	4	Edwards (1995)
<i>A. fusca</i>					
Brazil	64	18	13	5	Chiarello (1993)
Brazil	63	16	16	5	Gaspar (1997)
Brazil	73	13	11	3	Limeira (1997)
<i>A. caraya</i>					
Brazil	~60	~15	~20	~5	Bicca-Marques and Calegario-Marques (1994)

expenditure (Milton, 1980). However, diets in La Luz are relatively nutritious and most food sources abundant; accordingly, resting time is not elevated. Time spent feeding and resting is highest during the dry season, when young leaves and flowers comprise the majority of the diet. Milton (1980) observed a similar pattern, with time spent feeding increasing when foliage consumption was at its highest. She suggests that increased feeding time may result from the need to feed longer to reach satiation when eating foliage; this interpretation seems likely for howlers at La Luz as well, especially given that the rates of dry matter consumption per minute are higher for fruits and figs than for leaves (Chapter 4). Increased activity during the wet season is expected, as the availability of relatively abundant young leaves and flowers falls (Chapter 2). In the wet season, howlers include more fruits in their diets (particularly of *Spondias mombin*), which provide more ready energy that can be immediately mobilized for foraging, travel, and social activities. Fruit feeding also decreases the need to rest in order to maximize physiological activity on digestion of foliage (Smith, 1977; Gaulin and Gaulin, 1982). Increased fruit consumption during the wet season may also engender more travel time due to the somewhat patchier distribution of fruit sources (Chapter 5), increasing search time and travel distance.

Optimal Foraging and Shifting Strategies

Some of the resources used by howlers at La Luz, as at other sites, have a discontinuous distribution in both space and time, leading to the concentration of food resources in discrete patches surrounded by areas of low food density. However, the less

Table 3.14. Density of food species comprising >1% of the total diet at La Luz and other study sites.

Site	% Stems in Enumeration	Density/ha	Source
La Pacifica	22%	2.4	Glander, 1981
Santa Rosa	--	8.0	Chapman, 1988a
Barro Colorado Island	35%	3.4	Milton, 1980
La Luz	69%	4.1	This Study

diverse environment at La Luz results in patch distributions and dynamics that differ from those observed at other sites. Due to the relatively low density of trees, the overall number of *potential* food patches is reduced. The low diversity of tree species suggests that heterogeneity in nutrient content between patches will be lower. Finally, because many of the common trees in the shade plantation are used as food sources, a higher proportion of the trees available in the plantation are acceptable resources; therefore, although patches may be encountered less frequently, there is a greater chance that those found will be suitable food sources. The lower overall density of potential patches would suggest increased travel time between patches (as is observed), which, according to marginal value theorem, should result in longer patch residency times (Charnov, 1976; Pyke *et al.*, 1977). However, reduced heterogeneity in patch quality, coupled with a relatively high density of food tree species, would suggest that there are few costs in

leaving patches earlier as they become depleted because locating a food patch of comparable nutritional quality should not be difficult.

Although secondary and disturbed habitats are frequently characterized as poorer quality, low tree density and diversity may not negatively impact howlers if the remaining trees provide appropriate food resources throughout the seasonal cycle. Indeed, it appears that La Luz actually has a higher density of *feeding* trees than some sites at which *A. palliata* has been studied (Table 3.14), and that these trees provide higher quality forage. Although tree species accounting for $\geq 1\%$ of feeding time have a relatively high density at Santa Rosa (Chapman, 1988a), these trees are smaller than feeding trees at La Luz (mean diameter at breast height 62.6 cm versus 77.9 cm) and may therefore comprise a smaller proportion of the available crown volume than at La Luz.

A discussion of patch density may be appropriate only for certain fruits (and possibly flowers), because the currency likely maximized when feeding on these resources is net energy gain (versus a favorable ratio of nutrients to digestion inhibitors, as with leaves; Milton, 1979), fruits are rarer in the habitat (Chapter 2), and they generally occur in depletable patches (Milton, 1980; Chapman, 1988a; but see Chapter 5 for a discussion of patchy versus non-patchy fruit resources). However, similar differences are seen between sites even when fruit alone is considered. At La Luz, species whose fruits the howlers were observed eating account for 40.9% of trees in the vegetation enumeration. Conversely, fruit trees at La Pacifica and BCI account for only 14 to 26% of trees in vegetation enumerations (Glander, 1981; Milton, 1980). This pattern is likely an artifact of the superabundance of *Cecropia peltata*, whose fruits are more fibrous and quite

heterogeneous in sugar content (Chapter 4). Nevertheless, trees used for food at La Luz are relatively abundant and there are few differences in nutrient content between eaten and ignored resources, suggesting that patchiness is reduced in the shade coffee plantation.

In terms of food encounter rate and the *average* quality of the forage available, the habitat at La Luz may actually be considered of higher quality for howlers, which are able to consume and digest relatively high levels of fibrous foods (Chapter 4); one would therefore expect shorter patch residency times at this site (Murden and Risenhoover, 1993). Only Chapman (1988a) presents these data for *A. palliata*: mean time spent feeding in a patch is over three times as long at Santa Rosa than at La Luz (1275 versus 359 seconds, respectively). Regardless of what type of food is eaten, the time spent feeding in a patch is 2 to 4 times longer than at La Luz. However, it is unclear if this difference is merely a result of methodological differences, as Chapman calculated patch residency as group feeding time (i.e., the time from which the first group member began feeding in a patch to the time when the last group member stopped feeding in the same patch). I cannot reanalyze my data to determine how comparable they are; however, group members were generally highly synchronized in their behavior, particularly while feeding in large feeding trees, and I believe that were I to have collected comparable data, they would increase patch residency time by a factor of 1.5 *at the very most*.

The overall pattern of foraging behavior that emerges at La Luz is broadly similar to that of *Alouatta palliata* at other sites: both foliage and fruit comprise large parts of the diet; seasonally available items are favored as food sources; and foods are chosen

selectively, with certain commonly-found potential resources being largely ignored. However, subtle differences emerge that reflect effects of reduced tree density and diversity in the shade coffee forest. The howlers at La Luz demonstrate heavier reliance on staple foods than most conspecifics. Additionally, the howlers at La Luz rely heavily on species that are not frequent food sources at other sites. Taken together, these results suggest a somewhat less selective foraging strategy at La Luz. Low selectivity by howlers in La Luz is possible only because of the unusual nutritional characteristics of the foliage in the shade coffee plantations. In Chapter 4 I describe the nutritional qualities of the foods eaten and the consequences of diet selection for the energetics of howlers in the shade coffee plantation.

CHAPTER 4

NUTRITIONAL INTAKE AND ENERGY EXPENDITURE

INTRODUCTION

The foraging patterns of howlers in La Luz differ from those of conspecifics in their heavier reliance on a limited number of staple species, exploitation of species less frequently used at other sites, and dependence on relatively abundant food sources (Chapter 3). These differences likely relate to the relatively low tree density and species richness in the shade coffee plantation at La Luz. However, the overall dietary profiles of the La Luz howlers are similar to those of conspecifics, suggesting that dietary quality may not be compromised. Milton (1979, 1980), Glander (1981), and Estrada (1984) found that when selecting leaves, mantled howlers chose relatively rare species whose leaves had high protein to fiber ratios or high levels of digestibility. Consistent selection of rare food items is not as frequent at La Luz; however, the nutritional causes and consequences are unclear without a study of food phytochemistry.

The less discriminating feeding patterns seen by howlers in the coffee plantations may result in the ingestion of foods with less favorable protein to fiber ratios or high levels of toxins or chemical digestion inhibitors if the overall quality of foliage is poor. In this case, the less selective feeding pattern would be a consequence largely of low tree density and diversity and would result in higher energetic stress than seen in other populations of *Alouatta palliata*, either through a poor nutritional profile or energetic costs associated with impaired nutrient absorption or detoxification of a diet high in secondary

compounds (Freeland and Janzen, 1974; Guglielmo *et al.*, 1996; Robbins *et al.*, 1991). However, if the average foliage quality is high (i.e., contains relatively high levels of protein and low levels of fiber), low feeding selectivity would be an optimal strategy for the howlers, as the costs of increased foraging effort would outweigh the benefits (Murden and Risenhoover, 1993; Owen-Smith and Novielle, 1982). In this case, low selectivity would result because nutrients (or, conversely, high levels of feeding deterrents) are not limiting, and energy expenditure would not be expected to balance or outpace intake, regardless of dietary composition. In this chapter, I present data on the nutritional composition of diets of howlers at La Luz. I examine the nutritional makeup of their primary foods and contrast these to foods eaten by conspecifics to characterize the overall quality of the diet. I also consider the nutritional content of rarely and never eaten food sources. I predict that seasonally available food items will have a more favorable nutritional profile than perennially available mature leaves, that potential resources that are ignored will have higher levels of digestion inhibitors and toxins, and lower levels of nutrients such as protein and simple carbohydrates. I also predict that foods that are eaten in spite of high levels of fiber or toxins will have high levels of critical minerals or nutrients that are rare, and therefore limiting, in the habitat.

Variation in energy balance is expected within the La Luz population as a result of differing energetic needs of males of females and of feeding competition. Although folivorous primates are thought to endure little to no feeding competition (Janson and Goldsmith, 1995), recent studies have documented relationships between group size, foraging effort (Gillespie and Chapman, 2001; Koenig *et al.*, 1998; Steenbeck and van

Schaik, 2001), and net energy gain (Koenig, 2000) among colobine monkeys. Previous researchers have found evidence of feeding competition in howlers (e.g., Larose, 1996), suggesting that howlers at La Luz may also experience costs in net energy gain related to group living. I predict that individuals in larger groups will have lower net energy gain, and that females will endure larger energy deficits due to the energetic costs of pregnancy and lactation.

METHODS

Field Collection of Dietary Items

Collection of plant parts for phytochemical analysis concentrated on major dietary items used by the study subjects. However, in order to determine the role of nutritional and secondary compound composition in food selection, I also included examples of mature foliage and fruit that was abundant in the habitat but ignored by the howlers. A total of 100 samples from over 40 species were collected. Young leaves (N = 23) were collected from 17 species, mature leaves (N = 27) from 18 species, fruit (N = 24) from 15 species, and flowers (N = 10) from 8 species, and other parts (e.g., rachis, petioles, seeds, etc.; N = 6) from 7 species. Food samples were collected during the periods in which they were used, nearly always from the specific trees used by the monkeys. However, the collection of flower samples was frequently difficult, and these were sometimes gathered from more easily-accessible conspecifics, again during the period of their consumption by the howlers.

Samples were collected by cutting limbs with an extensible tree pruner, from broken branches that fell to the ground while the howlers were feeding, and directly from the ground where howlers had been feeding. Foods sampled by the howlers and then discarded were excluded from collection. Whenever possible, foods were collected on the day they were consumed. After collection, the samples were dried either in an electric food dehydrator or in a wire mesh drying rack using a low flame as a heat source. Samples were dried at $\leq 60^{\circ}$ C in paper bags until they reached a constant weight. Dried samples were then stored in zip lock bags with silica gel prior to grinding and analysis. Samples which developed mold were discarded. Although I attempted to collect at least 100 grams of dry sample, this proved impossible for some foods, and I did not have enough material to perform all tests; in these cases, some measures of content have been excluded. As the howlers swallowed fruits intact and passed seeds undigested, seeds were separated from fruit pulp prior to analysis for most samples. Attempts were made to separate seeds in *Ficus* and *Cecropia* fruits. However, the seeds of these species are extremely small and numerous, and some samples were processed with seeds, and some seeds are likely included in the fruit pulp sample even after separation.

Analyses of Nutrient Content

Analyses of nutritional components were carried out in the Wildlife Conservation Society's Nutrition Laboratory, under the direction of Dr. Ellen Dierenfeld. To determine water content, the dry weight of the samples was subtracted from the fresh weight. Samples were redried in a forced-draft oven at 60° C to a constant weight to

determine total dry matter (DM); all subsequent tests are reported as percentages of DM. To determine the content of inorganic matter (total ash content) samples were ashed in a muffle furnace at 500° C for 5 hours. Neutral detergent fiber (NDF), acid detergent fiber (ADF), and the sulfuric acid lignin content were determined using the methods described by Van Soest *et al.* (1991). The difference between NDF and ADF content represents hemicellulose content, while cellulose content is defined as the difference between ADF and lignin.

The total nitrogen content was determined using a macro-Kjeldhal procedure (Williams, 1984). To facilitate comparisons with other studies, crude protein (CP) content was then determined by the standard formula $N \times 6.25$ (Williams, 1984), although it has been suggested that a factor of 4.0 to 5.0 may be more appropriate for tropical leaves (Milton and Dintzis, 1981). A second Kjeldhal procedure was performed on residues from acid detergent extractions to determine available protein (AP) by subtracting resulting estimates of protein bound in insoluble fiber from total crude protein (Goering and Van Soest, 1970). Water soluble carbohydrate (WSC, i.e. mono- and disaccharides) content was measured via a phenol-sulfuric acid colorimetric assay using a sucrose standard (Strickland and Parsons, 1972). Crude fatty acid content was determined using a petroleum ether extraction (Association of Official Analytical Chemists, 1996). The content of calcium, chromium, copper, iron, magnesium, manganese, potassium, sodium, and zinc was measuring via atomic absorption spectrophotometry. Samples were ashed, digested in acid, and diluted in a 1% lanthanum

solution (Parker, 1963). Phosphorus levels were analyzed by colorimetric methods (Association of Official Analytical Chemists, 1996).

The metabolizable energy (the fuel value of the food that can be assimilated and used for metabolism; Robbins, 1993) content of primate foods is sometimes estimated using the standard equation for humans (NRC, 1989):

$$ME = (4 \times CP) + (4 \times NFE) + (9 \times CF)$$

where ME is the metabolizable energy of 100 g of dry matter of the given food, CP is crude protein, NFE is the nitrogen-free extract (i.e., carbohydrate), and CF is the crude fat fraction. This equation was developed based on the digestibility of human foodstuffs; as the foods eaten by wild primates are generally less digestible, with a larger proportion of cell wall constituents, it is likely that this equation overestimates the caloric content available to primate consumers (Ofstedal, 1991). Based on feeding trials conducted on temporarily caged howlers on BCI, Milton *et al.* (1980) found that mantled howlers digested 24 to 45% of total cell wall material and 74 to 94% of crude protein on various diets comprised of *Ficus* fruits or leaves. I therefore calculate an estimate of metabolizable energy for howlers using coefficients of digestibility of 41% and 89% for NDF and CP respectively (cf. Conklin and Wrangham, 1994):

$$ME_{AP} = (4 \times CP \times 0.89) + (4 \times NDF \times 0.41) + (4 \times (WSC + NFE)) + (9 \times CF)$$

where ME_{AP} is the metabolizable energy *Alouatta palliata* is able to extract from 100 g of dry matter, CP is crude protein, NDF is neutral detergent fiber, WSC is water soluble carbohydrates, NFE is remaining nitrogen free extract ($100 - (CF + CP + WSC + NDF$

+ ASH)), and CF is the crude fat fraction. Given the uniformly low levels of crude fat in all samples measured, ME_{AP} was calculated even if fat values were missing (i.e., crude fat content was assumed to be zero). The coefficients of digestibility are based on the average assimilation values for a diet comprised largely of *Ficus* leaves. Milton *et al.* (1980) determined digestibility of fiber by feeding howlers two test diets, one comprised primarily of *Ficus* fruits, the other of *Ficus* leaves; the leaf diet was more digestible due to the high proportion of indigestible fig seeds included in the nutritional analyses of Milton *et al.* (1980). Because the higher values of digestion efficiency derived from the leaf diet are more similar to those observed for other animals (Milton *et al.*, 1980), and because I analyzed the nutrient content of *Ficus* figs with at least some seeds removed, I use the higher values as digestion coefficients. Recent studies of digestion by *A. seniculus* also have found NDF digestibility of about 45% (Edwards, 1995), providing further evidence that howlers can assimilate a large amount of fiber.

All macronutrient analyses except crude fats were performed in duplicate and results represent the average values of the replicates; results were discarded if there was > 2% difference between replicates. Due to limited sample quantities, not all analyses were performed on all samples; tests of fiber and protein content were emphasized when sample quantities were limited. Because fig syconia have demonstrated differences from other fruits in their typical fiber and mineral contents (Conklin and Wrangham, 1994; O'Brien *et al.*, 1998; Silver *et al.*, 2000), they are considered separately in the analyses of nutritional content. When multiple samples of the same food species/phenophase were analyzed, the results were averaged for analysis.

Calculation of Individual Activity Budgets and Net Energy Gain

The scan data used to calculate group activity budgets (Chapter 3) cannot be applied to the description of activity patterns for age-sex classes because members of all age-sex classes may not be in view at all times; this is especially true for adult males, which are not numerous in the groups. Additionally, because individual identity was not noted in the scans, they cannot be used to calculate individual activity budgets.

Consequently, for comparisons of energy allocation and expenditure between age-sex classes and between individuals within groups, I use activity budgets calculated from day-long focal follows. For all full-day focal samples (where least 9 hours of contact data were recorded, excluding periods when the focal was lost or otherwise not visible), I calculate activity budgets based on the percent contribution of each activity state to the total contact hours recorded. Focal animals were most frequently lost during travel, and these activity budgets therefore likely underestimate the amount of time dedicated to movement; however, this bias should be consistent for all individuals, and the focal-based budgets should therefore be appropriate for inter-individual contrasts of activity patterns.

The same focal follows used to calculate individual activity budgets were also used to calculate daily dietary intakes. For each complete focal follow, the total time spent feeding on each food (i.e., each phenophase of each food species) was recorded. Feeding rates (units food consumed per minute) collected concurrently were used to calculate the approximate intake in grams of each food type. Food intake for each bout was calculated by multiplying the number of units food eaten per minute during the feeding bout, the length in minutes of the feeding bout, and the wet weight per unit of the food. All

feeding bouts in which a particular food was eaten were summed to determine the total intake for each food per day. If feeding rates were not available for a given bout, the focal animal's average feeding rate for the given resource on that day was used. If feeding rates for the given resource were not available for the focal animal, the average feeding rate for the food species and phenophase, based on data pooled from the focal individual's group, was used to calculate the amount of fresh matter eaten. I used Zootrition Dietary Management software (Wildlife Conservation Society, 2002) to calculate the nutritional content of the daily diets. If a food was not included in the nutritional analyses, either values for the same phenophase of a congener or the average values for the phenophase (i.e., mature leaflets, young leaves, mature fruit, flower bud, etc.) were used for values of protein, carbohydrate, fat, and caloric content; given the variability in mineral content (see Results), no attempt was made to estimate these values for unmeasured foods.

Estimates of nutritional and caloric requirements were derived from a number of sources. Mineral requirements are based on published data for nonhuman primates (NRC, 1978); requirements for primates are estimated to be: calcium, 0.56% dry matter; iron, 200 mg/kg; magnesium, 0.17% DM; manganese 44.4 mg/kg; phosphorus 0.44% DM; potassium, 0.89% DM; sodium, 0.33% DM; and zinc, 11.1 mg/kg. Although the dry matter protein needed to maintain nitrogen balance may be as low as 4 to 8% (Milton, 1979), to allow for potentially low digestibility of the protein fraction bound in cell wall constituents, and to avoid underestimating protein requirements, crude protein

requirements are estimated to be 16% of dietary intake on a dry matter basis (NRC, 1978).

Two methods are used for calculating energetic needs. Following Dasilva (1992), Nakagawa (2000), and Stacey (1986), to estimate daily metabolic requirements I use Harvey and Clutton-Brock's (1981) derivation of equations presented by Coelho (1977) to calculate average daily metabolic needs (ADMN):

$$\text{ADMN} = [(130W^{0.75} / 24) \times S] + [(89W^{0.75} / 24) \times (24 - S)] + T$$

where ADMN = daily metabolic costs in kcal per day, W = body weight (kg), S = number of non-resting hours each day, $130W^{0.75}$ estimates the active metabolic rate, and $89W^{0.75}$ the resting metabolic rate. An additional estimate of travel costs, T , is included (Tucker, 1970):

$$T = (0.1) 10^E (\text{kg} \times \text{km})$$

where T = travel costs per day in kcal and $E = 1.67W^{-0.216}$. T is then added to ADMN to provide a total estimate of energy expenditure. Travel costs may be underestimated by T because I measured DJL's on a planimetric scale without reference to topography or energetically-expensive vertical movement (Chapter 5). For example, Sprague (2000) found that modeling ranging behavior on a 3-dimensional representation of terrain increased estimates of travel distance and range size by a factor of approximately 1.2, while Gaulin and Gaulin (1982) estimated found average vertical movement to be approximately half the average day journey length. In their estimates of howler energy expenditure, Milton *et al.* (1980) triple T to account for these underestimates. I therefore

calculate ADMN using both T and $2T$ and contrast the results to see if one produces estimates of energy expenditure more in line with energy intake.

Activity budgets based on focal animal follows are used to calculate time spent active. To take into account the energetic costs of pregnancy and lactation, the ADMNs (prior to the addition of travel costs) of reproductive females were multiplied by a factor of 1.25 and 1.5, respectively (Coelho, 1974; Harvey and Clutton-Brock, 1981); pregnancy was determined by counting back from the appearance of a new infant and is considered to include the last 3 months before parturition. Although the resulting estimates of ADMN fall below the field metabolic rate of 84.8 kcal/kg/day measured by Nagy and Milton (1979b), calculations of ADMN are preferable for these analyses as they take into account the differing activity levels and travel distances of individuals and groups. For the purposes of these analyses, each individual focal follow is considered a separate data point, even though this method results in counting several follows of the same individual as individual data points. Although data points could be averaged across individuals to collapse these into one single data point, this would make analyses of differences between months (or between reproductive states among females) impossible. However, it is possible that this treatment leads to inflated sample sizes. When possible, I also analyze the data averaged for each individual (separated by reproductive status; female X while lactating is treated as a separate individual from female X while pregnant) to provide corroboration of results based on the original analyses.

RESULTS

Phytochemical Content of Foods

Results of all phytochemical analyses are presented in Appendices I (macronutrients) and II (micronutrients). There were differences between in the content of various macronutrients of mature leaves, young leaves, flowers, fruits, and figs used as food sources (Table 4.1). All foods had relatively high levels of fiber, with fig fruits having the highest fiber fractions. Leaves and flowers contain more crude protein than do fruits and figs. An unbalanced one-way ANOVA demonstrates significant differences between food categories in the content of water ($F_{[4,70]} = 10.436, P < 0.001$). Kruskal-Wallis ANOVAs demonstrate significant differences between foods in the content of water soluble carbohydrates ($H = 16.215, P = 0.003, N = 69$), crude protein ($H = 41.117, P < 0.001, N = 74$), available protein ($H = 15.690, P = 0.003, N = 39$), and the crude protein to ADF ratio ($H = 31.595, P < 0.001, N = 74$); no significant differences are observed in metabolizable energy content ($H = 4.871, P = 0.301, N = 69$), NDF ($H = 7.703, P = 0.103, N = 75$) ADF ($F_{[4,70]} = 1.485, P = 0.216$), or lignin ($F_{[4,70]} = 1.173, P = 0.330$). *Post hoc* comparisons demonstrate that mature leaves have significantly lower water content than all other plant parts. Non-fig fruits had significantly higher levels of water soluble carbohydrates than all other plant parts. Mature leaves, young leaves, and flowers had significantly more crude protein than figs or fruit. Young leaves had significantly higher crude protein to ADF ratios than figs or fruits, and flowers also had significantly higher values than figs. When young and mature leaves eaten were compared alone, significant differences were found in water ($U = 42, P < 0.001, N = 42$)

Table 4.1. Macronutrient, water, and energy content of plant parts eaten.¹

Part	N	Water	NDF	ADF	Lignin	WSC	CP	CP:ADF	ME _{AP}
Mature Leaves	15	60.4	48.4	36.6	18.0	4.6	19.5	0.60	2.8
<i>SD</i>		10.4	13.6	12.6	9.6	1.6	6.2	0.30	0.3
Young leaves	18	73.7	44.2	37.2	20.3	3.7	22.3	0.72	2.8
<i>SD</i>		6.0	11.6	11.4	9.3	1.6	8.1	0.53	0.3
Flowers	9	76.0	41.2	33.3	18.5	8.3	21.1	0.71	2.9
<i>SD</i>		12.3	8.4	9.1	6.6	4.4	4.6	0.34	0.2
Fruits	14	70.6	48.0	40.0	19.4	17.4	8.6	0.28	2.9
<i>SD</i>		7.9	17.9	15.7	10.1	15.1	3.8	0.23	0.4
Fig fruits	7	70.0	56.6	47.6	25.1	5.9	7.5	0.16	2.6
<i>SD</i>		8.7	7.7	8.4	4.4	5.1	1.1	0.03	0.2

¹Water is reported as percentage of fresh weight; NDF, ADF, lignin, WSC, and CP reported as percentage of dry matter; metabolizable energy as kcal/g dry weight.

Table 4.2. Micronutrient contents of plant parts eaten.¹

Part	n	Ca	Cu	Fe	K	Mg	Mn	Na	P	Zn	Ca:P
Mature Leaves	13	1.52	8.5	125.0	1.9	0.32	30.2	0.05	0.16	12.3	13.4
<i>SD</i>		1.01	4.3	43.7	1.1	0.17	19.0	0.02	0.10	7.0	14.2
Young leaves	13	0.68	16.3	89.6	2.9	0.52	23.3	0.02	0.34	31.5	2.4
<i>SD</i>		0.42	5.8	27.6	1.0	0.68	8.5	0.02	0.11	11.4	2.1
Flowers	5	0.80	16.7	93.1	2.2	0.36	23.4	0.03	0.30	30.8	2.9
<i>SD</i>		0.52	13.2	20.7	0.4	0.11	8.4	0.02	0.06	13.4	2.0
Fruits	14	0.49	14.7	52.9	2.0	0.24	10.7	0.01	0.17	17.8	3.5
<i>SD</i>		0.40	20.3	29.7	1.0	0.14	9.0	0.01	0.09	17.2	2.6
Figs	4	1.87	16.3	126.3	1.6	0.37	22.8	0.02	0.14	20.9	15.6
<i>SD</i>		0.71	9.0	20.3	0.8	0.08	4.7	0.01	0.06	4.6	9.3
ANOVA (F)		8.2***	3.2*	--	5.2**	3.3*	--	--	10.8***	11.7***	10.5***
Kruskal-Wallis (H)		--	--	25.7***	--	--	17.0**	21.5***	--	--	--
<i>Post hoc</i> tests		ML>YL	YL>ML	ML>YL	YL>ML	YL>FR	ML>FR	ML>YL	YL>FR	YL>ML	ML,FG>YL
		ML>FR		ML>FR	YL>FR			ML>FR	YL>FG	YL>FR	ML,FG>FL
		FG>FR		YL>FR					FL>ML	FL>ML	ML,FG>FR
				FG>FR					FL>FR	FL>FR	

¹Values of Na, Mg, Ca, and P reported as %DM; other minerals as $\mu\text{g/g}$ DM. ANOVAs are either parametric (one-way unbalanced, F statistic) or non-parametric (Kruskal-Wallis test, H statistic) when transformed data do not fit parametric assumptions. For both the F and H tests, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Results of *post hoc* tests for significant differences between food categories (Bonferroni's Adjustment): ML = mature leaves, YL = young leaves, FL = flowers, FR = non-fig fruits, FG = figs; > indicates a significant differences at the 0.05 level, with the part on the left having significantly higher levels of the mineral in question.

and water soluble carbohydrate content ($U = 102, P < 0.036, N = 37$), but no significant differences were found in any measures of protein or fiber content, nor were differences seen in ash, crude fat, or caloric content.

In spite of the lack of significant differences between plant parts in ash content ($F_{[4,70]} = 1.881, P = 0.123$), differences were found for all minerals analyzed (Table 4.2). Mature leaves had significantly more calcium than young leaves and fruits. Calcium-to-phosphorus ratios, a measure of calcium availability (Robbins, 1993), are significantly higher in mature leaves than in young leaves, fruits, and flowers. Mature leaves also contain significantly more iron and sodium than young leaves or fruits, and more manganese than fruits. However, young leaves have significantly higher copper, potassium, and zinc levels than mature leaves. Young leaves also have higher iron, potassium, magnesium, phosphorus, and zinc than fruit, and higher phosphorus than figs. Fruits generally have lower mineral content than other plant parts. Fig synconia, in contrast to other fruits, have relatively high mineral content, with significantly higher levels of calcium and iron than fruits, as well as higher levels of calcium-to-phosphorus ratios than young leaves, flowers, and fruits. Flowers also have high levels of phosphorus in comparison to mature leaves and fruits.

Resources from leguminous species have been singled out as particularly nutritious resources for other folivorous primates due to their high nitrogen (Oates *et al.*, 1990; Dasilva, 1994; Mowry *et al.*, 1996) and amino acid (Waterman and Kool, 1994) content. As expected, the foliage of the leguminous species eaten had significantly higher levels of both crude (mature leaves: $F_{[1,13]} = 17.793, P = 0.001$; young leaves: $F_{[1,16]} =$

12.864, $P = 0.002$) and available protein (mature leaves: $F_{[1,10]} = 13.902$, $P = 0.004$; young leaves: $F_{[1,9]}: 36.380$, $P = 0.001$). Other measures of nutrient content did not differ significantly between leguminous and non-leguminous species.

Food Selection in Relation to Nutrient Content

Howlers are thought to select food in relation to nutrient content (as opposed to relative abundance alone; e.g., Milton, 1979; Silver *et al.*, 2000), concentrating feeding on resources with high levels of protein or simple sugars and with low levels of fiber. However, many of the key foods eaten by howlers in La Luz (for example, mature fruits of *Cecropia peltata*, mature leaves of *Enterolobium cyclocarpum*) have relatively high fiber levels or low levels of crude protein or water soluble carbohydrates (Table 4.3). Rank correlations demonstrate no significant relationships between percent time feeding on a given species' phenophase and any measure of nutrient content. However, given that abundance may significantly affect food selection at La Luz (Chapter 3), relationships between selection and nutrient content may be obscured. If the index of selection (the proportion contribution to total feeding time of each part of each species, divided by the proportion contribution of each species to total basal area; Chapter 3) is used instead of percent feeding time, there are negative relationships between selection and all measures of fiber content that approach significance (NDF: $r_s = -0.297$, $P = 0.056$; ADF: $r_s = -0.261$, $P = 0.095$; lignin: $r_s = -0.254$, $P = 0.105$; $N = 42$ for all tests). No relationship is seen between selection ratio and water soluble carbohydrate, crude protein, available

Table 4.3. The nutrient content of mature leaves, young leaves, fruits, and flowers of the primary food species.¹

Species	Mature leaves			Young Leaves			Mature Fruits/Figs			Flowers		
	ADF	CP	WSC	ADF	CP	WSC	ADF	CP	WSC	ADF	CP	WSC
<i>Ficus costaricana</i>	--	--	--	52.9	12.0	3.0	38.1	5.8	12.1	--	--	--
<i>Enterolobium cyclocarpum</i>	45.7	22.5	4.6	30.9	30.5	3.7	--	--	--	29.3	29.1	6.2
<i>Spondias mombin</i>	--	--	--	43.4	22.2	2.0	20.7	8.6	31.2	--	--	--
<i>Cecropia peltata</i>	46.4	17.9	2.3	51.5	26.3	1.5	46.8	10.6	7.6	41.2	18.1	7.0
<i>Bursera simaruba</i>	32.5	14.0	6.2	41.8	16.5	--	--	--	--	32.3	19.2	--
Average (all foods)	36.6	19.5	4.6	37.2	22.3	3.7	42.5 ²	8.3 ²	13.6 ²	33.3	21.1	8.3

¹ADF, CP, and WSC reported as percentage of dry matter.

²Values for mature fruits and figs pooled.

protein, or the ratio of protein to fiber. These results suggest possible avoidance of cell wall constituents when abundance is taken into account.

The ANOVAs reveal no significant differences between young and mature dietary foliage in fiber or protein content, as would be expected if the howlers are selecting mature leaves with nutritional profiles similar to young leaves. Young leaves are generally considered to be a higher-quality food source than mature leaves due to lower fiber and higher protein levels. I analyzed the content of macronutrients in matched pairs for food and non-food species with nutritional information from both young and mature leaves. Although young and mature leaves did not differ significantly in fiber content, young leaves have significantly more water (Wilcoxon signed ranks test: $Z = -2.803$, $N = 10$, $P = 0.005$), crude protein ($Z = -2.666$, $N = 9$, $P = 0.008$), and water soluble carbohydrates ($Z = -2.197$, $N = 7$, $P = 0.028$), and have significantly higher crude protein to ADF ratios ($Z = -2.395$, $N = 9$, $P = 0.017$).

Samples of mature leaves and fruits abundant in the habitat but never eaten by the howlers were also analyzed for macronutrient content (Appendix II). When compared with mature leaves and fruits included in the diet, uneaten items do indeed have more fiber, less protein, lower levels of water-soluble carbohydrates, and lower ratios of crude protein to ADF (Table 4.4). However, for the most part these differences are not significant. Fruits that were eaten had significantly less neutral detergent fiber than uneaten fruits ($F_{[1,18]} = 4.900$, $P = 0.040$); both dietary fruits and foliage had significantly higher levels of water soluble carbohydrates than uneaten items (fruits: $F_{[1,18]} = 29.054$, $P < 0.001$; mature leaves: $F_{[1,22]} = 7.082$, $P = 0.015$).

Table 4.4. Mean nutrient content and standard deviations of eaten versus ignored mature foliage and fruits.

Phenophase	N	NDF	ADF	Lignin	CP	CP:ADF	WSC
Mature fruit (eaten) ¹	14	49.9 ± 17.9	40.2 ± 15.8	20.0 ± 10.0	8.8 ± 4.1	0.29 ± 0.23	17.6 ± 15.1
Mature fruit (ignored)	6	66.6 ± 15.8	49.6 ± 16.8	18.0 ± 9.3	10.7 ± 3.4	0.26 ± 0.17	1.0 ± 1.2
Mature Leaves (eaten)	16	48.3 ± 13.1	36.3 ± 12.3	17.6 ± 9.4	19.4 ± 6.0	0.56 ± 0.31	4.8 ± 1.7
Mature Leaves (ignored)	9	54.0 ± 9.9	41.6 ± 9.8	20.2 ± 6.4	16.4 ± 5.0	0.44 ± 0.22	2.9 ± 2.6

¹Not including *Ficus* fruits.

Analyses of secondary plant compounds (alkaloids, total phenolics, and condensed tannins) are ongoing. One may expect that the reduced tree species diversity at La Luz could lead the howlers at this site to consume higher levels of digestion inhibitors or toxins. However, preliminary analyses of the foliage at La Luz suggest that on the whole, levels of alkaloids and phenolics are fairly low at this site (Mowry, personal communication). Some food sources are high in secondary compounds: for example, the young leaflets of *Albizia guachepile*, although extremely high in protein and low in fiber (Appendix II) are also highly reactive with reagents testing for alkaloids, while the mature leaves of *Terminalia oblonga* have very high levels of protein-binding tannins. However, preliminary results suggest that these are the exception, and that secondary metabolite content is quite low.

Daily Food and Nutrient Intake

The howlers consumed an average 659.6 ± 230.0 g fresh matter and 173.1 ± 58.4 g dry matter on a daily basis. There are no significant differences between groups, seasons, age-sex categories, or reproductive status in the daily intake of fresh or dry matter (Table 4.5). There are no significant differences between males, females, and juveniles in ingestion rate, although females have higher rates per minute feeding time of fresh matter ingestion than males. However, rates of fresh weight ingestion are significantly higher in the wet season ($F_{[1,60]} = 6.031$, $P = 0.017$). When each focal is considered an independent datum, rates also differ significantly between groups ($F_{[2,60]} =$

Table 4.5. Daily fresh and dry matter intake by group, season, age-sex class, and reproductive status (females only).

Variable		N ¹	Fresh Matter Intake (g)	Dry Matter Intake (g)
Group	Group 1	11	682.6 ± 306.3	171.6 ± 83.2
	Group 2	24	610.2 ± 203.1	172.3 ± 56.2
	Group 3	26	695.5 ± 218.2	174.5 ± 50.0
Season	Wet Season	30	660.5 ± 215.5	178.1 ± 58.6
	Dry Season	31	658.8 ± 246.8	168.3 ± 58.7
Age-Sex Class	Male	23	675.8 ± 186.8	185.5 ± 54.3
	Female	35	651.2 ± 256.9	167.0 ± 60.9
	Juvenile	3	675.8 ± 186.8	185.5 ± 54.3
Female Status	Nonreproductive	9	613.3 ± 325.2	142.4 ± 59.2
	Pregnant (late)	5	583.8 ± 264.5	147.5 ± 57.1
	Lactating	21	683.4 ± 230.3	182.3 ± 60.3
All Data		61	659.6 ± 230.0	173.1 ± 58.4

¹N is the number of completed focal follows; several follows of the same individual may be included as different data points.

Table 4.6. Rate of fresh matter and dry matter intake for major food types.

Food Type	Fresh Matter Intake (g/min)	Dry Matter Intake (g/min)
Mature Leaves	6.57	2.60
Young Leaves	20.15	5.30
Figs	11.02	3.31
Other Fruits	23.10	6.78
Flowers	5.98	1.79

3.454, $P = 0.038$), with Group 3 having significantly higher rates than Group 2.

However, these differences are not significant if each individual is considered a datum ($F_{[2,24]} = 1.972$, $P = 0.161$). As observed by Gaulin and Gaulin (1982) and Oftedal (1991), although the majority of feeding time is spent eating foliage, the rate of dry matter intake is highest for fruits (Table 4.6). On a dry matter basis, the average daily diets comprise $41.7 \pm 6.5\%$ neutral detergent fiber, $38.7 \pm 6.2\%$ acid detergent fiber, $14.0 \pm 3.2\%$ crude protein, $9.5 \pm 6.7\%$ water soluble carbohydrates, and only $0.06 \pm 0.03\%$ crude fat. Given the average daily intake of 173.1 g dry matter, the howlers are estimated to consume an average of 72.2 g of NDF, 67.0 g of ADF, 16.4 g of WSC, and 24.2 g of crude protein per day. Unbalanced one-way ANOVAs demonstrate no significant differences between groups, seasons, age-sex classes or reproductive status in the macronutrient composition of diets on a dry matter basis, although differences between seasons in water soluble carbohydrates approach significance (Kruskal-Wallis: $H = 3.047$, $N = 60$, $P = 0.081$), with WSC intake higher in the wet season when consumption of ripe fleshy fruits peaks (Chapter 3).

On average, calcium comprises 0.97%, magnesium 0.56%, phosphorus 0.18%, potassium 1.84%, and sodium 0.02% of dry matter. Average iron content of the daily diets is 83.9 mg/kg dry matter, average manganese 17.0 mg/kg, and average zinc 22.0 mg/kg. Based on recommendations for primates (NRC, 1978), the average diet meets crude protein, calcium, magnesium, potassium, and zinc needs, but may be deficient in iron, manganese, phosphorus, and sodium. However, as not all foods were analyzed for mineral content, the mineral content of the average diets is probably underestimated and

may fall within acceptable limits. Although there are no significant differences between age-sex classes or classes of reproductive status in the amount of any mineral in the daily diet, there are significant differences between groups in the amount of calcium in the diet ($F_{[2,60]} = 3.606, P = 0.033$), with Group 2 consuming significantly more calcium than Group 1. This difference likely arises from the high consumption of calcium-rich *Ficus* fruits by Group 2 versus the relatively *Ficus*-poor diet of Group 1 (Chapter 3). Seasonally, the diets contain significantly more sodium and zinc during the dry season (Na: $F_{[1,60]} = 6.999, P = 0.010$; Zn: $F_{[1,60]} = 4.188, P = 0.045$); the fruits that comprise a large portion of the wet season diet have relatively low levels of both these minerals.

Activity Budgets, Caloric Intake, and Energy Expenditure

Analysis of activity data collected during focal animal sampling demonstrates energy budgets differ for individuals in different age-sex classes (Table 4.7). Adult females in all reproductive stages rest more than do males or juveniles; while non-reproductive adult females rest significantly more than adult males and juveniles, pregnant and lactating females do not. Conversely, males and juveniles move more than adult females, with adult males moving significantly more than non-reproductive adult females. Juveniles spend the most time feeding and adult females the least; among females, pregnant and lactating individuals feed more, although these differences are not significant. Juveniles and adult males spend more time in affiliative social interactions (e.g., play) than females, while lactating females spend the most time in agonistic social interactions, engaging in them significantly more often than adult males. The increased

Table 4.7. Mean age-sex class activity budgets calculated from continuous data collected during focal animal sampling (each complete follow is considered an individual datum), standard deviations, and differences between age-sex classes.¹

Age/Sex Class	N ²	Rest	Move	Feed	Affiliative	Agonistic	Vocalize	Other
Adult Males	23	73.0	8.6	16.6	1.0	0.1	0.6	0.1
<i>SD</i>		6.0	2.3	5.7	1.7	0.1	0.7	0.2
Adult Females	10	80.2	5.9	13.1	0.6	0.2	0.0	0.0
<i>SD</i>		6.3	2.4	5.8	0.6	0.2	0.0	0.0
Adult Females (pregnant)	4	74.8	8.1	16.6	0.4	0.1	0.0	0.0
<i>SD</i>		6.9	1.4	5.8	0.1	0.1	0.0	0.0
Adult Females (lactating)	21	77.2	6.8	15.2	0.5	0.3	0.0	0.0
<i>SD</i>		5.5	2.1	5.0	0.4	0.3	0.0	0.0
Juveniles	3	67.6	9.4	21.0	1.9	0.1	0.0	0.0
<i>SD</i>		7.1	3.9	1.3	2.1	0.1	0.0	0.0
ANOVA (F)		4.247**	3.720**	1.154	1.004	2.602*	1.525	1.157
<i>Post hoc</i> tests		AF > AM	AM > AF			AFL > AM		
		AF > J						

¹*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Results of *post hoc* tests for significant differences between age-sex classes: > indicates significant differences at the 0.05 level, with the class on the left engaging in the given activity significantly more often.

²N is the number of completed focal follows; several follows of the same individual may be included as different data points.

time lactating females spend in agonistic social interaction probably results from the increased harassment they face from both male and female group members when associated with a new infant (Chapter 6).

Based on my estimates of food intake and caloric content, on average the howlers consumed 441.3 kcal per day (range 129.5 to 940.4, $SD \pm 151.0$). Table 4.8 presents the metabolizable energy intakes by group, season, age-sex class, and reproductive status. The overall caloric intake of the three groups did not differ significantly, although the two larger groups have slightly higher caloric intakes. Slight seasonal differences exist, with average caloric intakes higher in the wet season, even though less time is spent feeding; however, a one-way ANOVA shows no significant difference between seasons in caloric intake. Differences are also seen among adult males, adult females, and juveniles in caloric intake, with males having the highest average intake, as would be expected given differences in body size. However, these differences are not significant. Nor are significant differences observed between reproductive states within adult females, although lactating females do have higher energetic intakes, as would be expected given the costs of reproduction for females.

The mean ADMN is 480.6 kcal/day (range 276.6 to 574.5, $SD \pm 80.3$), or, calculated using $2 \times T$, 486.4 kcal/day (range 270.5 to 579.7, $SD \pm 80.6$). The values of T are generally low (mean 5.8 kcal, range 1.6 to 15.8, $SD \pm 2.7$), and, as using $2 \times T$ makes little difference in estimated energy expenditure, I will present further results using T only. Significant differences are seen between groups in ADMN (Table 4.8), with Group

Table 4.8. Mean daily metabolizable energy intake, average daily metabolic needs, and energy budgets by group, season, age-sex class, and reproductive status (females only); each complete follow is considered an individual datum.¹

Variable		N ²	Intake (kcal/day)	ADMN (kcal/day)	Budget ³ (kcal)
Group	Group 1	11	437.5 ± 221.7	485.8 ± 92.5	-9.1 ± 71.6
	Group 2	24	433.0 ± 138.3	512.4 ± 56.7	-40.1 ± 27.7
	Group 3	26	450.7 ± 131.6	449.0 ± 84.1	41.0 ± 25.0
	ANOVA		F _[2,58] = 0.088	H = 6.631*	F _[2,58] = 1.731
Season	Wet Season	30	425.1 ± 154.5	468.5 ± 85.4	4.3 ± 29.5
	Dry Season	31	458.0 ± 148.1	493.1 ± 74.0	-4.1 ± 27.9
	ANOVA		F _[1,59] = 0.721	H = 0.740	F _[1,59] = 0.043
Age-Sex Class	Male	23	478.2 ± 150.0	472.5 ± 6.8	45.0 ± 31.3
	Female	35	421.8 ± 150.5	503.7 ± 83.4	-42.6 ± 25.2
	Juvenile	3	386.6 ± 157.7	273.0 ± 6.9	152.9 ± 88.0
	ANOVA		F _[2,58] = 1.496	H = 12.525**	F _[2,58] = 4.026*
Female Status	Nonreproductive	9	371.0 ± 149.8	375.2 ± 4.6	35.1 ± 49.1
	Pregnant (late)	5	367.3 ± 150.4	472.6 ± 5.4	-66.0 ± 66.2
	Lactating	21	456.5 ± 147.8	566.1 ± 5.3	-70.3 ± 31.7
	ANOVA		F _[2,32] = 1.435	H = 26.000***	F _[2,32] = 1.718

¹ ANOVAs are either parametric (one-way unbalanced, F statistic) or non-parametric (Kruskal-Wallis test, H statistic) when transformed data do not fit parametric assumptions. For both the F and T statistics, * $P < 0.5$, *** $P < 0.001$

² N is the number of completed focal follows; several follows of the same individual may be included as different data points.

³ Corrected for negative bias by adding 39.3 to all budgets to set the average budget to 0 kcal (perfect energy balance).

2, the smallest group, having significantly higher energy needs than Group 3. Although ADMN is higher in the wet season, these differences are not significant. ANOVAs using full-day follow as data points demonstrate significant differences in ADMN between age-sex classes, with females having the highest daily metabolic needs; males have higher energy needs than juveniles, and females expend significantly more energy than both males and juveniles. These differences are significant even when data are collapsed by individual ($H = 8.810$, $P = 0.012$, $N = 27$). High energy demands within females are a result of the energetic demands of pregnancy and lactation, with pregnant females expending significantly more energy than non-reproductive females; lactating females have significantly higher estimated ADMNs than both pregnant and non-reproductive females. As with age-sex differences, differences among females are significant even when individuals, rather than follows, are treated as data points ($H = 12.490$, $P = 0.002$, $N = 17$).

Subtracting the energy expenditure from the energy intake provides an estimate of energy balance (Coelho, 1986). The average energy balance is -39.3 kcal (range -276.0 to 466.7, SD 157.0). The majority of these energy budgets are slightly negative, suggesting that caloric requirements are not being met; however, given that the howlers were reproducing and had healthy body conditions, it seems unlikely that they were incurring regular energy deficits. It seems more likely that the discrepancy arises from the assumptions used in calculating caloric content and energy expenditure. Nevertheless, these data should be appropriate for comparative purposes within this study. To provide a more realistic baseline, I apply a correction factor to the energy budgets by adding 39.3

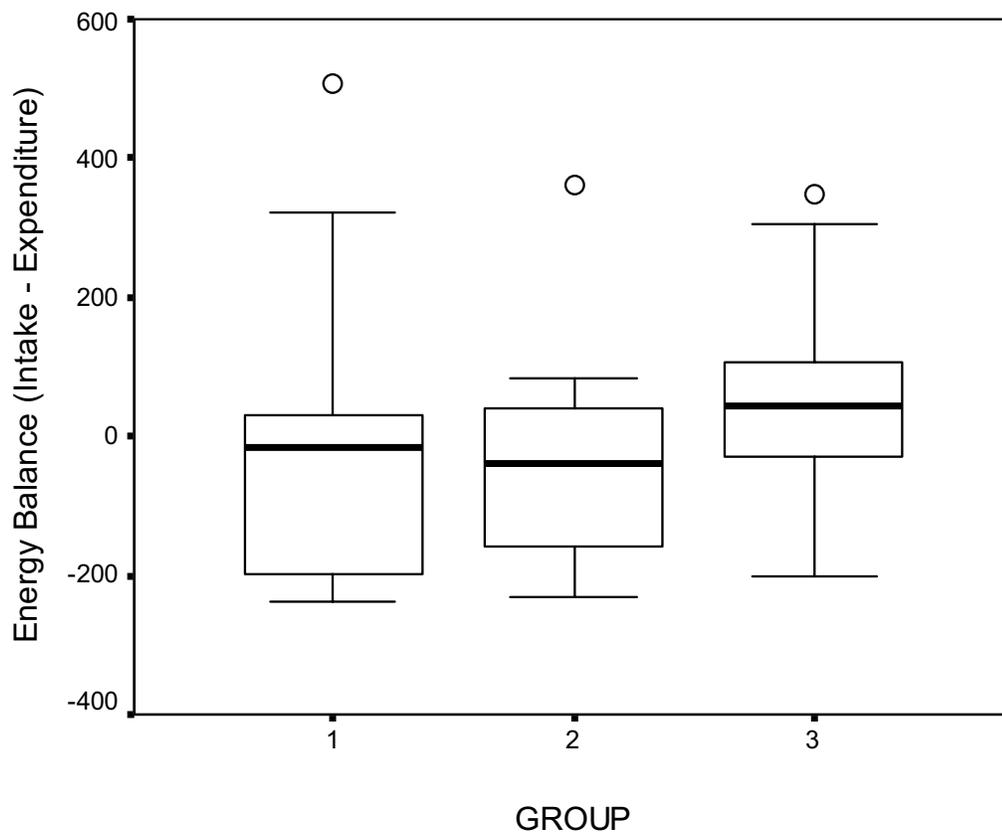


Figure 4.1. Median (dark line) energy balance of the three groups, with the interquartile range (box) and high and low values (whiskers), excluding outliers (circles).

kcal to all budgets, so that the average budget is 0 (i.e., energy intake matches expenditure). Mean energy balance differs between groups (Table 4.8), although not significantly. Contrary to expectations regarding levels of within-group feeding competition in relation to group size, the smallest group has the highest deficit. To a certain extent, this result is a consequence of a skewed data distribution with a few outliers; a consideration of median values demonstrates that Group 1 and 2 have similar energy deficits (Figure 4.1). Age-sex classes differ in their energy balance, with females having higher deficits than males or juveniles. An ANOVA demonstrates significant differences between the age-sex classes, with females having significantly lower energy balances than both adult males and juveniles; however, considered on an individual basis, this difference is not significant ($F_{[2,24]} = 2.462, P = 0.107$). Given that females bear the energetic burden of pregnancy and lactation, a lower energy balance is expected. Lactating females have higher energy deficits than pregnant females, which in turn have, on average, a more negative energy balance than non-reproductive females. However, differences among reproductive states within females are not significant. In spite of variation in diet, time spent feeding, and foraging effort (Chapters 3 and 5), energy balance does not show any seasonal effect, as energy expenditure rises with caloric intake during the wet season.

DISCUSSION

Foliage Selection and Nutrient Content

As has been observed for many folivorous primates (e.g., *Alouatta palliata*: Milton, 1979; Glander, 1981; Estrada, 1984; *Alouatta seniculus*: Gaulin and Gaulin, 1982; *Colobus satanas*: McKey *et al.*, 1981; *Colobus polykomos*: Dasilva, 1994; *Presbytis entellus*: Koenig *et al.*, 1998; *Presbytis johnii*: Oates *et al.*, 1980; *Procolobus verus*: Oates, 1988), the howlers at La Luz ignore the foliage of several common species, feeding instead on leaves from a circumscribed subset of the available trees (Chapter 3). However, the La Luz howlers differ in that their primary sources of foliage are quite abundant. Although other studies of howlers have found significant differences in protein and fiber content between mature and young leaves eaten, and between eaten and uneaten items (e.g., Milton, 1979; Glander, 1981; Estrada, 1984; Silver *et al.*, 2000), these differences are not as pronounced at La Luz. As observed by Glander (1981) at La Pacifica, there were no significant differences in protein and fiber content between the young and mature foliage that was eaten, even though mature leaves in general have more cell wall material. However, Glander also found significant differences between fiber and protein levels in eaten versus ignored foliage, a pattern not observed at La Luz. Indeed, the most frequently consumed mature leaves (those of *Enterolobium cyclocarpum* and *Bursera simaruba*) have higher fiber levels and lower protein levels, respectively, than do other mature leaves eaten. Likewise, the young leaves of *Ficus costaricana*, the most frequently used source of immature foliage, are high in fiber and low in crude protein in comparison to other young leaves eaten. These results underscore that although the howlers are indeed selective in

Table 4.9. Crude protein and fiber content of foliage consumed at La Luz and other sites.

Study Species	Mature Leaves				Young Leaves				Reference
	%CP	%NDF	%ADF	CP:ADF	%CP	%NDF	%ADF	CP:ADF	
<i>Alouatta palliata</i>	12.6	--	--	--	16.7	--	--	--	Estrada (1984)
<i>Alouatta palliata</i>	12.4 ¹	--	37.5	--	12.0 ¹	--	33.7	--	Glander (1981)
<i>Alouatta palliata</i>	9.3 ¹	43.0	--	--	15.0	42.0	28.7	0.6	Milton (1979), Milton <i>et al.</i> (1980) ²
<i>Alouatta palliata</i>	19.5	48.4	36.6	0.6	22.3	44.2	37.2	0.7	Present Study
<i>Alouatta pigra</i>	18.3	53.9	33.7	0.6	23.6	49.4	35.0	0.8	Silver <i>et al.</i> (2000)
<i>Alouatta seniculus</i>	16.6	57.2	40.5	0.4	21.2	54.4	36.4	0.6	Oftedal (1991) ³
<i>Colobus polykomos</i>	12.4	--	40.6	0.3	21.8	--	29.3	0.7	Dasilva (1994)
<i>Nasalis larvatus</i>	9.9	43.0	30.5	0.4	--	--	--	--	Yeager <i>et al.</i> (1997) ⁴
<i>Presbytis johnii</i>	10.7	41.6	32.6	0.4	16.0	37.6	33.4	0.6	Oates <i>et al.</i> (1980)
<i>Trachypithecus auratus</i>	13.4	--	34.4	0.4	--	--	--	--	Kool (1992) ⁵

¹ Protein values are for summed amino acids, rather than crude protein; crude protein levels are likely higher.

² Mature leaf values include some non-dietary foliage, young leaf values based on nutrient content of leaves in feeding trials.

³ "Major" food items only.

⁴ Young and mature leaves eaten pooled.

⁵ Includes non-dietary foliage.

their feeding behavior, food choice in certain cases may be more strongly influenced by factors other than nutrient content.

Although the leaves most often consumed by the howlers have relatively low protein to fiber ratios compared to other, less abundant foliage available in the habitat, the forage available at La Luz may be of relatively high quality in comparison to that at other sites where howlers and other folivorous primates have been studied (Table 4.9). The average crude protein content of mature leaves eaten at La Luz (19.5%) is higher than that reported in other studies of *A. palliata* and other studies of folivorous colobines (12.6 to 18.3%), and the protein content of the mature leaves of *Enterolobium cyclocarpum* is 22.5%. Average protein levels of both young and mature foliage are well in excess of recommendations for non-human primates (16.7% of food on a dry matter basis; NRC, 1978). Howlers at La Luz consume, on average, an estimated 24.2 g of crude protein daily. In spite of lower food intakes, their protein consumption exceeds that of howlers with more selective patterns of foliage consumption (*Alouatta seniculus*: 13.0 g CP/day, Gaulin and Gaulin, 1982; ~20.2 g CP/day, Edwards, 1995). The mean value of the crude protein to fiber of all mature leaves calculated with data weighted on basal area (cf. Waterman *et al.*, 1988) is 0.66, well above levels seen at various sites in Africa, Asia, and Madagascar where colobine and lemur biomass have been related to leaf chemistry (Waterman *et al.*, 1988; Oates *et al.*, 1990; Ganzhorn, 1992; Chapman *et al.*, 2002). It therefore appears that protein (alone or in relation to fiber levels) may not be a limiting factor at this site, leading to foliage selection based more strongly on availability than protein content. A similar pattern was observed by Kool (1992), where protein levels of

abundant foliage are relatively high, and by Mowry *et al.* (1996), where selection among young leaves was influenced primarily by abundance if the protein to fiber ratio exceeded a threshold value of 0.5.

The high protein levels and favorable protein to fiber ratios at La Luz may result from a number of factors. Firstly, La Luz has an abundance of pioneer species characteristic of secondary forest (e.g., *Cecropia peltata*), perhaps due to the relatively open canopy, which should favor rapidly-growing sun-loving species. Pioneer species invest less in structural and chemical leaf defense, dedicating resources instead to rapid growth (Coley and Barone, 1996); pioneer species may therefore be of relatively higher quality as they invest less in feeding deterrents (Kool, 1992). Secondly, there is an abundance of leguminous species in the plantation because they are favored as shade trees due to their nitrogen-fixing abilities (Chapter 2). Foliage from these trees, particularly those from the subfamilies Mimosoideae and Papilionoideae, generally have high nitrogen levels (Waterman *et al.*, 1988); these subfamilies predominate in the shade coffee forest. Leguminous species are frequently found growing on nutrient-poor soils (Waterman *et al.*, 1988), and soil quality has been implicated as a factor leading to high levels of chemical feeding deterrents (particularly phenolics) in mature foliage (e.g., Janzen, 1974; Gartlan *et al.*, 1978). Volcanic soils can vary significantly in nutrient content; however, the volcanic soils of western Nicaragua are generally nutrient-rich (Stevens, 1964). Although they have not been analyzed, the soils at La Luz may also be of high quality, and this may explain the apparently low secondary compound content of the foliage.

The role of secondary plant metabolites in foliage feeding has not been systematically addressed in this analysis. As with nutrient content, the effects of phenolic, tannin, and alkaloid content on foliage selection are variable: in some cases primates do avoid foliage high in secondary plant metabolites (e.g., Oates *et al.*, 1977; Oates, 1988; Glander, 1978b, 1981), while other studies have failed to demonstrate a consistent relationship between levels of chemical feeding deterrents and food selection (e.g., Estrada, 1984; Milton, 1979; Mowry *et al.*, 1996; Oates *et al.*, 1980; Silver, 1997). It has even been suggested that low levels of tannins and phenolics may enhance foliage digestibility by some colobines (Kool, 1992). Ultimately, the efficacy of plant chemical defenses is dependent upon the plant's relative abundance and the abundance of other plants in the environment (Belovsky and Schmitz, 1991). Diverse diets may be a behavioral strategy for circumventing the problems posed by plant secondary compounds and structural feeding deterrents (Glander, 1978b; Milton, 1978) by allowing animals to avoid excessive consumption of any single toxin or deterrent. The apparently low levels of secondary compounds suggest that alkaloids and tannins may have only weak effects on food selection, although definitive conclusions are precluded without a complete analysis.

Phytochemical Influences on Fruit and Flower Feeding

Selection of fruits and flowers appears more closely tied to nutrient content. In this case, it appears that water soluble carbohydrates are limiting and that fiber is avoided. For example, the mature fruits of *Ficus costaricana*, which account for 14% of all observed

feeding, differ from other figs in their low levels of fiber (38.1% versus 50.8% ADF), high simple sugar content (12.1% versus 2.9% WSC), and high ratios of calcium to phosphorus (26.7 versus 8.9). The mature fruits of *Spondias mombin*, the most frequently consumed non-*Ficus* fruit, have lower levels of ADF (20.7% versus 41.3%) and higher sugar levels (31.2% versus 16.8%) than other fruits consumed. Similarly, with the exception of *Cecropia*, flowers have low fiber and high protein and sugar content, and are heavily consumed during their brief periods of availability; during certain months they account for over 40% of feeding time (Chapter 3). Even though mature leaves provide some energy, either via their small contributions to simple sugar intake or via fermentation of structural carbohydrates in the hindgut (Milton *et al.*, 1979; Milton and McBee, 1983), fruits, ripe figs, and flowers provide the main sources of ready energy.

Mineral Content and Food Selection

As observed by Silver *et al.* (2000), mature leaves apparently are important sources of minerals, especially of calcium, iron and manganese; they generally exceed young leaves in mineral content, making them potentially valuable food sources, in spite of their higher fiber levels. The average values of various minerals in leaves, fruits, and flowers closely resemble those reported by Silver *et al.* (2000, Table 1) for *Alouatta pigra*. Mineral values for foliage at La Luz are higher than those reported by Yeager *et al.* (1997); however, as found in this study, the leaves eaten were deficient in calcium, iron, and phosphorus in comparison to estimated requirements for non-human primates (NRC, 1978).

Consumption of certain substances (foods with high levels of secondary plant metabolites

or otherwise poor nutritional profiles, soils and other inorganic materials) by folivorous primates has been linked to mineral content (e.g., Oates, 1978; Oates *et al.*, 1980).

The selection of certain food resources can be explained in relation to mineral content. The minimum daily requirement of iron recommended for primates, 200 mg/kg dry matter of feed, is met only by some mature leaflets of *Gliricidia sepium* (Appendix III). In spite of their high alkaloid levels (Glander, 1977; Mowry, personal communication), the leaflets of *Gliricidia sepium* are occasionally consumed in small amounts, perhaps in part to meet iron needs. Similarly, the mature leaves of *Terminalia oblonga* are eaten in spite of their high content of protein-binding tannins; however, they are one of the few resources to meet manganese requirements. Young leaves of *Spondias mombin*, also eaten sparingly, meet phosphorus requirements. Extensive fig consumption, in spite of their high fiber levels, may be related to their high calcium content and high protein to fiber ratios, a pattern seen throughout the tropics (O'Brien *et al.*, 1998; Silver *et al.*, 2000). No measured food approaches sodium requirements, and the howlers may have difficulty maintaining sodium balance. However, not all foods were collected for nutritional analyses, and of those that were collected, due to limited sample quantities, not all were analyzed for mineral content. It is possible that one of the food sources *not* examined for mineral content has high enough sodium levels to meet the howlers' needs.

Food Intake and Energy Expenditure

The feeding rates (660 g/day fresh matter, 173 g/day dry matter) and caloric intakes estimated for the howlers in La Luz are roughly similar to those estimated by

other researchers for howler monkeys. The daily intakes by weight are lower than values reported for *A. palliata* in Panama (782 g/day fresh matter, 258 g/day dry matter; Nagy, 2001) and *A. seniculus* in Columbia (1230 g/day fresh matter, 266 g/day dry matter; Gaulin and Gaulin, 1982); however, they exceed those reported for Venezuelan red howlers (544 g/day fresh, 151 g/day dry; Edwards, 1995), suggesting food intake rates within the range of variation observed for the genus. Energy expenditure, as estimated via ADMN, is below the field metabolic rate estimated by Nagy and Milton (1979) of $1.98 \times \text{BMR}$ (approximately 85 kcal/kg body weight), and exceeds that estimated by Coelho *et al.* (1976) for *A. pigra* (~350 kcal/day).

Although the many assumptions involved in calculating the energy intake and expenditure preclude a definitive finding on the exact caloric intake and metabolic needs of the howlers, biases in the estimates are the same for all individuals, meaning that energy budgets are suitable for internal contrasts. Based on these estimates, it appears that females may experience more energetic stress than males. Given the metabolic costs of pregnancy and lactation, it is not surprising that females had the highest energy deficits. Like other conspecifics (Serio-Silva *et al.*, 1999), females at La Luz increase energy intake during pregnancy and lactation. However these increases do not meet their higher energetic demands, and reproductive females face the highest energy deficits. If females are metabolizing energy stores during reproduction, presumably they build energy stores during periods when they are not pregnant or nursing dependent offspring. However, I do not have enough data on nonreproductive females to test this hypothesis.

It seems likely that females endure periods when caloric intake does not meet their energetic needs, during which they depend on the metabolization of body tissues; presumably, they rely on deposition of fats when neither pregnant nor lactating to buffer the later costs of reproduction.

Feeding Competition and Net Energy Gain

Socioecological theory predicts that individuals in larger groups will face higher levels of within-group feeding competition, leading in turn to reduced foraging efficiency (Janson and Goldsmith, 1995; Sterck *et al.*, 1997; van Schaik, 1989). Competition may lead to reduced net energy gain for individuals in larger groups, via reduced food intake, increased energy expenditure related to foraging, or both (e.g., Janson, 1988a). Although the groups at La Luz do not differ in their average caloric intake, the energy expenditures do differ slightly. It appears, however, that group size is not the primary factor influencing net energy gain: the largest and smallest group had nearly identical median net energy gain (based on median values; Figure 4.1). These small differences are consistent with the competitive regimes that generally characterize folivorous primates, in which overall levels of within-group competition are low, most competition comprises within-group scramble, and the costs of living in large groups, at least in terms of feeding competition, are relatively low (Koenig *et al.*, 1998; Steenbeck and van Schaik, 2001).

However, these results do not indicate that feeding competition is therefore unimportant for howlers at La Luz. As observed for other folivorous primates (*Gorilla gorilla*: Watts, 1988; *Presbytis thomasi*: Steenbeck and van Schaik, 2001; *Procolobus badius*:

Gillespie and Chapman, 2001), group foraging does entail costs, especially for females. However, these costs are lower than those faced by primates (both frugivorous and folivorous) with less abundant, patchier, and more energy-rich food sources (e.g., Janson, 1988a; Koenig, 2000). Additionally, the costs of competition may not necessarily be reflected in net energy gain. Larger groups may compensate for potentially reduced food intake through larger home ranges and longer day journey lengths to increase the number of food sources encountered per day (Janson and Goldsmith, 1995; Isbell, 1991; Chapter 5). The costs of competition are, therefore, not reflected in net energy gain, and may be reflected in reduced time for other activities, such as resting, socializing, mating, and vigilance (Cuthill and Houston, 1997; Stacey, 1986). Costs of within-group scramble competition may be reflected in increased travel costs, discussed in the next chapter.

CHAPTER 5

RANGING BEHAVIOR

INTRODUCTION

Ranging behavior is thought to reflect foraging effort, which, in many primate species, increases with group size and concomitantly high levels of feeding competition (Isbell, 1991; Janson and Goldsmith, 1995). Examination of variation in home range size and daily path length can therefore be used to examine the strength of feeding competition acting in a population. Among many primate species (particularly non-folivores), measures of ranging activity increase with group size and decrease with habitat quality on both long (annual measures of home range) and short (day journey length) time scales (Clutton-Brock and Harvey, 1977; Gillespie and Chapman, 2001; Isbell, 1991; Janson and Goldsmith, 1995; Milton and May, 1976; Steenbeck and van Schaik, 2001). Presumably, individuals in larger groups experience more within-group feeding competition (van Schaik, 1989; Sterck *et al.*, 1997). Unless individual food intakes are reduced, larger groups are predicted to require larger home ranges and longer day journey lengths in order to meet the foraging needs of all group members (Isbell, 1991; Janson and Goldsmith, 1995). These relationships are not universal: relationships between ranging and group size are generally much weaker for folivorous primates (Janson and Goldsmith, 1995), presumably because leaf sources are less easily depleted. However, analyses accounting for variables of habitat quality and social stability have demonstrated

minor, but significant, relationships between group size and ranging parameters in folivores (e.g., Gillespie and Chapman, 2001; Steenbeck and van Schaik, 2001).

Although mantled howling monkeys rely on foliage as a key food source, most populations also consume substantial amounts of fruit (Glander, 1978, 1981; Milton, 1980; Stoner, 1993). Fruit exploitation generally reflects the availability of fruit in the habitat, with consumption tracking seasonal availability. Remis (1997b) uses the term “seasonal frugivores” in discussing similar patterns of opportunistic fruit exploitation by lowland gorillas; this term applies equally well to howlers. Howlers opportunistically exploit fruits – a patchier and more easily-depleted resource with a higher rate of energy intake per unit feeding time (Chapter 4) – when they are more widely available in the habitat. It is reasonable to expect that howlers will therefore show variation in foraging effort throughout the year, with intra-group competition increasing during periods of increased fruit consumption. Consistent with such expectations, among lowland gorillas (Remis, 1997a) and proboscis monkey (Boonratana, 2000) measures of ranging are higher when fruit comprises a larger portion of the diet.

In this chapter, I describe the ranging behavior of the howlers in La Luz. Given the established relationships between ranging and aspects of habitat quality, it is expected that ranging patterns will differ between groups and between this and other populations of other howlers. Home range size is known to vary with habitat quality (i.e., food density and nutritional value); given the high-quality foliage available at La Luz (Chapter 4), I do not expect home ranges at La Luz to be substantially bigger than at other sites. However, the relatively low density of food trees, the howlers may have to travel more to

locate certain resources, and I predict that at La Luz day journey lengths will exceed those observed for conspecifics at less-disturbed sites. Between groups, within-group scramble competition should lead to increased patch depletion, reducing the density of food resources and increasing the need to search for food patches. I therefore predict that larger groups will have larger home ranges and longer day journey lengths than smaller groups. Finally, within groups I expect that ranging area and day journey length will increase as the consumption of less-widely distributed fruits increases; these differences may reflect both increased scramble competition for an easily-depleted resource and the lower abundance of fruit food trees in the habitat. Data presented on home range size, range overlap, intensity of range use, and day journey length allow me to explore the basic ranging patterns of the population, to contrast these with the ranging behavior of conspecifics at other sites, and to explore the role of habitat characteristics and intragroup feeding competition in shaping the ranging behavior of howling monkeys.

METHODS

All accessible feeding trees were mapped using differential GPS. I used two Ashtech ProMARK X 10-channel GPS receivers. One unit was connected to an external high-gain antenna and used to map trees, while the other was connected to an external multipath-resistant antenna and served as a base station for post-processing differentially collected GPS fixes, providing 3-m accuracy. Analyses of home ranges were conducted in ArcView GIS 3.2 software with the Animal Movement Analysis Extension (Hooge and Eichenlaub, 1997). For the purposes of estimations of annual range size, I exclude data

collected on Group 2 during the last 3 months of the study, as this group underwent a radical shift in ranging area, abandoning their former range in response to social disturbance caused by the replacement of the previous resident male by two young males (see Chapter 6).

The locations of feeding trees were used to estimate home range size via two methods. First, I estimated home range sizes using the commonly employed Minimum Convex Polygon (MCP) method (White and Garrott, 1990). All points are bounded by the smallest-area polygon with internal angles less than or equal to 180°. Although the MCP method is commonly used in primatological studies, it can include large areas of habitat not actually used by the study groups (White and Garrott, 1990). I therefore also used a GIS-based method developed by Ostro *et al.* (1999), Digitized Polygons (DP), which provides more accurate estimates of home range size and shape. Day journey paths were mapped based on movements between feeding trees and are calculated as straight lines between consecutive feeding trees. These lines were then surrounded on each side (“buffered” in GIS terminology) by a 10-meter width, producing a 20 m wide band with the approximate travel path in the middle. Twenty meters was chosen because it represents both the maximum error of the GPS points and the minimal group spread. The resulting shapes, based on each day’s paths, were joined into one shape. Small internal lacunae (gaps) were included with the home range. Finally, the 20 m buffer zone was trimmed based on the borders of the MCP home range.

Day journey lengths were calculated by summing the straight-line distances between consecutive feeding trees. Trees used for travel were also included to increase

accuracy. Nevertheless, the assumption of straight paths between points underestimates travel distance (Isbell *et al.*, 1999). Only paths from complete (10-12 hours) days are included in these analyses. Travel velocity was calculated by dividing the day journey length by time in minutes spent moving (derived from group activity budgets; Chapter 3). Both range lengths and sizes are presented as planimetric distances and areas, respectively. Given the topography of the site, actual distances traveled and surface areas used are likely to be larger (Sprague, 2000). However, the lack of detailed topographic maps for the area prevents analysis of the actual surface area used.

To determine if the howlers were using certain habitats more frequently than encountered, I used a chi-square test to compare the number of days spent in each habitat type with the expected number of days based on the habitat composition of their entire home range. For this analysis I followed Stoner (1996). The habitat in which the howlers were first encountered each day was used; to reduce interdependence between observations, only the first and third days of each follow are used. To characterize the intensity of range use, I used the amount of time spent feeding at each marked tree to calculate a surface that models the time spent feeding. This process produces a topography of feeding intensity and is analogous to a topographic map representing elevation; in this case, total feeding seconds, rather than elevation data, are used to provide a visual representation of the intensity of feeding in a given area. I used ArcView's surface analyst extension to interpolate a surface of each group's feeding intensity using the location of each feeding tree as point locations and total feeding seconds as the z-value data source. Total feeding seconds were log-transformed to

reduce the number of extreme values and to approximate a normal distribution. Based on these values, I calculated a triangulated surface of each group's feeding behavior in order to create a continuous surface estimating the concentration of feeding in areas of the ranges without data points. Although triangulation produces jagged surfaces with sharp slopes, it is the most appropriate interpolation method for unevenly spaced data points and surfaces with high relief features (Hu, 2001). The resulting surfaces were then circumscribed based on the borders of the digitized polygon home ranges so that areas which the howlers never entered are excluded from the final topography.

RESULTS

Annual Home Range Size and Overlap

The MCP home ranges are shown in Figure 5.1. Based on these estimates, the home range size of Group 1 was 21.9 ha, 15.8 ha for Group 2 (first 9 months only), and 21.3 ha for Group 3. However, the MCP method produces large home ranges that include areas not actually entered by the groups. When home ranges are calculated using the DP method, smaller home ranges result that more closely encompass the areas used by the groups (Figure 5.2). Based on the DP method, home range size estimates are 20.3 ha for Group 1, 13.7 ha for Group 2, and 17.3 ha for Group 3. Regardless of method used, the largest group, Group 1, had the largest home range, while Group 2, the smallest group, had the smallest home range. Differences in calculated home range size between these two methods approach significance (Wilcoxon signed ranks test: $Z = -1.064$, $P = 0.109$, $N = 6$).

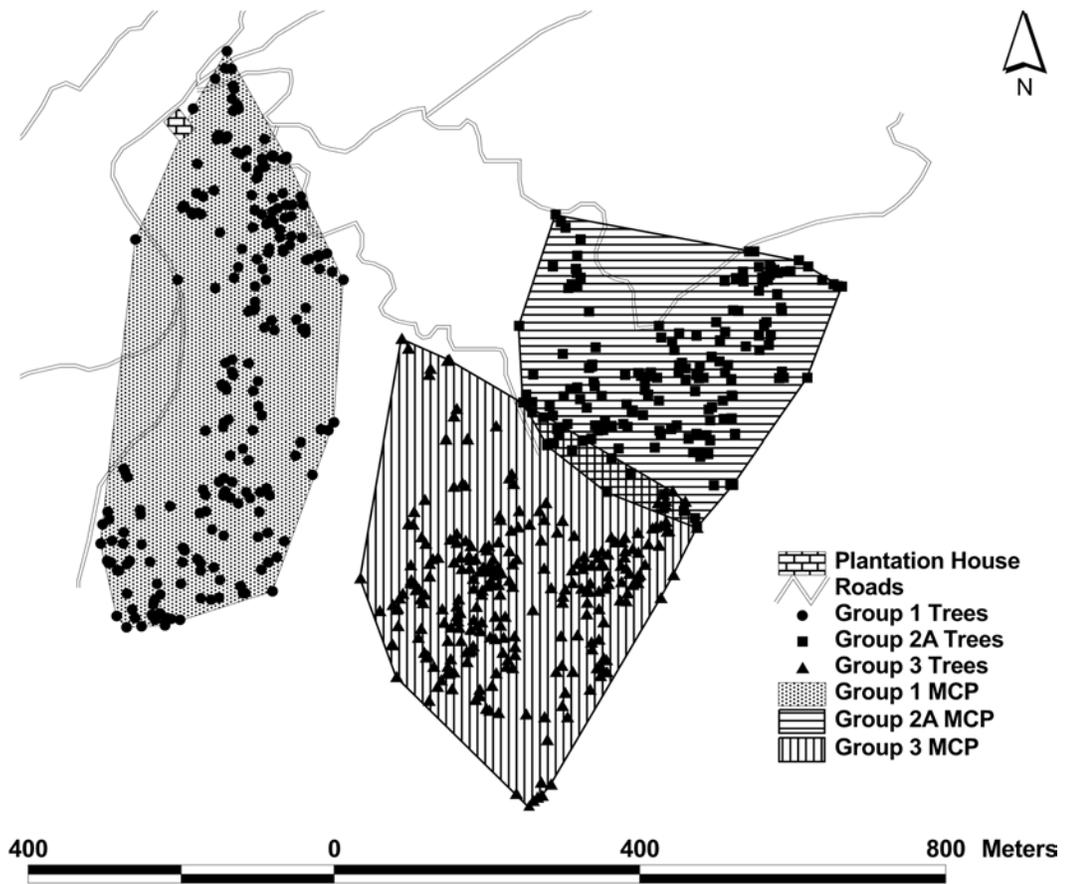


Figure 5.1. Feeding tree locations and minimum convex polygon (MCP) home ranges of study groups. Home ranges are calculated by bounding all feeding trees in the least-area polygon with no internal angles exceeding 180° .

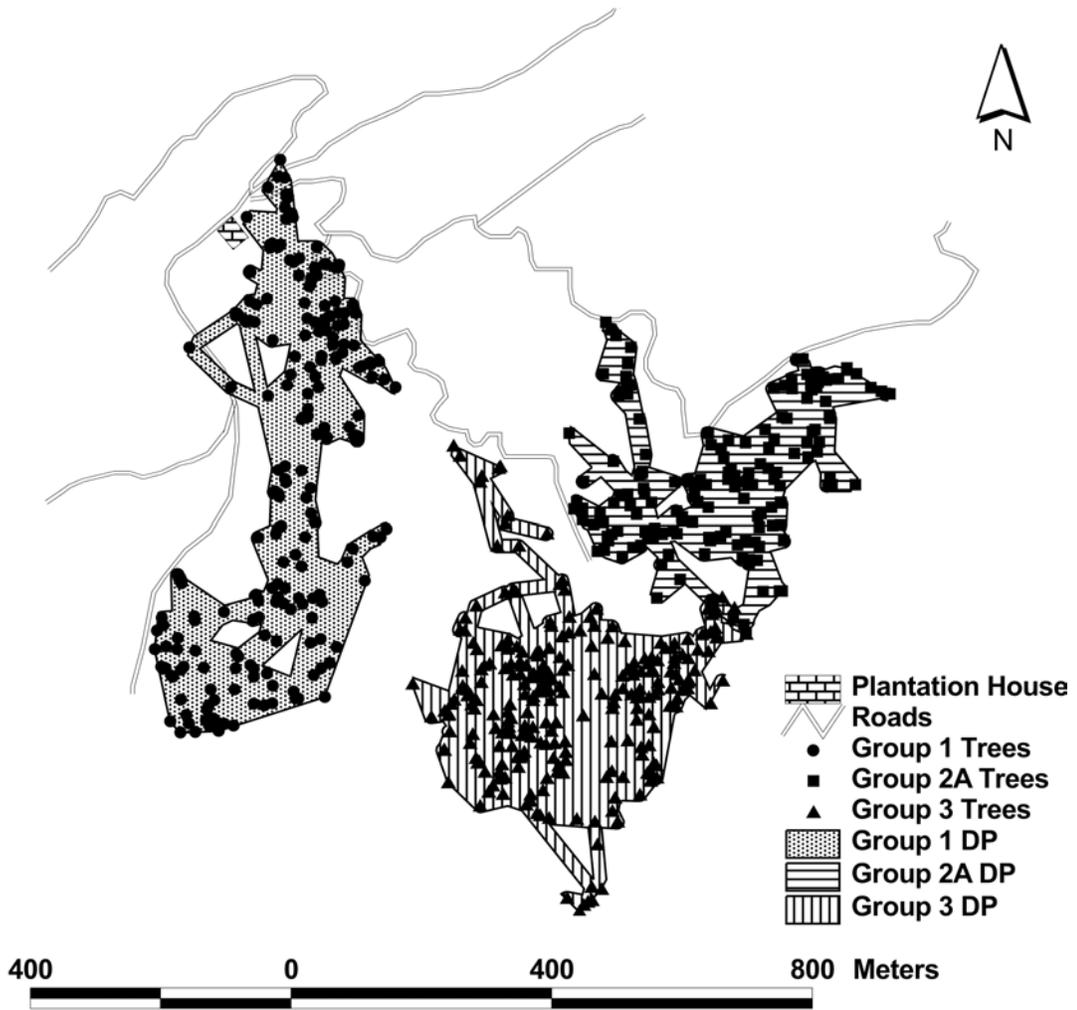


Figure 5.2. Feeding tree locations and digitized polygon (DP) home ranges of study groups. Home ranges are calculated by plotting the paths between feeding trees and then adding a 10 meter buffer to each side of the line.

A plot of the cumulative area used by each group over the course of the study (Figure 5.3) yields a curve that approaches an asymptote for both Groups 1 and 3, suggesting that most of their annual home range was characterized during the course of the study. The curve levels out for Group 2 after Month 7 (April 2000) of the study; however, the area used begins to increase steadily during the last 3 months of the study. This increase corresponds with social disturbance and a shift to a previously unoccupied area by the group. However, the leveling of the curve before this point suggests that the estimate of range size from the first 9 months of the study accurately estimates total home range size before range abandonment.

Figures 5.2 and 5.3 also demonstrate that there was little range overlap between the groups; additionally, there was little overlap with other howler groups not included in the study. Group 1 shared 0% of its range with the other study groups, Group 2 shared 7% of its range with Group 3, and Group 3 shared 5% of its range with Group 2. Additionally, Group 1 shares only the southern tip of its range with another group, while Group 2 shares its northeastern area with another group. Solitary animals and transient groups of 5 or fewer individuals are sometimes seen both within group ranges and in the interstices between groups.

Monthly Range Area

In addition to the size of the annual range, I considered the area used by each group on a month-by-month basis: the DP method was used to calculate range areas

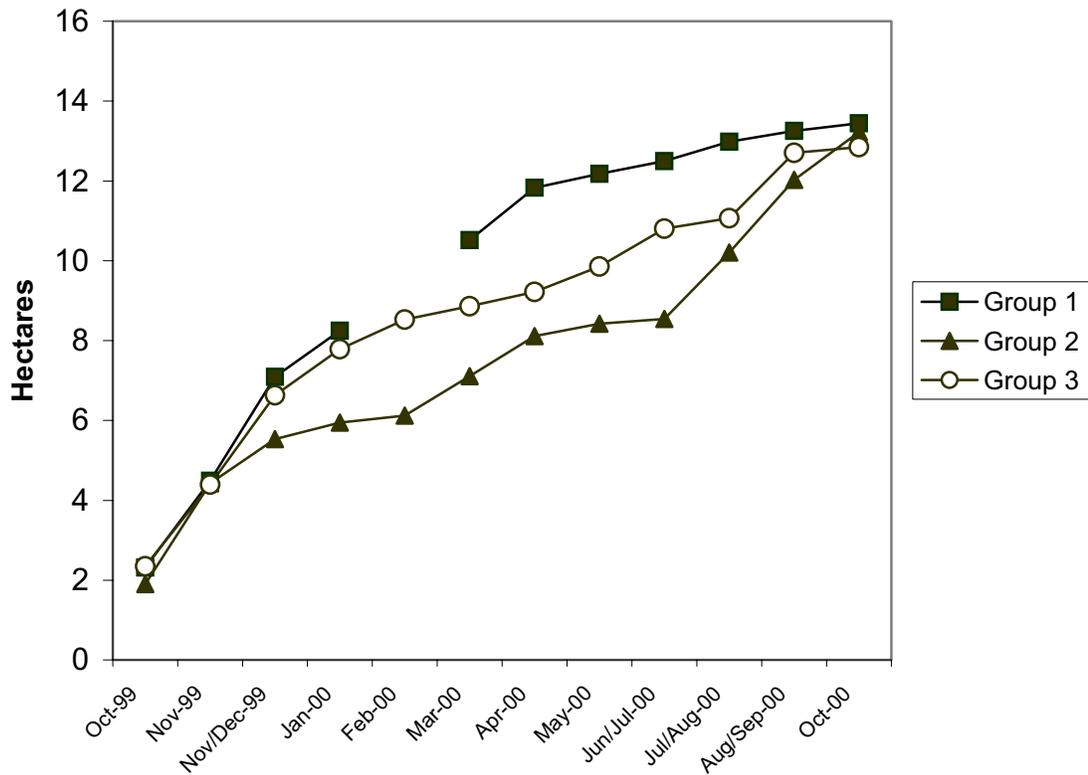


Figure 5.3. Cumulative area used by the study groups.

from the travel paths from the 4-day follows conducted on each group to provide an estimate of monthly range use. The area used by each group during the 4-day follows averaged 3 hectares for all groups over the course of the study (Table 5.1). The average monthly area used by Group 1 was 3.59 ha (range 2.31 – 4.99, SD \pm 0.73, N = 11), for Group 2 was 2.21 ha (range 1.00 to 3.62, SD \pm 0.89, N = 12), and for Group 3 was 3.22 ha (range 1.51 – 6.50, SD \pm 1.40, N = 12). As with annual home range size, the areas used on a monthly basis were higher for larger groups. Area used per month also shows

Table 5.1. Area used on a monthly basis (ha) by the three study groups.

Group (No. Inds.)	Average Monthly Area	Average Dry Season Monthly Area	Average Wet Season Monthly Area
Group 1 (26)	3.59 ± 0.73	3.94 ± 0.81	3.40 ± 0.67
Group 2 (15)	2.21 ± 0.89	2.11 ± 0.94	2.27 ± 0.92
Group 3 (20)	3.22 ± 1.41	2.40 ± 0.75	3.81 ± 1.51
<i>La Luz Population</i>	<i>2.99 ± 1.19</i>	<i>2.74 ± 1.11</i>	<i>3.16 ± 1.23</i>

seasonal variation. For Groups 2 and 3, monthly areas were larger in the wet season (Table 5.1). The average monthly area used for all groups was 2.74 ha during the dry season (± 1.11 SD, $N = 14$) and 3.16 ha during the wet season (± 1.23 SD, $N = 21$).

There are no significant seasonal differences in the size of the monthly area used ($F_{[1,33]} = 1.406$, $P = 0.310$). Monthly ranges differ between groups, the larger groups having larger ranges as expected; these differences are significant, ($F_{[2, 32]} = 5.369$, $P = 0.010$), with Group 1 having a significantly larger monthly areas than Group 2.

Habitat Selection and Intensity of Range Use

The home range of Group 1 comprised 32% coffee cultivation, 25% regeneration, 38% secondary forest, and 5% other (abandoned coffee, other agriculture, etc.). Group 2's home range was 90% coffee, 23% regeneration, and 3% older secondary forest. Group 3 was intermediate, with 74% of its range consisting of coffee, 23% of

younger regeneration, and 3% of older secondary forest. Chi-square tests comparing the number of days spent in each habitat with the expected number of days based on the habitat composition of the home ranges reveal no significant differences between observed and expected values for any of the groups, although Group 1 did spend more time than expected in areas of coffee cultivation, and, in fact, all groups were most frequently found in shade coffee areas. However, Group 1 also spent large amounts of time in areas of regeneration and secondary forest, and if these two habitat types are considered together, Group 1 was most frequently found in these areas of forest regeneration.

Figure 5.4 shows the interpolated surfaces of feeding intensity for all 3 groups. Rather than concentrated core areas, all groups have several small patches of high-intensity use scattered throughout their ranges. There are also several patches of low-intensity use in all groups' ranges. A comparison with the location of habitat patches (Figure 5.5) demonstrates that all groups have areas of high-intensity foraging in areas of active coffee cultivation. Group 1's areas of high use fall largely in coffee plantation in the northern part of their range and in regenerating and uncultivated areas in the southern part of their ranges. Group 2's areas of intense foraging are scattered throughout areas of shade coffee. Group 3 has a central area of intense foraging that falls largely in shade coffee. Areas of frequent use did not overlap with those of other groups. The presence of high use areas in regions of shade coffee cultivation suggests that the shade trees in La Luz provide important resources for the howlers and that groups are not necessarily dependant upon patches of less-disturbed habitat for their survival.

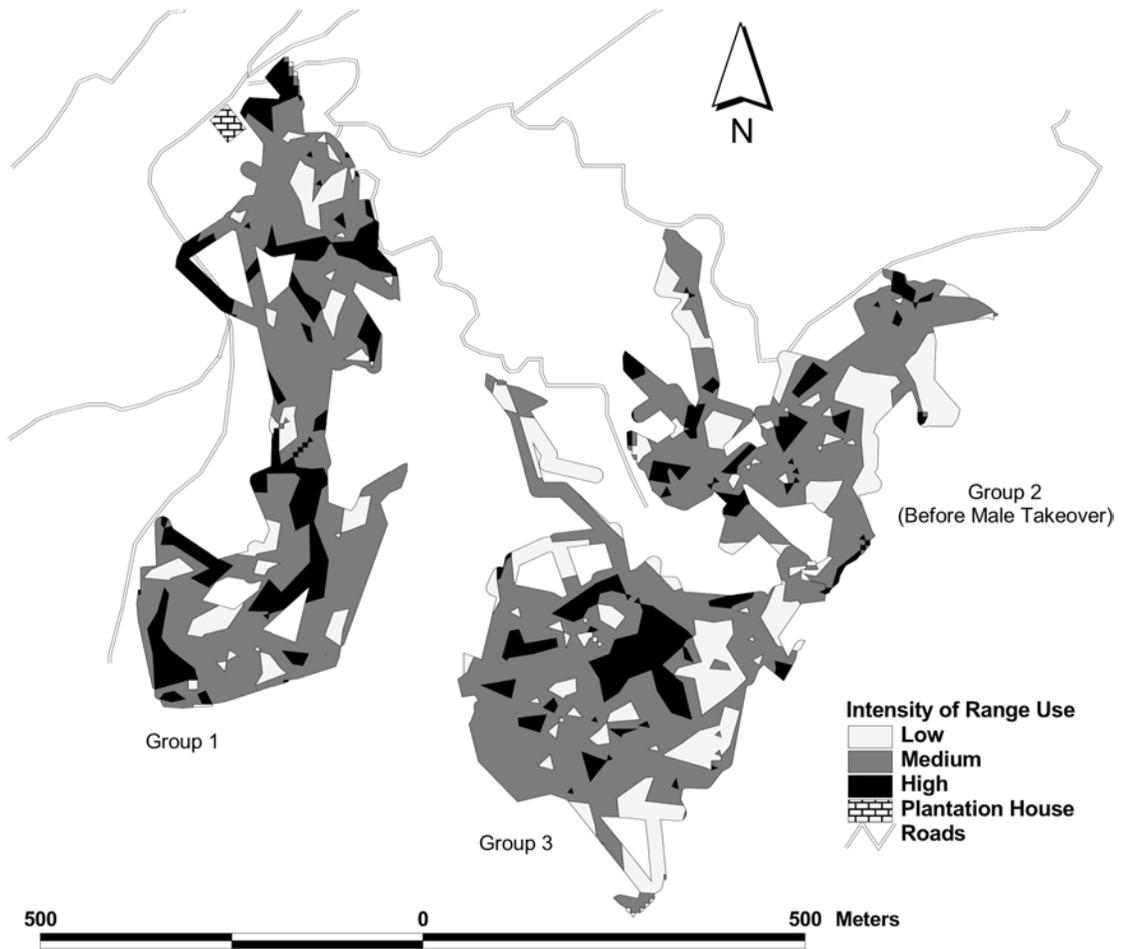


Figure 5.4. Topographic surfaces of intensity of habitat use by the three howler groups. Total feeding seconds are used to model a surface representing the time spent feeding.

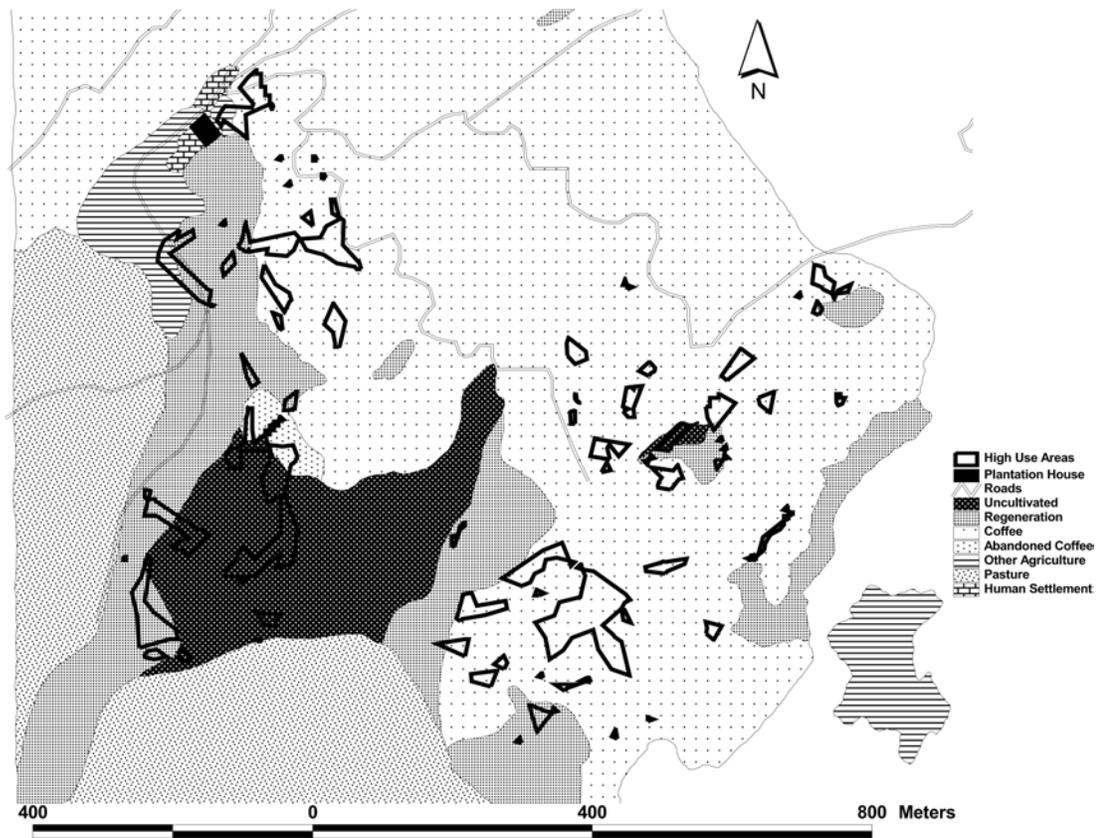


Figure 5.5. Locations of areas of high-intensity foraging in relation to habitat.

Day Journey Length and Travel Rate

Day journey lengths averaged 617 m for all groups during the course of the study (Table 5.2). As with home range size, day journey lengths were higher for larger groups. Day journey lengths also show seasonal variation and were longer in the wet season; the average daily travel distance for all groups during the dry season was 535 m (± 269 SD, $N = 50$) and 675 m during the wet season (± 295 SD, $N = 70$). Day journey lengths differ significantly between groups ($F_{[2,32]} = 5.034$, $P = 0.013$), with Group 1 traveling significantly farther than Groups 2 and 3. Day journey length does not differ significantly between seasons ($F_{[1,10]} = 2.634$, $P = 0.136$). While moving, the howlers travel an average of 1.3 ± 0.4 meters per minute; although rates are slightly higher for larger groups and during the wet season, these differences are not significant based on one-way ANOVAs. Average day journey length per month correlates with total area used per month when all data are pooled ($r_s = 0.536$, $P = 0.001$, $N = 35$), although within groups these relationships are positive but not significant.

Phenophase Availability and Seasonal Variation in Ranging Patterns

The habitat-wide abundance of mature leaves, young leaves, fruits, and flowers varied over the course of the study and roughly tracked monthly precipitation (Chapter 2). Both new leaves and flowers are produced largely during the dry season, when many trees drop mature leaves. Although the production of all fruits peaks in the dry season (Figure 5.6, dashed line), this peak largely represents the production of hard, dehiscent

Table 5.2. Daily Journey Lengths (m) traveled by the three study groups.

Group (No. Inds.)	Average Total DJL	Average Dry Season DJL	Average Wet Season DJL
Group 1 (26)	752 ± 292	709 ± 333	779 ± 270
Group 2 (15)	568 ± 256	542 ± 256	608 ± 254
Group 3 (20)	572 ± 301	446 ± 186	664 ± 337
<i>La Luz Population</i>	617 ± 292	535 ± 269	675 ± 295

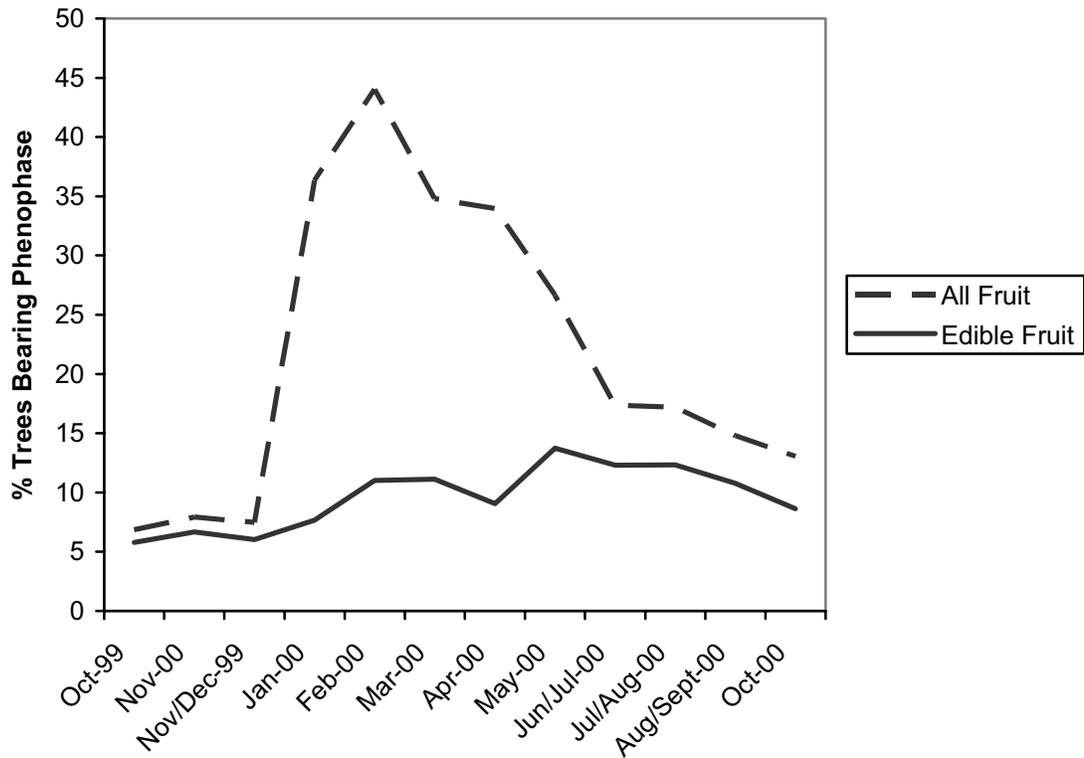


Figure 5.6. Percent of trees in vegetation enumeration bearing fruit (dashed line) and percent trees bearing edible fruit (solid line).

fruits typical of the leguminous tree species that dominate the vegetation community in the shade coffee plantation. Howlers ignore these fruits in favor of succulent fruits. When species whose fruits contributed to the howlers' diets are considered alone (Figure 5.6, solid line), fruit production increases during the dry season but peaks during the rainy season, during periods of increased fruit consumption (Chapter 3).

Table 5.3 describes the Spearman rank correlation coefficients between monthly ranging area, average daily journey length per month, and monthly indices of plant part production (food species only). On a group by group basis, relationships between the ranging variables the production of edible plant phenophases are variable. Ranging has variable relationships with mature leaf production (weakly positive or negative, with no consistent pattern). Young leaf and flower production essentially show no relationship with ranging. Consistent with expectations, ranging does generally show a positive relationship with fruit production, although within groups these relationships are not always consistent between monthly area and day journey length. However, when data for all groups are pooled, both the average monthly ranging area and average day journey lengths show positive correlations with the availability of fleshy fruits (monthly area: $r_s = 0.587$, $P = 0.045$; DJL: $r_s = 0.469$, $P = 0.124$), suggesting that for the La Luz howlers as a whole, foraging effort does increase in response to fruit availability.

Fruits comprise approximately 30% of the howlers' annual diet, with fruit consumption peaking during the wet season at over 45% of the diet (Chapter 3). A Spearman rank correlation of ranging variables and monthly proportions of various food

Table 5.3. Spearman rank correlation coefficients between ranging variables and indices of phenophase production (for feeding trees only).¹

Ranging Variable	Mature Leaves	Young Leaves	Fruits	Flowers
G1 Monthly Area	-0.574 ^T	-0.055	0.445	0.1
G2 Monthly Area	0.270	-0.137	-0.203	-0.056
G3 Monthly Area	0.350	-0.231	0.441	-0.245
Average Monthly Area	0.130	0.105	0.587*	-0.399
G1 DJL	0.264	0.064	-0.264	-0.191
G2 DJL	-0.411	-0.399	0.616*	0.011
G3 DJL	0.217	0.336	0.427	-0.315
Average DJL	-0.112	-0.021	0.469	-0.133

¹N = 11 for all G1 cells, N = 12 for all other cells; all tests are 2-tailed. ^T $P < 0.10$, * $P < 0.05$.

types in the diet (Table 5.4) suggests that there are variable relationships between individual groups' ranging and the amount of fruit and other phenophases in the monthly diet. Mature leaf consumption shows no strong relationship with monthly ranges and positive relationships with day journey length, significantly so for Group 3. Young leaves generally have slightly negative relationships with ranging. For fruit consumption, relationships on a group by group basis are weak and variable. However, the average monthly ranging area shows a significantly positive relationship with fruit consumption with the average amount of fruit in the monthly diet ($P = 0.031$) and a significantly negative correlation between monthly area used and the average amount of young leaves

Table 5.4. Spearman rank correlation coefficients between ranging variables and diet composition.¹

Ranging Variable	% Mature Leaves in Diet	% Young Leaves in Diet	% Fruit in Diet	% Flowers in Diet
G1 Monthly Area	-0.482	0.318	-0.118	0.164
G2 Monthly Area	-0.203	-0.322	0.28	0.217
G3 Monthly Area	0.371	-0.182	0.238	-0.270
Average Monthly Area	0.140	-0.608*	0.622*	0.028
G1 DJL	0.391	-0.218	0.064	-0.374
G2 DJL	0.27	-0.354	-0.165	0.333
G3 DJL	0.601*	-0.315	0.364	-0.340
Average DJL	0.392	-0.182	-0.014	-0.469

¹N = 11 for all G1 cells, N = 12 for all other cells; all tests are 2-tailed. * P < 0.05

in the diet ($P = 0.036$). Average day journey length, however, shows a slightly negative, non-significant relationship with both fruit and young leaf consumption. Although there is no strong relationship between day journey lengths and any aspect of monthly diet, the relationship between monthly area used and fruit consumption is consistent with expectations that the howlers increase foraging effort during periods of fruit consumption.

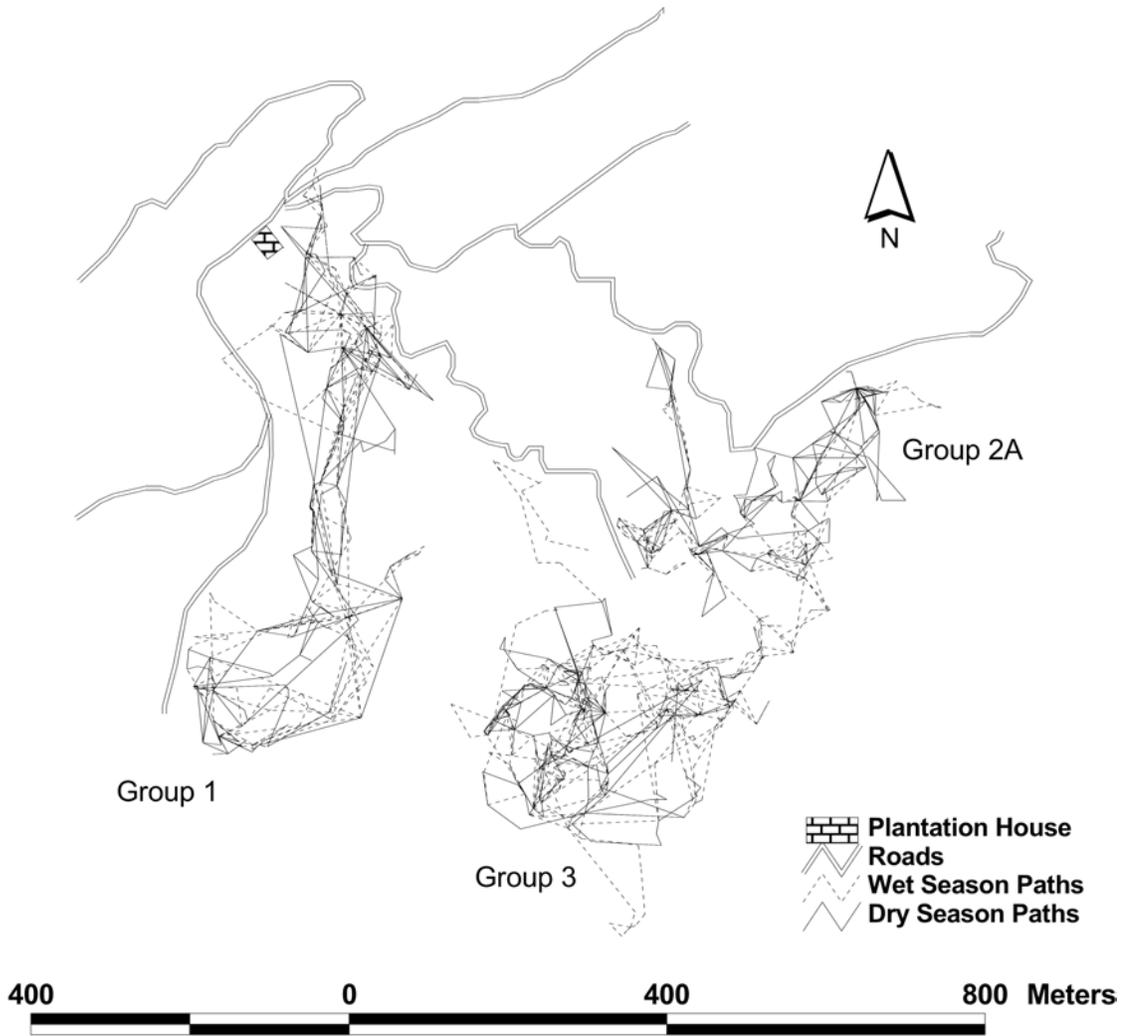


Figure 5.7. Travel paths in wet (dashed lines) versus dry (solid lines) seasons.

While fruits provide a nutritious, carbohydrate-rich food source, they are also less abundant and more patchily distributed than the leaves that comprise the majority of the howlers' diet. As described above, there is a significant difference in the day journey lengths between seasons, with day journey lengths being longer during the wet season. This apparent increase in foraging effort is reflected in other aspects of their ranging behavior. Figure 5.7 presents the travel paths of all groups during the wet and dry seasons. During the wet season, all groups not only traveled further each day, but also used more areas of their ranges, making more frequent excursions to peripheral areas of their ranges. These excursions generally were to large fruiting trees during periods of production of sweet, fleshy fruits.

Tree Density and Distribution

Tree abundance and distribution in the home ranges differ between groups; for example, the average number of marked feeding trees per hectare of home range varies between groups, with the largest groups having the fewest trees per hectare of home range (Group 1: 10.3/ha; Group 2: 18.1/ha; Group 3: 15.3/ha), suggesting that intergroup differences could simply result from feeding tree density and distribution. Given that fruit feeding trees are less widely distributed in both space and time than leaf feeding trees, longer day journey lengths could simply be a result of the spatial distribution of fruiting trees. To explore the effects of food tree distribution on ranging patterns, I considered the average distance between all feeding trees used during each 4 day follow, between trees where fruit was consumed, and between trees where other

phenophases were consumed. Average distance was calculated as the average of all possible pair-wise distances between feeding trees. The average distance between feeding trees was 132 ± 56 m for Group 1, 71 ± 25 m for Group 2, and 79 ± 18 m for Group 3. There are significant differences between groups in the average distance between all monthly feeding trees ($F_{[2,32]} = 9.590, P = 0.001$), with Group 1's trees being farther apart than those of the other two groups. However, there were no significant seasonal differences in the average distance between all feeding trees ($F_{[1,33]} = 2.102, P = 0.157$).

The average distances between fruiting trees were larger than those between trees used for other types of food (Group 1: 176 m vs. 152 m; Group 2: 107 m vs. 88 m; Group 3: 124 m vs. 90 m). However, these differences are significant only for Group 3 ($F_{[1,22]} = 10.333, P = 0.004$). Additionally, while there are positive Spearman rank correlation coefficients between day journey length and the average distance between fruit trees, none of these relationships are significant. It is therefore possible that some or all of the variation within groups in foraging effort may reflect differences in the distribution of fruit versus non-fruit feeding trees. However, Groups 1 and 2 demonstrate no significant within-group differences in the distances between trees providing fruits and trees used for leaves and flowers; it therefore seems unlikely that seasonal variation in the groups' ranging behavior results exclusively from the spatial distribution of fruit trees.

Summary of Ranging Behavior at La Luz

Annual home range sizes at La Luz vary from 14 to 20 hectares, with larger groups having larger home ranges. Little range overlap is observed. Areas used on a monthly basis (1.0 to 6.5 ha) and day journey lengths (244 to 1,133 m) also show positive relationships with group size. Differences between groups also correlate with habitat differences: larger groups have larger home ranges, but their ranges also have lower densities of feeding trees and comprise less shade coffee. Seasonally, both monthly area used and day journey length increase during the wet season, when more fruits and mature leaves are included in the diet. There is a positive relationship between the average values for these ranging variables and the production of edible fruit, but on a group-by-group basis these relationships are generally variable and not significant. Seasonal variation in ranging behavior does not correlate with the average distance between feeding trees (considered as a whole or as fruit versus other feeding trees).

DISCUSSION

Given that the habitat in La Luz is disturbed, with low tree species diversity and stem density, one might expect the La Luz howlers to have large home range sizes and day journey lengths in comparison to conspecifics at other sites. However, the home range sizes of the La Luz howlers fall well within the range of variation for the species (Table 5.4). Range sizes at sites where studies encompassing a full annual cycle have been conducted vary from 9 ha (Glander, 1978) to 60 ha (Estrada, 1984). Relatively small home ranges do not reflect unusually small group sizes at La Luz: the home range area

per individual or per kilogram of group biomass also falls at the low end of the range of variation. Given the low population density of Mombacho howlers, the relatively small home ranges of the howlers at La Luz probably do not reflect crowding or habitat contraction, as has been observed at other sites (Baldwin and Baldwin, 1972). Although the density of individual trees is lower at La Luz than at less-disturbed habitats, several of the tree species used have high densities and often have large basal areas, suggesting that resource availability may not be as low as stem density or tree species diversity would suggest.

Perhaps more importantly, as measured by average protein to fiber ratios, the foliage at La Luz is of relatively high quality (Chapter 4), which may mean that. There is a relationship between average protein and fiber ratios to the *population* biomass of colobines (Oates *et al.*, 1990; Waterman *et al.*, 1988), lemurs (Ganzhorn, 1992), and, possibly, Amazonian howlers (Peres, 1997): areas with higher quality foliage support more primate biomass per unit area, suggesting the carrying capacity of a habitat for folivorous primates relates directly to the average nutritional content of mature foliage. Comparable data for the Mombacho area are not available, as censuses conducted in the area do not account for group overlap (McCann *et al.*, 2003). My intention in highlighting this point is not to compare the group biomasses which I present in Table 5.5 with those published in studies relating primate community biomass to forage quality, but to point out that Mombacho may be able to support a higher density of howlers than is currently observed. The extent to which these population-level relationships are reflected in the ranging patterns of individual groups remains unclear. However, given the high quality forage

available at La Luz and the apparent relationship between forage quality and primate biomass, it seems reasonable to argue the area may be able to support more howlers per unit area than other study sites.

In contrast to the typical sizes of their home ranges, day journey lengths are higher than reported at most other sites (Table 5.5). It is not immediately clear why day ranges should be longer at La Luz than at other sites. Longer day ranges at La Luz probably do not reflect methodological differences in calculating day journey lengths, which are generally calculated by other researchers as distances between successive feeding and travel trees; in fact, given that I do not incorporate topographic effects into my measures, my estimates are, if anything, too low. It is more likely that longer path lengths reflect increased foraging effort on shorter time scales. Given that most food sources are abundant and nutritious in the shade coffee plantation, it is perhaps surprising that the howlers at La Luz should travel further than conspecifics. Day range length is more sensitive to patterns of food distribution than is home range size (Isbell, 1991), and the long distances traveled may relate specifically to the distribution and density of foods containing limiting nutrients, which, based on nutritional analyses (Chapter 4) are ripe fruits and other sources of simple carbohydrates. Edible leaves and fruits of moderate nutrient value (relatively high in fiber and low in simple sugars, such as fruits of *Cecropia peltata* and *Ficus obtusifolia*) are abundant, but energy-rich fruits are not. For example, the fruits of *Spondias mombin* fruits are large and sugar-rich and are heavily exploited when available; however, *Spondias* trees have a density of only 1 individual per hectare, and these individuals have a clumped distribution (Chapter 2).

Table 5.5. Ranging parameters of *Alouatta palliata* at La Luz and other study sites.

Study Site	Group Size	Home Range (ha)	Group Biomass (kg) ¹	Space Used (ha/ind)	Space Used (ha/kg)	Overlap	Day Range (m)	Min Day Range (m)	Max Day Range (m)	D ²	Source ³
Mexico (Los Tuxtlas)	14	60	58	4.29	1.03	--	123	11	503	0.28	1
Costa Rica (Finca La Pacifica)	13	10	56.6	0.77	0.18	--	596	207	1261	3.34	2
Panama (BCI)	17	32	80.5	1.88	0.40	High	443	104	792	1.39	3
Nicaragua (La Luz G1)	25	22	107	0.88	0.21	0%	761	279	1646	2.88	4
Nicaragua (La Luz G2)	15	16	63	1.07	0.25	7%	627	196	1143	2.78	4
Nicaragua (La Luz G3)	19	21	91	1.11	0.23	5%	627	244	1553	2.42	4

¹ Calculated based on published weights for adult males, adult females, juveniles, and infants.

² Defensibility index (Mitani and Rodman, 1979) calculated as Mean Day Range/Home Range Diameter.

³ 1: Estrada (1984); 2: Glander (1978); 3: Milton (1980); 4: Current study.

Howlers derive significant energy from hindgut fermentation (Milton and McBee, 1983). Nevertheless, their ability to assimilate energy from fibrous foods is limited (Milton *et al.*, 1980), and to meet energy needs they must rely on mature fruits and nectar-rich flowers. During the dry season, flowers with high soluble carbohydrate content are superabundant; throughout the rest of the year, the howlers must seek out rarer, more widely-dispersed fruits, necessitating more travel on a short-term basis. Similar patterns are seen among mantled howlers at other sites: conspecifics in seasonal habitats in Costa Rica (Glander, 1978) and Panama (Milton, 1980) also increase ranging during the rainy season, when fruits are more abundant and comprise a higher proportion of the diet. Although the combination of small ranges with long day journey lengths could indicate that territorial defense is a possibility at this site, little territorial behavior (e.g., monitoring of home range edges, intergroup encounters) was observed. The low home range overlap between groups reflects low population density rather than active range defense or high rates of inter-group competition.

Differences between and within groups in ranging behavior may result from factors additional to food competition. Most importantly, differences in food availability certainly underlie some of the differences observed between groups. The large area of secondary forest occupied by Group 1 differs in tree density and species composition from the shade coffee which comprises the ranges of Groups 2 and 3, notably in its paucity of *Ficus costaricana* and *Enterolobium cyclocarpum*. As data were not collected on species composition and phenology in the secondary forest, these potential confounding factors cannot be systematically explored; however, that measures of ranging differ as

predicted between Groups 2 and 3, which occupied very similar habitat, suggests that scramble competition is acting. In fact, a reanalysis of the data with Group 1 excluded demonstrates more highly significant differences between groups in monthly range area and day journey length.

The weak relationship between each group's fruit consumption and its ranging behavior may result from the inclusion of widely-available fruit sources in the diet. Not all fruits are equally rare, in space or in time, and different levels of scramble competition should be expected when feeding on different fruit sources. *Cecropia peltata*, for example, accounts for 10% of annual fruit consumption; however, it comprises 16% of individual trees in the coffee plantation and produces fruit throughout most of the year. Individual patch depletion is offset to some extent by general patch abundance. Effects of scramble competition should be higher than when feeding on less abundant fruit sources. Trees such as *Spondias mombin* and *Manilkara chicle*, which yield large, fleshy fruits, have limited fruiting periods, and occur at low densities, are more likely to produce feeding competition due to their clumped spatial pattern, intermediate size, and less abundant crops.

Although the effects of feeding competition are generally weak for folivores (e.g., Gillespie and Chapman, 2001; Steenbeck and van Schaik, 2001; Watts, 1988) and the relationships between temporal fluctuations in resource abundance and ranging patterns within primate groups over time are highly variable (Di Fiore, 2003), the howlers at Finca La Luz demonstrate patterns of between and within group variation in ranging that are consistent with predicted increases in within-group feeding competition. Between group

comparisons are robust, and seasonal comparisons, while more ambiguous, nevertheless support the hypothesis that fruit abundance affects ranging due to increased feeding competition. These patterns are reflected in increased time spent feeding and traveling by larger groups, and by all groups in the wet versus dry season (Chapter 3). As “behavioral folivores” (Milton, 1998), significant consumption of reproductive parts when available appears integral to the howler foraging strategy. The degree to which shifting dietary bases affect competition levels has remained largely unexplored. Fruits are generally considered not only depletable (thereby engendering scramble competition) but also monopolizable, which should lead to the occurrence of contest competition in some feeding contexts. In the next chapter, I investigate whether contest competition is found at La Luz, if it occurs more frequently than in other populations of howlers, and how contests affect the social structure of howlers at this site.

CHAPTER 6

GROUP COMPOSITION, CONTEST COMPETITION, AND PATTERNS OF GROUP TRANSFER

INTRODUCTION

The previous chapter describes the possible effects of scramble competition, in which food encounter rate is decreased for all group members equally (Terborgh and Janson, 1986; van Schaik, 1989; Sterck *et al.*, 1997). In and of itself, scramble competition should not cause conspicuous differences in *per capita* net energy gain within groups, and is therefore thought to lead to relatively undifferentiated relationships between female primates (Sterck *et al.*, 1997; Koenig, 2002). However, when resources are distributed such as to allow monopolization, significantly increasing net energy gain, females are expected to contest access through agonistic encounters, as female reproductive success should be closely tied to nutritional status (Trivers, 1972). Aggressive behavior when feeding constitutes within-group contest competition, and is manifest in the dominance systems between females within a group (Sterck *et al.*, 1997). Given their exploitation of relatively large and abundant food patches, contest competition should be relatively rare among howlers, although it has been documented to occur at low levels (Larose, 1996). However, mantled howlers demonstrate some characteristics of social structures generally associated with strong levels of within-group competition, such as linear dominance hierarchies among females (Jones, 1980) and increased reproductive success with increasing dominance (Glander, 1992).

These apparently inconsistent aspects of howler societies have been explained in reference to factors other than resource characteristics, such as infanticide avoidance or habitat disturbance (Crockett and Janson, 2000; Sterck *et al.*, 1997). A study of howlers in yet another disturbed habitat, upon first inspection, may not seem like a viable means of further exploring these contradictory results. However, La Luz has demonstrably different food abundance and distribution from other sites where *Alouatta palliata* has been studied, as demonstrated in the proceeding chapters. Although trees are less dense and the community less species rich at La Luz, those that are exploited as food resources are frequently large, generally abundant, and of relatively high quality, possibly reducing the costs associated with living in large groups. The reduced nutritional heterogeneity and lower population density may reduce the costs of dispersal from natal groups. Contest competition is expected to be relatively unimportant, although given that fruits may be limiting at certain times of the year, it is expected, particularly when feeding on energy-rich foods. If resources are less limiting the habitat is not saturated in the shade coffee plantation, a closer fit with the “dispersal-egalitarian” social patterns should be seen at La Luz.

METHODS

Whenever possible, all individuals in each study group were counted and assigned to an age sex category (categories distinguished based on criteria presented in Neville *et al.*, 1988). Given the large group sizes, groups were occasionally dispersed over distances of up to 200 meters (generally during travel; groups were more coherent while resting and

feeding), and some members were difficult to locate during periods of inactivity (in particular, adult females are less conspicuous than males and juveniles), counts generally could only be conducted during group progressions in which the all members followed the same arboreal pathway. Additionally, whenever other groups were encountered, as many individuals as possible were counted.

Social behavior was recorded during the course of focal animal sampling. All agonistic and affiliative interactions were recorded, regardless of duration. As social encounters were generally brief, they are treated as individual events rather than states. When social activity was observed, I noted the behavior (e.g., groom, inspect, bite, avoid, supplant, etc.), its duration if it continued for more than 3 seconds, whether it was affiliative or agonistic, the individuals interacting with the focal animal (when they could be identified), and whether the interaction occurred in a feeding context. Interactions were considered to occur while feeding if either the actor or recipient of a behavior was feeding immediately before or after the interaction. When agonism took place in a feeding context, the individual tree and food type were noted to allow comparisons of rates of agonism in relation to food species and phenophase consumption. Rare events, such as intergroup interactions and chases between resident and extra-group males were recorded on an *ad libitum* basis. During such dramatic events, focal animal sampling was suspended to record as much information as possible about the encounter.

Overall rates of affiliative and agonistic interactions are calculated by dividing the number of interactions by the total hours observation. Rates on a group-by-group basis are calculated by dividing by total observation time dedicated to each group. Rates of

interaction between age-sex classes are determined by summing all observed interactions for the age-sex class pair and dividing by the total focal time spent observing each age-sex class (for example, female-male interactions and male-female interactions are added, and then divided by the total time spent observing males plus time spent observing females). All instances of agonism, including those related to weaning and establishment or maintenance of dominance, were included in this analysis. As these were not scored as having occurred in a feeding context, their inclusion should not affect examination of rates of contest competition over food. Rates of social behavior are also calculated on a daily basis: the number of each type of social behavior (agonistic or affiliative, feeding or other context) are summed and divided by the total number hours of data recorded for a focal animal on a given day; these data are used in Kruskal-Wallis ANOVAs to test for differences between groups, seasons, and age-sex classes in the rates of social behavior.

RESULTS

Group Compositions

The groups varied in size and composition over the course of the study due to births, transfers, and, presumably, deaths. Table 6.1 presents the compositions of the three groups based on modal values from monthly counts of males, females, subadults, juveniles, and infants; Table 6.2 describes the temporal variation in composition of the three focal groups. Modal values are used because some of the variation probably arises from difficulties in obtaining accurate counts: unless all group members followed a single

Table 6.1. Compositions of the three study groups (modal values based on repeated counts) and two neighboring groups, number of males per female, and number of infants per adult female.

Group	# Counts	Males (range)	Females (range)	Subadults (range)	Juveniles (range)	Infants (range)	Total (range)	M:F	I:F
La Luz 1	7	2 (2)	10 (10-12)	4 (3-5)	5 (5-8)	3 (2-5)	26 (24-28)	0.20	0.30
La Luz 2	10	1 (1-2)	8 (7-9)	0 (0-1)	2 (1-4)	5 (1-6)	16 (14-17)	0.13	0.63
La Luz 3	12	1 (1-4)	7 (5-9)	5 (2-9)	5 (4-7)	1 (0-4)	19 (17-24)	0.14	0.14
San Emilio	1	2	9	5	2	3	21	0.22	0.33
San Joaquín	1	1	6	0	3	4	14	0.16	0.67

Table 6.2. Variation in group composition of the three study groups throughout the course of the study (M, number of adult males; F, adult females; SA, subadults that could not be reliably sexed; J, juveniles; I, infants).

Month	Group 1					Group 2					Group 3				
	M	F	SA	J	I	M	F	SA	J	I	M	F	SA	J	I
Oct-99	--	--	--	--	--	--	--	--	--	--	1	6	3	4	4
Nov-99	2	10	4	5	3	--	--	--	--	--	1	8	2	6	2
Dec-99	--	--	--	--	--	1	7	1	3	4	1	5	5	5	1
Jan-00	2	10	5	6	3	1	7	1	2	5	1	7	5	5	0
Feb-00	--	--	--	--	--	1	7	1	2	5	1	7	5	6	0
Mar-00	2	12	4	5	5	1	9	0	2	5	1	7	5	7	1
Apr-00	2	12	3	8	2	1	8	0	1	6	1	7	5	5	1
May-00	2	10	4	8	3	1	8	0	2	5	2	7	9	5	0
Jun-00	2	11	3	7	3	1	8	0	3	2	--	--	--	--	--
Jul-00	--	--	--	--	--	2	8	0	3	3	2	7	7	5	0
Aug-00	--	--	--	--	--	2	8	0	4	2	2	7	7	5	1
Sep-00	2	12	3	6	3	--	--	--	--	--	4	9	4	5	2
Oct-00	--	--	--	--	--	2	7	0	4	1	4	9	2	5	1

path during a progression, it was difficult to obtain a complete count. However, the modal values obscure some important variation in group size that resulted from changes in group composition, particularly for Group 3 (see “Female Transfer and Male Takeovers”). Group sizes were relatively large for the species, and infants were born in all groups during the course of the study. Birth rates were particularly high in Group 2, where at least 5 infants were born during the course of the study; three of the births took place in November and December of 1999. Group 1 had 3 births between March and May of 2000; Group 3 also had three births, one in March 2000 and two in August 2000. Both Groups 1 and 3 had 1 infant disappear; in at least one case, the disappearance coincided with an influx of adult and subadult males into the group. Group sizes and compositions are consistent with those observed for groups in neighboring coffee plantations (Table 6.1). Transfer of adults into and out of groups is discussed below.

In addition to these large bisexual groups, a number of solitary and small groups of howlers were observed. The extent to which these were long-term associations is unclear. Small groups of animals, particularly of adult and subadult males, were observed in the areas between Group 2’s original range and Group 1’s range in the shade coffee plantation (Figure 6.1). The all-male groups appeared to have fluctuating membership, although the continued presence over a number of months of some recognizable males suggests that these associations were not completely ephemeral. Additionally, small bisexual groups were sometimes observed, ranging in size from two (a male-female pair) to five (two females, one juvenile, and two males) individuals. These bisexual groups were seen only one time each, and it is unclear whether they represent new groups in

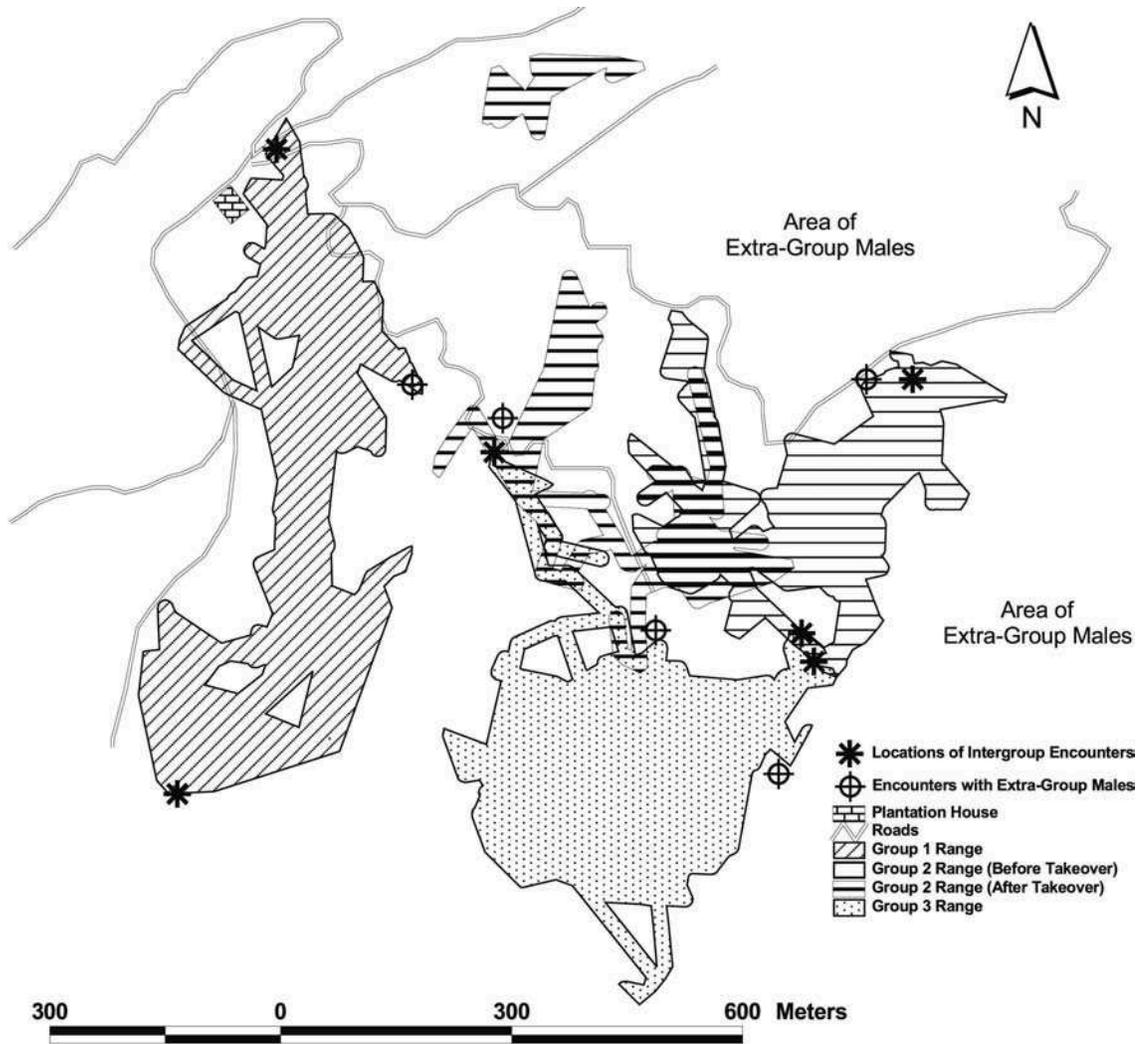


Figure 6.1. Locations of all howler groups in the study area, intergroup encounters (stars), and encounters between group males and extra-group males (circles).

formation, attempting to establish a home range, or more opportunistic associations of otherwise nomadic and/or dispersing individuals. On two occasions, lone females were observed.

Patterns of Social Interactions

During the course of focal animal sampling, a total of 1,588 social interactions were recorded. There were 953 affiliative interactions, 609 agonistic interactions, and 26 interactions that could not be clearly classified. As focal animals were in view for a total of 1,037 hours, the rate of all social interactions is 1.53 per hour, based on all data pooled. There were 0.92 affiliative social interactions and 0.59 agonistic interactions per focal hour. For the most part, interactions did not take place during feeding bouts (only 20.7% of all interactions occurred in feeding contexts). However, while only 7.2% of affiliative interactions took place while feeding, 42.0% of agonism occurs while feeding (Table 6.3).

Differences between Groups. It might be expected that, by virtue of having a greater pool of potential partners, larger groups would have higher rates of social interactions. However, Groups 2 and 3 have higher rates of both agonistic and affiliative interactions than Group 1, the largest group. A Kruskal-Wallis ANOVA demonstrates no significant differences between groups in the rates of all social behaviors per hour ($H = 3.325$, $N = 128$, $P = 0.190$). While there were significant differences between groups in the rates of agonistic encounters while feeding (Table 6.3), differences were not in the expected direction: the medium sized group had the highest rates of contest competition,

Table 6.3. Frequency of agonistic and affiliative social interactions and rates (number per observation hour) for each study group.¹

Group (Size)	N ²	Agonistic		Affiliative		Focal Hours Observed
		Feeding	Other ³	Feeding	Other ³	
1 (26)	40	59	99	11	200	288.7
<i>Rate</i>		<i>0.204</i>	<i>0.343</i>	<i>0.038</i>	<i>0.693</i>	
2 (16)	44	87	151	30	244	372.2
<i>Rate</i>		<i>0.234</i>	<i>0.406</i>	<i>0.081</i>	<i>0.656</i>	
3 (19)	44	110	103	28	440	376.4
<i>Rate</i>		<i>0.292</i>	<i>0.274</i>	<i>0.074</i>	<i>1.168</i>	
All Data Pooled		256	353	69	884	1037
<i>Rate</i>		<i>0.247</i>	<i>0.340</i>	<i>0.066</i>	<i>0.852</i>	
Kruskal-Wallis (H)		9.075*	1.843	4.143	4.779 ^T	
<i>Post hoc</i> tests		G3>G1	--	--	--	

¹ For tests for between-group differences: ^T $P < 0.10$, * $P < 0.05$; for *post hoc* tests (pair-wise K-W tests), “>” indicates that the group on the left has significantly higher rates.

² Number of focal follows per group; rates per hour per follow used in statistical tests.

³ Includes interactions related to mating, dominance, and weaning.

Table 6.4. Frequency and rates of agonistic and affiliative social interactions for the wet and dry seasons.¹

Season	N ²	Agonistic		Affiliative		Focal Hours Recorded
		Feeding	Other ³	Feeding	Other ³	
Wet	74	166	262	43	681	594.0
<i>Rate</i>		<i>0.28</i>	<i>0.44</i>	<i>0.07</i>	<i>1.15</i>	
Dry	54	92	91	26	203	443.2
<i>Rate</i>		<i>0.21</i>	<i>0.21</i>	<i>0.06</i>	<i>0.46</i>	
Kruskal-Wallis (H)		2.234	5.963*	0.792	21.204***	1037

¹ For tests of between-group differences: * $P < 0.05$, *** $P < 0.001$.

² Number of focal follows per group; rates per hour per follow used in statistical tests.

³ Includes interactions related to mating, dominance, and weaning.

while the largest group had the lowest. These differences could result in part from habitat and dietary differences (see below).

Differences between Seasons. Significant differences are observed between seasons in the rates of both affiliative and agonistic social behavior (Table 6.4). Rates of all social interactions pooled are significantly higher in the wet season (Kruskal-Wallis: $H = 20.234$, $N = 124$, $P < 0.001$). Given the increased exploitation of patchier fruit resources during the wet season, it would be reasonable to expect increased agonistic encounters, especially related to feeding contests. However, the only significant contrasts are between affiliative and agonistic behaviors in non-feeding contexts. These seasonal patterns appear to arise from differences in Group 1's interaction rates between seasons. All

contrasts, except for rates of affiliative behavior while feeding, are significant for Group 1; however, for Groups 2 and 3, the only significant differences between seasons are in rates of affiliative behavior while feeding.

Differences between Age-Sex Classes in Affiliative Interactions. Of the 953 observed affiliative interactions, 484 were observed while following females, 361 while following males, and 108 while following immatures. These do not represent unbiased assessments of patterns of affiliative interactions between age-sex classes, as adult males and females comprised the majority of focal individuals. If these values are divided by the contribution of each age-sex class to focal animal sampling, females engaged in affiliative social interactions at a rate of 0.78/hour, males at a rate of 1.01/hour, and immatures at a rate of 1.71/hour. The high rates of affiliative interactions observed for immature animals reflect the large amount of time spent playing; adult males also regularly played with juveniles. Rates and frequencies of interactions between age-sex classes are presented in Table 6.5 (data from all groups combined). The highest interaction rates are seen for pairs of immatures, the lowest for male-male pairs. Rates of interactions for females are fairly constant, regardless of the age-sex class of their partner. These patterns of affiliative behavior are reflected in the activity patterns of each age-sex class (Chapter 4), with adult males and juveniles spending significantly more time in affiliative interactions than adult females. However, based on rates of affiliative behavior calculated from each focal follow, differences between males, females, and juveniles in overall rates of affiliative behavior are not significant.

Table 6.5. Numbers and rates per hour of all affiliative and all agonistic social interactions between pairs of age-sex classes.¹

	Age-Sex Class	Male	Female	Immature ²	Observation Time (hours)
Affiliative	Male	8	291	172	356.1
	Rate	<i>0.02</i>	<i>0.30</i>	<i>0.41</i>	
	Female	--	175	213	617.8
	Rate	--	<i>0.28</i>	<i>0.31</i>	
	Immature²	--	--	71	63.3
	Rate	--	--	<i>1.12</i>	
Agonistic	Male	4	162	24	356.1
	Rate	<i>0.01</i>	<i>0.17</i>	<i>0.06</i>	
	Female	--	245	119	617.8
	Rate	--	<i>0.40</i>	<i>0.17</i>	
	Immature²	--	--	6	63.3
	Rate	--	--	<i>0.09</i>	

¹ Excludes interactions for which one partner could not be reliably assigned to an age-sex class.

² Includes all immatures (juveniles, infants, and subadults).

Differences among Age-Sex Classes in Agonistic Interactions. There are significant differences between males, females, and juveniles in the overall rates of agonistic behavior ($H = 23.419$, $N = 128$, $df = 2$, $P < 0.001$), rates of agonism while feeding ($H = 12.438$, $P = 0.002$), and rates of agonism in non-feeding contexts ($H = 19.397$, $P < 0.001$). Females engage in aggressive encounters significantly more frequently than males in both feeding and non-feeding contexts, and juveniles significantly more than males while feeding. A total of 609 agonistic encounters were recorded during the course of the study, 469 while following adult females (0.76/hour), 100 while following males (0.28/hour), and 40 while following juveniles (0.63/hour). In considering all agonistic behavior by age-sex class, an essentially opposite pattern emerges from that of affiliative encounters. Males and immatures generally exhibit low rates of agonistic behaviors, while females apparently endure or engage in frequent harassment. Given the low rates of interactions and the difficulty in identifying all group members, dominance hierarchies ranking individual animals cannot be determined. However, the patterns of agonistic encounters are consistent with those observed for other mantled howlers, with males dominant to all females and females dominant to juveniles.

Aggressive encounters are most frequently seen between females, who compete not only for food, but presumably also for group membership and, subsequently, dominance within the group (Zucker and Clarke, 1998). Females are frequently subject to harassment by other females when they have young infants. Young infants are attractive to other group members, and both females and (less frequently) males will pursue new mothers in attempts to touch, grab, hold, or carry infants. As observed by

Clarke *et al.* (1998), many interactions between non-mothers and infants were aggressive in nature and mothers would threaten and/or flee from persistent harassment. In non-feeding contexts, significant differences were found in rates of agonistic encounters between females with and without infants ($H = 4.327$, $N = 76$, $df = 1$, $P = 0.035$), with mothers engaging in agonism more than non-mothers.

Contest Competition and Food Type. Given the importance of contest competition in structuring group size and social relationships in primates, I consider agonism in feeding contexts in more detail. Fruits are more energy rich, more defensible, and less abundant in a tree crown than other foods, and it is therefore expected that a disproportionate amount of contests will take place while feeding on fruit; conversely, given the abundance of the mature leaves eaten (Chapter 3), one would expect agonistic encounters less frequently when feeding on mature leaves. Of the 256 aggressive encounters recorded during feeding, 91 were observed while subjects were eating fruit, 86 while eating mature leaves, 52 while eating young leaves, 23 while eating flowers, and 4 while eating other plant parts. Although most contests do take place while feeding on fruit, based on the time spent feeding on each food category, only mature leaves are contested more often than expected, while young leaves are contested less often than expected (all groups combined: $\chi^2 = 16.658$, $df = 4$, $P = 0.002$; Figure 6.2). This result is exactly opposite of that predicted, and is observed in all three groups; only in Group 3 do contests occur more than expected while feeding on fruit.

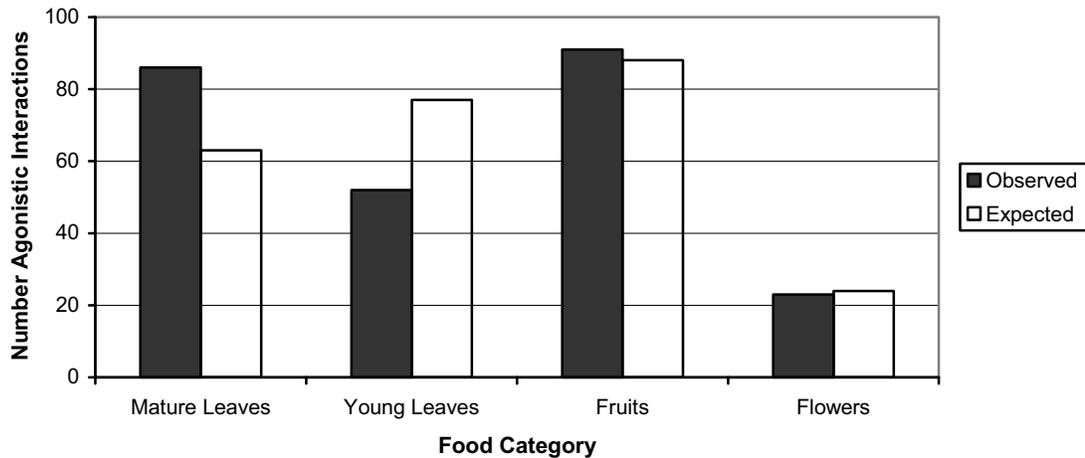


Figure 6.2. Observed versus expected (based on total time spent feeding) frequencies of agonistic interactions while feeding on mature leaves, young leaves, fruits, and flowers.

Contest Competition and Food Species. Agonistic encounters were observed in 32 tree species, and were also observed when feeding on epiphytes and vines. Most of these were in primary food species, such as *Ficus costaricana*, *Enterolobium cyclocarpum*, and *Cecropia peltata*. While there is a significantly positive correlation between the number of contests per species and time spent feeding on that species ($r_s = 0.804$, $N = 38$, $P < 0.001$), there is no relationship between agonism and the selection ratio (percent contribution to the diet divided by percent contribution to basal area; Chapter 3), suggesting that rarer resources are not more frequently contested. Rather, contests occur roughly in proportion to the time spent feeding on a given species.

Within species, patterns of agonism vary in response to food type eaten, as seen by considering the 5 most important food species. For *Ficus costaricana* (69 contests observed), more contests took place while feeding on fruits than expected, while fewer than expected were observed while eating young leaves ($\chi^2 = 9.741$, $df = 3$, $P = 0.021$). Similarly, contests took place more than expected when eating *Cecropia peltata* fruit and less than expected when eating mature leaves, young leaves, and flowers (24 contests: $\chi^2 = 13.763$, $df = 3$, $P = 0.003$). Twenty-five contests were observed while animals were feeding on *Enterolobium cyclocarpum*, with no significant differences between observed and expected frequencies ($\chi^2 = 3.579$, $df = 3$, $P = 0.311$). A similar pattern was observed for *Spondias mombin* (14 contests; $\chi^2 = 0.583$, $df = 1$, $P = 0.445$) and *Bursera simaruba* (12 contests; $\chi^2 = 1.221$, $df = 3$, $P = 0.543$). Contest competition for mature leaves took place more often than expected in a few leguminous species (*Albizia guachapele*, *Lysiloma aurita*) and while feeding on epiphytes.

Female Transfer and Male Takeovers

The sizes and compositions of all groups varied throughout the study. As it was impossible to identify all group members, exact changes in group composition due to immigration and emigration cannot be described. However, it was possible to confirm both male and female transfer in this population. At least 3 recognizable females emigrated from the study groups during data collection. One young female left Group 1 in early 2000 and was subsequently observed with the large group ranging to the south of

Group 1. A subadult female emigrated from Group 3; she was subsequently seen once in the area south of Group 3's range. Finally, a fully adult female and her 11-month old juvenile emigrated from Group 2 and joined a small bisexual group with 1 other female and two males; given the fully adult status of this female, this likely represents a secondary transfer and was a result of persistent harassment from a male which had recently joined Group 2 (see below). I observed no instances of adult or subadult females attempting to enter the study groups, although such transfers may have taken place outside of the 4-day follows; nor were females observed persistently harassing juveniles or subadults in apparent attempts to expel them from groups.

Juveniles sometimes endured persistent agonism from adults that appeared related to forcing their emigration from the group. At least 2 juveniles disappeared from Group 2 during the study, after harassment from the resident adult male. One of these was subsequently observed attempting to reenter the group; the adult male persistently chased this individual away from the group, and after a period of days it was no longer observed in the vicinity. Because the testes of mantled howlers do not descend until sub adulthood (Neville *et al.*, 1987), is difficult to determine if juveniles that disappeared from the groups were male or female.

Although male emigration from the study groups is difficult to document, males clearly entered the groups. Both Groups 2 and 3 saw dramatic male transfers and takeovers. Just before the commencement of data collection, the resident male of Group 2 was presumably expelled by a lone male which remained the resident male for nine months. During his tenure, there were no unexplained disappearances of infants or

young juveniles. Presumably, this male was not the father of the infants in the group. However, he was rarely observed interacting aggressively with juveniles and infants, in contrast to some other males in the study population (see below). He would attempt to carry young infants, although these interactions were met with furious protests from both the infant and mother. This male disappeared between the ninth and tenth months of the study, and two males were observed in the group during the last three study months. Unlike their predecessor, the dominant of the two males was persistently aggressive towards juveniles and their mothers. All females with young juveniles or infants endured harassment from this male. A female and her 11-month old juvenile were most frequently subject to bullying, to the extent that both left the group together and joined a small mixed sex group. These high rates of social disturbance were accompanied by range abandonment by the group (Figure 6.3), during which time the group began to occupy areas of the coffee plantation where only solitary animals and groups of bachelor males had been seen.

Infanticide related to male takeovers of groups has been documented in several species of *Alouatta* (Crockett and Janson, 2000); in spite of male turnover in Group 2, there were no coincident disappearances of infants. However, this is not the case with Group 3, which saw an influx of subadult and adult males. For the first several months of the study, there was only one adult male in this group, but between the sixth and seventh months, at least 1 adult and 3 to 4 subadult males joined the group. The adult male, which had distinctive markings, had been observed several times either with bachelor groups or on the periphery of the group, where he was chased by the resident

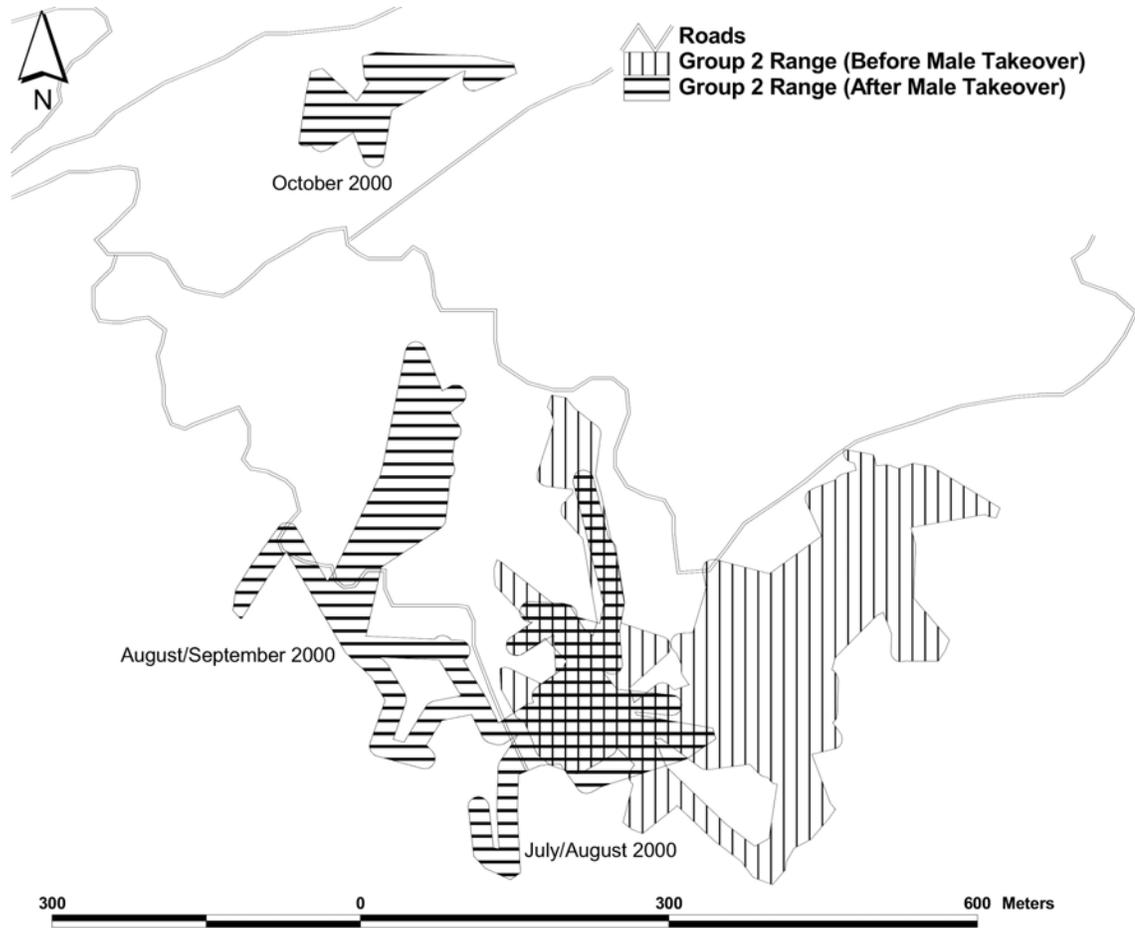


Figure 6.3. Range abandonment by Group 2 after a group takeover by two males: after the males were first seen in the group, the group abandoned farther west and south than previously seen (Month 10); the group shifted its range further west (Month 11) and then further north (Month 12).

male, Choco. After this influx of males, the original male remained in the group but was observed mating less frequently. One female's infant disappeared during this time, and within a month she was observed mating with the new adult male. Although Choco maintained affiliative social relationships with both adult females and juveniles in the groups, playing with juveniles and holding infants, the second adult male rarely engaged in play or other affiliative behavior with immatures.

Intergroup Encounters and Between Group Competition

Interactions with extra-group animals, either solitaires or in other permanent social groups, were relatively rare. Only five intergroup interactions were observed during the 1,300 hours of data collection; two more were observed during collection of phenological data. Encounters with extra-group animals nearly always took place on the peripheries of the groups' ranges (Figure 6.1). Although groups were rarely observed in proximity, members of all groups reacted strongly to the presence of other groups with howling and chases. There were no observed instances of bisexual groups remaining in proximity without accompanying vocal and visual displays. Adult males always participated in these conflicts, with howling and chases; females without dependent juveniles would sometimes participate to a lesser extent, trailing after males during chases. During one interaction, a Group 2 female was observed mating with the Group 3 male. On at least two occasions, intergroup encounters apparently were related to access to fruiting *Ficus* trees, with one group (Group 3) apparently evicting the other and then feeding in the contested tree. In both of these cases, the smaller of the two groups

(Group 2) retreated. Other intergroup encounters took place near fruiting trees but were less clearly related to access. There is no evidence that the howlers are regularly patrolling the edges of their home ranges, and given the rarity of these conflicts, the lack of overlap between home ranges seems a result not of active defense, but of low population density.

Single or small groups of males were sometimes observed on the peripheries of established groups, apparently in attempts to transfer in. These incursions were always met with resistance from resident males, who would usually engage in low-speed but persistent chases of these individuals, who were always observed to withdraw. No direct physical contact was observed during these chases, although the high incidence of injuries (torn lips, broken fingers and toes, and missing eyes) among males suggests that aggression can reach extreme levels. Most females, in contrast, lacked scars or evidence of permanent injury.

DISCUSSION

Group sizes at La Luz and throughout the Mombacho region (see McCann *et al.*, 2003) are within the range of variation for the species (Table 6.6). The ratio of infants to females (a rough estimator of birth rate; Treves, 2001) is also within the range of variation. However, unimale groups occur frequently at Mombacho (McCann *et al.*, 2003), and within La Luz, male to female ratios in permanent bisexual groups are among the lowest known for *Alouatta*. The variation in group size and composition at La Luz is unexpected and difficult to explain. Crockett and Eisenberg (1987) suggest that recently-formed howler groups are more likely to have only one male; given that the population of

Table 6.6. Average bisexual group compositions, ratio of males to females in permanent bisexual groups, and ratio of infants to females in bisexual groups of *Alouatta palliata* at La Luz and other sites.

Site	Males	Females	Juveniles	Infants	Total	Males: Females	Infants: Females	Source
La Luz ¹	2.0	9.6	4.3	2.7	18.6	0.21	0.28	Current Study
Los Tuxtlas (Mex)	3.0	4.1	1.6	1.5	9.1	0.73	0.36	Estrada (1982, 1984)
Santa Rosa (CR)	2.8	5.4	2.5	1.9	12.7	0.52	0.35	Fedigan <i>et al.</i> (1998)
La Pacifica (CR)	3.0	9.8	2.2	2.2	15.5	0.31	0.21	Clarke <i>et al.</i> , 1986
La Selva (CR)	3.3	4.0	2.4	1.3	11.0	0.82	0.32	Stoner (1994)
Ometepe (Nic)	5.5	8.0	3.5	3.5	20.5	0.69	0.44	Garber <i>et al.</i> (2000)
Barro Colorado (P)	3.2	5.8	4.3	2.3	16.2	0.55	0.40	Milton (1982)
Barro Colorado (P)	1.2	4.5	1.4	0.9	8.0	0.27	0.20	Collias and Southwick (1952)

¹ Based on average of monthly counts for three groups; subadults that could be confidently sexed included with adults, others pooled with juveniles.

howlers in Mombacho is currently expanding, many of Mombacho's smaller unimale groups may represent recently established social groups. Ostro *et al.* (2001) argue that for black howlers (*Alouatta pigra*) at low population densities, unimale social groupings are advantageous for males competing for female access, as there is less need for cooperative defense of breeding opportunities when the frequency of intergroup and lone male encounters is reduced. Population density at Mombacho is relatively low, and it is clear that intergroup interactions are quite rare. However, although this explanation may account for the prevalence of unimale groups in Mombacho, it does not explain the low male to female ratios seen in La Luz. Extra-group males seeking female access are clearly prevalent in the area, and it would be expected that males would, in fact, benefit from cooperative mate defense, particularly when there are so many females per male to monitor.

Sterck *et al.* (1997) relate female evictions and difficulties female howlers face during transfer to habitat disturbance. If fragmentation and elimination of predators leads to habitat saturation, high dispersal costs for females will result, leading to unusually large group sizes and more despotic social hierarchies amongst unrelated females. Consistent with hypothesis, mantled howlers, which have usually been studied in disturbed habitats, generally have larger groups with more adult females at higher population densities (Fedigan *et al.*, 1998). Unfortunately, habitat saturation does not seem a wholly appropriate explanation for howler group composition at La Luz: while they are not subject to predation, the habitat seems far from saturated, given the large areas of apparently suitable habitat that are currently unoccupied. As it was difficult to

identify individuals, I cannot comment extensively on the linearity or stability of female dominance systems in this population; however, agonistic interactions between recognizable females were rare, and there were reversals in half the dyads for which multiple aggressive encounters were observed.

Low male to female ratios may result in part from the size and distribution of food trees in the shade coffee plantation. Many of the feeding trees used by howlers in shade coffee plantations are either large (e.g. *Enterolobium cyclocarpum*, *Ficus costaricana*) or small but highly abundant (*Cecropia peltata*). Their size and distribution may mean that more females can feed concurrently in a single patch than at other sites, allowing one or two males to monopolize access to a group of more cohesive females. However, this possible proximate mechanism fails to explain the impetus for females forming large groups in the first place. All predators have been eliminated, and the howlers are not subject to hunting, so large female groups do not reflect predation pressure. Although females may group in response to infanticide, sharing males for protection (Sterck *et al.*, 1997), very large groups of females are thought to be more prone to male takeovers and subsequent infanticide attempts (Crockett and Janson, 2000; although the largest group at La Luz was the only one which did not see male turnover). Given the potentially increased risk of infanticide in large groups, the release from predation pressure, and the fact that most contest competition occurs between females, immediate benefits to large numbers of females in groups are unclear. These groupings may not be an adaptive response to anything, reflecting instead recent population and group history (Chapman

and Balcomb, 1998; Crockett, 1996), which cannot be documented with the limited information currently available.

The rates and patterning of agonistic interactions are consistent with studies of mantled howlers which demonstrate low rates of contest competition (Zucker and Clarke, 1998; Larose, 1996). Female-female agonistic interactions occur at a rate of 0.38/hour at Finca La Pacifica (Zucker and Clarke, 1998), nearly identical to that observed at La Luz. At Santa Rosa, Larose (1996) observed much lower rates of agonistic interactions (0.12/hour for all agonistic interactions pooled, versus 0.59/hour at La Luz), although this disparity may be a result of methodological differences. Nevertheless, the *patterns* of contest competition observed by Larose do differ in important ways: contests were more frequent while feeding on fruits and flowers and during the dry season, when seasonal food items comprise a larger portion of the diet. These discrepancies reflect the both the extreme seasonality observed at Santa Rosa, resulting in periods of strongly limited food availability, and the high quality, large patch sizes, and abundance of food species at La Luz, which should act to make food less limiting, and access therefore less contested.

Relatively low rates of contest competition in the large group could result in part from dietary and habitat differences from the other two study groups. Group 1's range encompasses a large area of older regeneration, with marked differences in vegetation composition. *Bursera simaruba* is much more common in these areas, and *Ficus* much rarer; similarly, the diet of Group 1 is higher in mature leaves, especially those from *Bursera*, and lower in its reliance on *Ficus*. Given that the most important component of the Group 1 diet is mature leaves from a species relatively abundant in its range, it is

perhaps not surprising that rates of contest composition are lower. Groups 2 and 3, which have similar diets and ranges, exhibit similar rates of interference competition.

Competition is quite frequent when feeding on some leaves, and more sporadic in some fruit sources, an unexpected pattern. Competition for access to the mature leaves of epiphytes can be easily explained, as these generally occur in circumscribed areas within the crowns of large trees. However, many of the foliage sources in which aggressive encounters most frequently occur are neither unusually rare nor extraordinarily nutritious in comparison to foliage resources that are not contested, making the high incidence of agonism in these feeding trees difficult to explain. Lower than expected incidence of competition in fruit trees may result in part because main fruit sources are generally large, able to accommodate most or all group members feeding at once, with a disperse distribution of fruits within the tree crowns. This is particularly the case with large trees of *Ficus costaricana*.

The howlers at La Luz resemble conspecifics in the relatively high rates of agonism between females. Females seem to bear the burden of aggressive interactions, both while feeding and in other contexts, and competition likely impacts them more than it does other group members (Chapter 7). However, the costs to females at La Luz of group living and group transfer may potentially be reduced. The primary costs to dispersing mantled howler females are increased predation risk, conflicts with conspecifics, loss of the first infant, and reduced nutrient intake as a result of unfamiliarity with the habitat (Glander, 1992). There are no predators to speak of aside from occasional human hunting for sport, and, against a human predator, a female is

probably better off alone and inconspicuous than with an easily-located large social group. Low population density at the very least reduces the probability of meeting other conspecifics, and the lack of evidence of severe injuries to females suggests that intraspecific agonism may be less intense. Finally, the relatively high quality of abundant foliage may impose fewer nutritional costs associated with dispersal. Consistent with this hypothesis, I never observed the fights and chases between dispersing and resident females or the harassment of juveniles described by Glander (1992).

Patterns of contest competition and general patterns of agonism among the mantled howlers of La Luz are consistent with expectations for a primate feeding on relatively abundant, low quality foods (van Schaik, 1989; Sterck *et al.*, 1997). Low levels of contest competition are evident, and it is possible that the howlers at La Luz conform more closely to predictions based on current socioecological theory than do other populations of *Alouatta palliata*. With a complete description of foraging strategy, nutritional condition, and patterns of contest competition, it is now possible to present a broader picture of howler behavioral ecology at La Luz (Chapter 7).

CHAPTER 7

CONCLUSION

REVIEW AND SYNTHESIS

In the preceding chapters, I have presented data on the habitat characteristics and phenological patterns in a shade coffee plantation, and the ways in which foraging, ranging, and activity patterns of mantled howling monkeys change in response to seasonal pressures. These basic features of the howlers' ecology are also related to the demands of group living in primates, which vary with the abundance and distribution of food resources. I contrasted the behavior and ecology of howlers in the coffee plantation to that of conspecifics and discussed how site-specific patterns of foraging, ranging, and social organization reflect the patterns of resource abundance and distribution in the agroforest of Finca La Luz. This study is unique in that it is the first study of any primate in Nicaragua that spans an entire annual cycle, it is the first study of primates living in coffee plantations, and it is one of the few studies of primate behavioral ecology that integrates detailed ecological, behavioral, nutritional and energetic data.

Generally strong support is provided for the prediction that howlers in a shade coffee plantation would demonstrate a less-selective foraging strategy, although perhaps not for the reasons I initially anticipated. The howlers at La Luz certainly feed very heavily from a limited number of species. Nevertheless, they also fed at least once from nearly every species in the plantation, and, in fact, feed on more tree species than were present in the vegetation enumeration. However, it is unlikely that the howlers are

expending much effort while foraging in order to maintain a diverse diet. Rather, diversity generally reflects sampling of trees encountered while moving between primary feeding trees. While the howlers are not indiscriminate in their food choices, disregarding some common tree species, they rely primarily on a few common species, some of which are present at other sites but largely ignored as food sources. Travel time is increased and resting time decreased, but, contrary to expectations if food is of lesser quality, time spent feeding is comparatively low – the howlers are not feeding more to compensate for what I had expected to be a nutritionally poor diet.

An initial examination of the nutritional content of the howlers' diet reveals little selectivity in food choice, with staple foods showing few significant differences in protein or fiber content from rarely or never eaten items. Howlers in a less diverse, and, presumably, less favorable habitat would be expected to focus on the most digestible and nutrient-rich resources, so this result is initially puzzling, even in light of expectations that primates in disturbed habitats might experience increased energetic and nutritional stress. However, a closer inspection of the average protein and fiber content of foliage in the shade coffee plantation reveals an apparently abundant supply of high-quality foliage. Low selectivity may therefore be an optimal foraging strategy in this environment because the typically choosy pattern of folivory seen at other sites is simply unnecessary. However, howlers probably cannot live on foliage alone. Location of sugar-rich fruit and flowers is likely the limiting factor in this environment, thus the heavy exploitation of sweet *Ficus* and *Spondias* fruits. During certain periods of the dry season, flowers are extremely abundant, and some are high in sugar content (e.g., those of *Diphyssa robinoides*,

Lysiloma aurita, and *Gliricidia sepium*). During other times of the year, howlers must rely on fruits for soluble carbohydrates. Some, such as those of *Ficus costaricana*, are available throughout the year but only moderately high in sugar, some are abundant but high in fiber and heterogeneous in simple carbohydrate content (*Cecropia peltata*), and some are sweet, low in digestion inhibitors, but sparsely dispersed and available only during limited periods (*Spondias mombin*, *Manilkara chicle*, *Simarouba glauca*). Searches for and depletion of these resources account for the very long travel paths seen during the rainy season.

These patterns of resource abundance and quality engender patterns of feeding competition and social behavior that may diverge somewhat from those observed at other study sites. Firstly, given that some nutrients, particularly simple sugars and perhaps sodium, are rare in the environment and occur in discrete, depletable patches, scramble competition at the very least is expected. Measures of foraging effort, as estimated by ranging behavior, are consistent with expectations that at least some resources are limiting. However, evidence of contest competition – which is expected to be higher in fruit and flower food patches, as these resources are both nutrient dense and patchily distributed in the environment and in individual tree crowns – is more equivocal in that competition is, surprisingly, more frequent than expected when feeding on mature leaves. Additionally, there are no systematic relationships between net energy gain and group size or season, suggesting that the ultimate effects of competition may be weak. To a certain extent, the differing energetic needs of certain age-sex classes confound analyses of between-group differences. The smallest group has the lowest average net energy gain, but also has the most lactating females, which are most likely to enter negative energy

balance. Unfortunately, I do not have enough data to explore group differences in the energy balance of females unburdened by offspring.

It is clear that females bear the brunt of the costs, however low, of within-group competition. The lack of variation between groups, seasons, and age-sex classes in average energy intake suggests that some upper limit of ingestion has been reached; given the particular resources available in the habitat, and the limited gut capacities of these relatively small-bodied herbivores, the howlers generally may not be able to ingest more calories. However, pregnant and lactating females have high energetic burdens imposed by reproduction (Hanwell and Peaker, 1977; Trivers, 1972). Although scramble competition affects the food encounter and ingestion rate of all group members equally (Watts, 1993), the effects on females are disproportionate given their already high energy deficits. Additionally, females endure an unequal amount of agonism and contest competition, which may interfere with foraging efficiency and possibly lead to harm of dependent offspring. These pressures make the large female groups observed at La Luz difficult to explain.

The competitive regime observed in La Luz is best described as low within-group scramble and even lower within-group and between-group contest competition, and the patterns of female dispersal and social relationships are consistent with the dispersal-egalitarian system anticipated by current socioecological theory (Sterck *et al.*, 1997). As I could not identify all females, I cannot unequivocally establish whether or not they demonstrate the strong linear hierarchies observed for other mantled howlers (Jones, 1980). However, that dominance cannot be clearly established for most dyads and that

no female evictions were observed is at least consistent with the La Luz howlers having a social system more in line with theoretical expectations. Ultimately, the lack of a perfect fit between group size associated costs of group living is itself expected. As Sterck *et al.* (1997) and others point out, the “optimal” group size is never an equilibrium state: if smaller groups experience less feeding competition, leading to higher net energy gain, the consequence should be higher female reproductive success (as is possibly seen in Group 2), resulting in growth in group size through births and preferential female transfer, which, in turn, leads to reduced foraging efficiency but not a concomitant reduction in group size. Finding a group at “optimal” size is in itself unexpected, and the favorable demographic conditions that are engendered should ultimately lead to the demise of these very circumstances.

The group organizations observed at La Luz, if they are not a short-term response to an unidentified ecological or demographic pressure, have some implications for the evolution in the population. If group males are monopolizing access to larger numbers of females, fewer males are doing more of the breeding. This pattern could potentially result in decreased genetic diversity, although short male tenure lengths could act as a counterbalancing force. Zucker and Clarke (1998) suggest that female transfer in howlers is, in part, an adaptation to reduce competition between kin. While it is clear that the consequences of scramble competition are greater for female reproductive success, it also appears that feeding competition is relatively moderate at La Luz. If the levels of competition are reduced in comparison to other populations, it is *possible* that there may be less pressure for female migration. Evictions of females by same sex group mates

were never observed, and recognizable females that did disperse were found later in neighboring groups; dispersal to nearby groups is not observed at La Pacifica, and Clarke *et al.* (1998) suggest that this is a mechanism to reduce between-group competition among resident versus dispersing kin. It may be that both within and between group competition are reduced at La Luz; this could result in a potential relaxation of constraints on the frequency and patterns of female migration. This situation may account for the high female to male ratios observed, in that females are less constrained by competition with group mates for access to food, allowing social groups to become larger before females emigrate in response to the pressures of competition. Males, however, would still be constrained by the need to defend mating exclusivity and protect offspring from conspecific aggression, and would therefore still monopolize access to females. The high numbers of extra-group males observed in La Luz suggest that the *population's* sex ratio is more species-typical, and that males may be competing intensively for group membership.

SURVIVAL AND CONSERVATION IN A DISTURBED HABITAT

The Importance of *Ficus*

Throughout the study, the importance of several resources key to the howlers' survival has been emphasized. Foremost among these is the tree *Ficus costaricana*, a large hemi-epiphytic fig tree found throughout Central America (Croat, 1974). This species is probably integral to the survival of the howlers at La Luz. A consideration of the nutritional characteristics of the parts eaten does not reveal a particularly outstanding

nutritional profile: among the figs, the synconia of this species are more sugar rich and less fibrous in comparison to the other species available; however, the fruits of many other species have far higher levels of sugar and lower levels of fiber. Although the nutritional profiles of their young leaves and leaf buds vary, they have relatively low protein to fiber ratios, so that the reliance on this species cannot be explained in nutritional terms alone. *Ficus* is a staple food source for many primates, although the reasons for such reliance have been at times unclear, given the variation in nutritional quality observed in the genus (Conklin and Wrangham, 1994).

The intense exploitation of the species at La Luz may result from several factors. Firstly, these trees are moderately abundant, and given their asynchronous phenological patterns, can serve as fallback resources during periods when the abundance of other seasonal phenophases is low. Secondly, given the reduced nutritional constraints at La Luz, macronutrient content may not be as important in food selection; the high levels of minerals, particularly calcium, may be in part what attracts howlers to this resource (O'Brien *et al.*, 1998). Also, as these trees are generally very large, they can accommodate the entire group while feeding, which may reduce rates of contest competition. Finally, the foods eaten from *Ficus costaricana* may be particularly digestible or palatable due to low levels of secondary compounds. However, I cannot determine if this is the case with the data I have available at this time.

Primate Conservation in Agroforests

Although preserving large tracts of undisturbed habitat would best ensure the protection of primates and other organisms (Soulé and Simberloff, 1986), such lands currently comprise a mere 5% of the earth's land surface, an insufficient amount for maintaining viable populations of most organisms (Meffe and Carroll, 1994). The conservation of biodiversity will require active efforts both *within and outside* of park boundaries (Western, 1989). Agricultural fields, rangelands, and managed forests fall outside of our usual conception of "wilderness", but they may play a key role in long-term biodiversity preservation (Western, 1989; Vandermeer and Perfecto, 1997). These areas have not been adequately explored as potential refuges for primates.

It has been argued, quite reasonably and logically, that habitat disturbance is detrimental to primate populations (Struhsaker, 1997). For example, some investigations of the responses of primates to selective logging have demonstrated resultant declines in numbers (e.g., Skorupa, 1988; Struhsaker, 1997). However, it is also clear that anthropogenic habitat change does not always result in reduced population density for all primate species (Johns, 1992; Plumptre and Reynolds, 1994), and that due to certain patterns of disturbance, some folivorous primates may in fact encounter more food resources, experience reduced predation pressure, or demonstrate higher population densities in logged or otherwise disturbed areas (Clavert, 1985; Plumptre and Reynolds, 1994). Although attempts to integrate human economic activities with tropical forest conservation can be unarguably disastrous under many circumstances (Oates, 1999), there may exist viable opportunities for conservation in some forested areas largely dedicated to

human use. Preserving primary, undisturbed habitat is undoubtedly critical for primate conservation; however, the conservation potential of secondary and disturbed habitats like shade coffee plantations should not be overlooked.

Perhaps one of the more surprising conclusions of the study is that howlers are not struggling to survive in Mombacho's shade coffee plantations, but apparently are thriving. Although their densities are relatively low, this appears to result not from poor habitat quality or high mortality, but from recent population history (McCann *et al.*, 2003). Due to the predominance of leguminous and pioneer species and, perhaps, rich volcanic soils, the agricultural habitat in La Luz is of high quality, at least from the point of view of a howler monkey, and may in fact provide higher than usual amounts of food (or at least foliage) resources. Given the high human population density and hunting pressures, the Mombacho habitat is clearly not suitable for many large mammals. However, as the howlers are subject to neither predation nor hunting by humans (for food or the pet trade), they are apparently not only surviving, but flourishing, in this habitat. Contrary to my initial expectations, the presence of the howlers in Mombacho is not tied to patches of less disturbed forest: the howlers feed, travel, and rest almost entirely in areas of active shade coffee cultivation. Based on my conversations with other researchers studying biodiversity and ecological processes in shade coffee plantations, the permanent residence of primates in coffee plantations is apparently quite rare.

A number of factors account for the persistence of howlers in Mombacho's shade coffee areas. Unlike spider and capuchin monkeys, howlers are considered neither tasty nor companionable, so they are not subject to hunting for food or the pet trade. It is

unclear the extent to which shade coffee plantations could serve as refuges for these other primates; as these species, like howlers, demonstrate labile dietary patterns (Chapman, 1988b), the low fruit abundance during certain times of the year should not in and of itself preclude their presence in coffee plantations, and capuchins are found in some of Mombacho's less-disturbed areas. Additionally, some long-term residents of Mombacho claim that all three species were found in La Luz in the past. Reasons for their absence today are not clear, although it seems probable that the same hunting pressure that severely reduced howler populations during the 1980's may have led to severe reductions in capuchin populations and the local extirpation of spider monkeys. Presently low population densities may reflect factors other than habitat disturbance *per se*. The howlers may in fact benefit from the lack of interspecific competition with other primates and frugivorous mammals for certain resources (cf. Fedigan *et al.*, 1998).

The nature of howler foraging and social adaptations play a key role in their ability to survive in coffee plantations and other disturbed habitats. Their dietary breadth and ability to eat a wide variety of foliage allow them to persist in a wide variety of habitats (Neville *et al.*, 1988). Additionally, that both sexes disperse from their natal groups (Glander, 1992) means that nearly all individuals must undergo periods of range shifting, during which time they must adapt to unfamiliar areas, learn to exploit new resources, and anticipate unique temporal and spatial patterns of resource abundance (Sterck *et al.*, 1997; Clarke *et al.*, 1998). Habitat characteristics in tropical forests may vary widely over relatively small distances, so that even an animal dispersing over only a few kilometers will face previously unknown environmental characteristics. That both males and females

must clearly adapt to new range may make howlers more adept at dispersing into a wider variety of habitat, including secondary and degraded areas (Clarke *et al.*, 2002a).

A third aspect permitting the continued survival of howlers in the plantation is the rich assemblage of large trees used as shade cover. I have made much of the low species diversity in the La Luz forest, and, in comparison to the most rustic of shade coffee plantations, the La Luz plantation is not as species rich or structurally diverse (Moguel and Toledo, 1999). However, the shade coffee plantations of Mombacho are among the most diverse and structurally intact that I have observed in southern Central America. In other areas of Nicaragua and Central America, shade trees frequently comprise a monoculture of one genus (typically *Inga*, as it is fast growing and easily managed), or shade trees may be small with crowns that do not touch (Moguel and Toledo, 1999; Rappole *et al.*, 2003), both of which rule out long-term primate habitation as a certain minimal level of food tree diversity is probably necessary for howlers to survive long-term in a habitat. Similarly, shade coffee plantations using a monoculture of small shade trees differ little from sun coffee plantations in the diversity of birds supported (Greenberg *et al.*, 1997), underscoring the need to specify the *kind* of shade system being promoted as a conservation tool.

The use of leguminous species as shade trees at La Luz may also be critical to the howlers' survival, as, at least in this environment, they apparently provide high protein and/or low fiber foliage upon which the howlers can fall back. The broken canopy may also encourage the growth of *Cecropia* and some *Ficus* species which grow particularly rapidly in full sunlight and serve as staple foods for primates throughout the Neotropics.

Fruit trees like *Spondias* and *Manilkara* are also preferentially left standing; although people do not harvest *Ficus costaricana* fruits, they are also favored as shade trees due to their large, spreading canopies, and their presence is clearly critical to the survival of the howlers. Although I did not collect data on the recruitment of seedlings, regeneration does occur, for example in temporarily-abandoned areas of coffee cultivation and in small forest fragments. The howlers themselves play an important role in forest regeneration by dispersing the seeds of their favorite fruit trees. The shade coffee plantation, in spite of control by humans, is a renewing system whose habitat can be maintained or even improved to provide habitat for native fauna.

The long-term persistence of this population is therefore possible with appropriate management and intervention. The situation in Mombacho presents a unique opportunity to connect conservation and agricultural production in an effective way. Although Mombacho's coffee growers are unlikely to abandon current shade growing practices in the near future (the climate in this area is relatively hot and dry, necessitating the use of shade trees to filter moisture from the air; the few sun coffee plantations in the area have not fared well), the current fluctuations and depressions of the world coffee market underscore the need for incentives to reward the use of minimal-impact agricultural practices in the tropics: as coffee prices have plummeted, widespread unemployment and population displacement has resulted throughout Latin America (Gonzalez, 2001), conditions which could easily lead to increased resource extraction by landless, and now jobless, plantation workers. Coffee exporting economies require the development of specialty coffees, such as organic, shade-grown, and fair trade varieties

that command premium prices less vulnerable to capricious markets (Forero, 2001). Additionally, stronger regulation of coffee production by the International Coffee Organization is critical to preventing future overproduction, which results in plummeting coffee prices, deforestation, and conversion of shade coffee to other, higher-yield agricultural production (O'Brien and Kinnaird, 2003). Integrating primate conservation, sustainable agriculture, and coffee certification and purchasing programs in Mombacho is key to the long-term survival of the howlers and other fauna in the shade coffee plantations (McCann *et al.*, 2002).

Suggestions for Long-Term Management

The Wildlife Conservation Society continues to work with coffee growers and distributors in the United States and Nicaragua to develop a “monkey-friendly” coffee certification program that will guarantee higher prices for growers whose plantations support primate populations and who plant trees used by the howlers and other animals, and return funds to the Mombacho community for environmental education and community improvement. Recently, Green Mountain Coffee has expressed interest in partnering with WCS on this initiative. Based on my data and recent insights regarding conservation initiatives in shade coffee plantations (e.g., see O'Brien and Kinnaird, 2003; Rappole *et al.*, 2003), I provide some suggestions for the development of a long-term management plan for primate conservation in Mombacho and a coffee certification program incorporating primate conservation into its criteria.

Primate conservation in Mombacho should have at least three foci: (1) the maintenance and improvement of habitat in shade coffee plantations for wildlife; (2) the protection and restoration of habitat in the Reserva Natural Volcán Mombacho (RNVM) and the extension of the reserve; and (3) benefits to landowners, coffee plantation workers, and other stakeholders which are directly tied to the maintenance of primate and wildlife populations. Given that the majority of Mombacho's forests are shade coffee plantations, integrating coffee production and biodiversity conservation is critical to the survival of wildlife in this area. Howlers can serve as an umbrella and focal species for conservation in this area; maintaining habitat for howlers should also conserve habitat for other arboreal mammals (e.g., kinkajous, coatis, porcupines, etc.), resources for frugivorous terrestrial mammals (agoutis and pacas), and habitat for numerous birds and reptiles. The density of howlers in Mombacho is known to vary inversely with habitat disturbance (McCann *et al.*, 2003), meaning that howler presence and density may be a useful measure of habitat quality in coffee plantations. A certification program for Mombacho's shade coffee plantations could provide incentive for maintenance and restoration of forested areas in plantations. Certified shade coffee can be marketed to consumers as biodiversity friendly, selling for a higher price in order to provide incentives to growers to maintain wildlife habitat (Rappole *et al.*, 2003). A number of coffee certification systems have been developed which incorporate ecosystem and wildlife conservation, forest preservation and reforestation, reduced agrochemical input, community relations, fair wages and conditions for workers, and planning and monitoring (Conservation International *et al.*, 2001; Rainforest Alliance, 2002).

A key aspect of shade coffee certification in the Mombacho area should be maintaining the presence and density of howlers in the shade coffee plantations. Bird diversity has sometimes been used as a measure of a shade coffee plantation's ability to serve as wildlife habitat (Greenberg *et al.*, 1997). However, monitoring birds is difficult as it requires experienced observers who can recognize birds upon brief sightings or by calls (or who have the specialized skills necessary to trap and release birds), standardization by time of year to account for variation in the presence of migratory species, and determination of the degree to which the bird community represents forest versus open-habitat specialists (presence of the latter suggesting that the coffee plantation is not serving as wildlife refuge for native forest species). This makes reliable wildlife monitoring by plantation owners and workers difficult. However, monitoring the presence of primates is much easier for lay people. Primate groups have localized home ranges (meaning that their presence more accurately reflects local conditions than does the presence of more mobile bird species), species, groups, or even individuals can be recognized, and it is relatively simple to maintain counts of group size and composition. Initial membership in a certification program should include the presence of howlers in the property and the regular monitoring of groups by both the certifying organization (possibly Green Mountain Coffee or a partner NGO) and the plantation owners. A "bounty" or added financial reward could be offered for exceeding a certain primate density or for troops which are maintaining their size or producing offspring. These rewards would serve as incentive to discourage harassment of primates and could also be tied to cessation of hunting and tree removal within a plantation.

Based primarily on relationships between habitat characteristics and avifauna diversity, Rainforest Alliance (2002) has developed a system of shade coffee certification criteria that can be applied or modified for use in Mombacho. They recommend that: shade trees comprise at least 12 native species which are “well distributed” throughout the plantation; that the density of trees be at least 70 stems/ha; emergent trees be present throughout the farm; shade be structurally complex, with at least 2 strata; and that “enough” of the shade trees are non-deciduous to provide continuous shade and habitat. La Luz probably meets all of these criteria; however, it is not clear that these criteria meet the needs of La Luz’s primates. To maintain howler populations, plantations should contain a suite of species that constitute key food resources so that edible phenophases are available throughout the year. Rather than focus on species numbers *per se* (which should presumably constitute 20 or more species for howler survival; Chapter 3), community composition is more critical. Certified plantations should contain sufficient *Ficus* trees to support primates and other arboreal frugivores, a number of other trees that provide pulpy fruit at various times of the year (for example, *Spondias*, *Manilkara*, *Brosimum*, *Cecropia*), and a variety of leguminous species (i.e., not just *Inga* and *Gliricidia*) to provide year-long access to high-quality foliage and seasonally-available flowers. Existing shade tree communities should be enhanced through reforestation of native trees (possibly through a nursery program) and careful monitoring of tree pruning to maintain arboreal habitats and sufficient canopy cover.

Coffee certification must be coupled with the protection of existing forests and reforestation when possible. Increased coffee prices can lead to the conversion of forest

to coffee plantation (O'Brien and Kinnaird, 2003), and shade coffee certification must proceed in such a manner that discourages this degradation. Ravines and areas not suitable for cultivation should be left undisturbed, or even reforested with native species. Fragments of less-disturbed forest should be identified and preserved intact; although howlers may prefer shade coffee to some regenerating areas, these fragments are probably critical to the long-term regeneration of Mombacho's forests, and serve as habitat for other wildlife less able to exploit shade coffee. Preservation of these areas, including prohibition of timber extraction and all hunting, should be made a condition of certification. Preservation and extension of the RNVM is also critical to primates: howlers probably use the area as a corridor for dispersal, while capuchins and possibly spider monkeys are largely confined to the less-disturbed habitat available in this area. Fines and/or removal from the certification program should result if growers make incursions into the reserve or allow resource extraction by employees. Ideally, in the future the reserve should be expanded, with the government or an NGO buying out the more rustic plantations on Mombacho's eastern flanks to reforest these areas and extend the reserve.

Finally, wages and living conditions must be improved for employees in coffee plantations, and funds generated from sales of coffee and tourism to the reserve must be returned to the Mombacho community through education and infrastructure improvement. It has been argued (e.g., Oates, 1999) that conservation initiatives tied to such development projects are ultimately detrimental to conservation goals because they attract new settlers to an area of previously low human density. While this may apply in

more remote areas, Mombacho is already very densely settled with a population of permanent residents who turn to resource extraction when their wages do not meet their needs. My subjective impression is that improved education, roads, and wages (or, alternately, food bonuses from employers) will not attract a new wave of settlers from nearby urban areas. However, with improved wages or food access, initiatives to ban all hunting (none of which is likely to be sustainable given the very high numbers of humans and very low numbers of prey species) are more likely to succeed due to reduced needs for cash and protein. Although there are few health clinics and no paved roads, Mombacho does boast several primary schools, which nearly all children attend. Fundación Cocibolca already conducts environmental education in these community schools, and information and activities centered on primates can easily be incorporated. Just as important is taking this message to the broader community of plantation owners, managers, and employees. One-on-one conversations, town hall meetings, tours, and the distribution of literature and posters, in conjunction with the financial incentives of certification, would increase environmental awareness and interest in protecting wildlife in Mombacho, a critical component of Mombacho's primates are to survive in the long-term.

CONCLUSION

In this dissertation, I have described the ecology and behavior of howling monkeys living in a shade coffee plantation and related my results to predictions based on foraging theory, primate socioecology, and expectations regarding primate response to

habitat disturbance. Additionally, I have discussed the conservation implications of my research and presented some options for future management of the population. My research has a number of theoretical and practical implications. Firstly, this work demonstrates that optimal foraging theory can be used to predict herbivore food choice (in a broad sense) when the constraints of nutrient mix, fiber content, and secondary metabolite content are taken into consideration. Folivorous primates are not obligated to feed selectively when nutrient content (or, in the case of structural feeding deterrents, digestive capacity) is not limiting. My research also demonstrates the great importance of information on both food abundance and nutrient content in explaining primate food selection; without *detailed* data on both of these aspects, patterns of food choice by the La Luz howlers would have been difficult to explain.

My research also corroborates the explanatory power of the “ecological model” of primate social relationships in relation to resource quality and distribution. In fact, the howlers at La Luz seem to conform to predictions better than some conspecifics, demonstrating the variability in basic aspects of primate social structure, such as patterning and strength of dominance relationships, seen in one primate species inhabiting different environments. La Luz howlers may differ from those studied at La Pacifica in fundamental aspects of female social relationships. In spite of the many studies conducted on mantled howlers, social organization and dominance has been studied at few sites, and perhaps results from Finca La Pacifica should not be taken as the norm for the species. Additionally, I demonstrate that competition, even at very low

levels, can be detected and may have demonstrable, if subtle, effects on primate behavior, even amongst folivores.

Perhaps most significantly, I have demonstrated that howlers can survive in the shade coffee plantations of Mombacho Volcano. Contrary to my initial expectations, these forests are not areas of occasional excursions, but, in fact, comprise the core range for many of Mombacho's howlers. These results challenge the common assumption that secondary areas constitute "poor" habitats and highlight the importance of explicitly stating the criteria used to characterize habitat quality. For example, from the point of view of howler conservation, Mombacho's shade coffee plantations are all but ideal, with abundant high-quality forage and few competitors or predators. However, from the point of view of conserving entire biotic communities characteristic of tropical ecosystems, shade coffee plantations are depauperate, and can only serve as buffer zones, population sinks, and dispersal corridors. Nevertheless, the persistence of primates and other wildlife in these agricultural areas in the absence of any formal management attests to the value of secondary and degraded habitat in landscape-level conservation plans. Although intact and undisturbed forest is clearly preferable for preserving tropical biodiversity, the value of agricultural lands, such as shade coffee plantations, in connecting reserves and providing some resources for humans must not be overlooked as the world's remaining wild areas become increasingly rare.

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APPENDIX I. Tree species composition in La Luz.

Family and Tree Species	Common Name	No. Stems	% Stems	% Basal Area	I_p^1
Anacardiaceae					
<i>Astronium graveolens</i>	Ron-rón	3	0.61	0.75	0.52*
<i>Spondias mombin</i>	Jocote jobo	6	1.22	1.08	0.15
Annonaceae					
<i>Annona purpurea</i>	Anona	2	0.41	0.19	--
Bigoniaceae					
<i>Tabebuia rosea</i>	Roble	1	0.20	0.15	--
Bombacaceae					
<i>Ceiba pentandra</i>	Ceiba	2	0.41	0.68	0.0
Boraginaceae					
<i>Cordia alliodora</i>	Laurel	7	1.42	0.77	0.36
Caesalpiniaceae					
<i>Hymenaea courbaril</i>	Guapinol	1	0.20	0.56	--
Cecropiaceae					
<i>Cecropia peltata</i>	Guarumo macho	80	16.26	11.70	0.52*
Combretaceae					
<i>Terminalia oblonga</i>	Guayabón	3	0.61	0.67	0.52*
Elaeocarpaceae					
<i>Muntingia calabura</i>	Capulín	1	0.20	0.08	--
Euphorbiaceae					
<i>Croton panamensis</i>	Sangredrigo	1	0.20	0.11	--
<i>Sapium macrocarpum</i>	Palo de leche	4	0.81	0.43	-0.08
Fabaceae					
<i>Albizia guachapele</i>	Gavilán	11	2.24	1.77	0.09
<i>Diphysa robinoides</i>	Guachipilín	2	0.41	0.33	--
<i>Enterolobium cyclocarpum</i>	Guanacaste	32	6.50	15.28	0.20
<i>Erythrina fusca</i>	Gallito	4	0.81	0.90	0.34
Fabaceae sp.	?	1	0.20	0.10	--

Family and Tree Species	Common Name	No. Stems	% Stems	% Basal Area	I_P^1
<i>Gliricidia sepium</i>	Madero negro	113	22.97	18.35	0.50*
<i>Inga</i> sp. 1.	Guabillo	7	1.42	0.99	0.08
<i>Inga</i> sp. 2	Guabillo	10	2.03	1.58	0.09
<i>Inga</i> sp. 3	Guabillo	2	0.41	0.41	--
<i>Inga vera</i>	Guabillo río	27	5.49	3.57	0.50*
<i>Leucaena leucocephala</i>	Leucaena	2	0.41	0.25	--
<i>Lonchocarpus</i> sp.	?	1	0.20	0.14	--
<i>Lysiloma auritum</i>	Quebracho	1	0.20	0.28	--
<i>Pithecellobium saman</i>	Genízaro	9	1.83	2.36	0.63*
Lauraceae					
<i>Persea americana</i>	Aguacate	5	1.02	0.66	0.52*
Meliaceae					
<i>Cedrela odorata</i>	Cedro real	39	7.93	4.84	0.52*
<i>Guarea glabra</i>	Tololo	4	0.81	1.16	-0.12
<i>Trichilia</i> sp.	?	6	1.22	0.77	0.15
Moraceae					
<i>Castilla elastica</i>	Hule	1	0.20	0.24	--
<i>Ficus costaricana</i>	Chilamate	23	4.67	10.78	0.12
<i>Ficus obtusifolia</i>	Matapalo	17	3.46	3.09	0.30
Myrtaceae					
“Cafecillo”	Cafecillo	1	0.20	0.18	--
<i>Eugenia salamensis</i>	Guacuco	1	0.20	0.21	--
Rubiaceae					
<i>Calycophyllum candidissimum</i>	Madroño	1	0.20	0.26	--
Rutaceae					
<i>Zanthoxylum</i> sp.	?	3	0.61	0.35	-0.08
Sapotaceae					
<i>Manilkara chicle</i>	Níspero Silvestre	8	1.63	2.41	0.52*
<i>Mastichodendron capiri</i>	Tempisque	6	1.22	1.96	-0.19

Family and Tree Species	Common Name	No. Stems	% Stems	% Basal Area	I_P^1
Simaroubaceae					
<i>Simarouba glauca</i>	Aceituno	1	0.20	0.07	--
Solanaceae					
<i>Acnistus arborescens</i>	Guitite	6	1.22	1.52	1.00*
Sterculiaceae					
<i>Guazuma ulmifolia</i>	Guácimo	23	4.67	3.65	0.50*
Tiliaceae					
<i>Luebea speciosa</i>	Guácimo de molenillo	4	0.81	2.37	- 0.78*
Verbenaceae					
<i>Vitex guameri</i>	Balona	6	1.22	1.57	0.45
Family/Species Unknown					
“3 Nervios”	?	1	0.20	0.07	--
“Araliaceae”	?	1	0.20	0.11	--
“Aspen Desconocido”	?	1	0.20	0.08	--
“Red fruit Desconocido”	?	1	0.20	0.15	--

¹ Morisita's standardized index of dispersion: values above 0 indicate a clumped distribution, values below 0 indicate a uniform distribution; * $P < 0.05$, significant departure from random distribution.

APPENDIX II. Water, Ash, Macronutrient, and Estimated Energy Content of Samples Analyzed.¹

Species/Part	Eaten ²	Water	Ash	NDF	ADF	Lignin	CP	AP	CP:ADF	WSC	Fat ³	ME _{AP}
<i>Albizia guachapele</i>												
Mature fruits (including seeds)	N		3.789		37.196	10.217	13.819		0.372			
Mature leaflets	Y	54.5	0.262	62.329	40.688	20.875	27.386		0.673	3.908		240
Young compound leaves	Y	71.3	3.111	26.939	17.086	8.191	39.205	37.287	2.295	3.355		307
<i>Annona purpurea</i>												
Immature fruits	R	73.1	5.800	66.785	56.101	21.864	10.645	4.352	0.190	3.199	0.083	215
Mature fruits	Y	70.8	5.832	65.836	54.174	17.939	10.674	5.445	0.197	4.097	0.029	217
<i>Astronium graviolens</i>												
Mature leaflets	Y	45.3	4.824	37.670	26.486	12.401	24.370		0.920	1.997		281
Young compound leaves	Y	68.9	3.923	21.913	17.754	6.940	29.414		1.657	2.255		320
<i>Bursera simarouba</i>												
Flowers	Y	80.0	7.924	38.588	32.364	22.441	19.239		0.594			
Immature fruits	R	75.1	8.160	57.194	44.865	14.948	10.751	7.195	0.240	3.047	0.083	228
Mature leaflet bases	N	60.2	9.296	42.343	32.475	12.674	14.084		0.434	5.764		257
Mature leaves	Y	60.4	12.101	43.154	32.490	13.947	13.962	6.157	0.430	6.239	0.039	244
Young leaflets	Y	77.1	9.099	46.509	41.849	28.213	16.467		0.393			
<i>Carica papaya</i>												
Mature fruits	R	83.0	12.723	14.265	12.806	1.401	11.985	10.996	0.936	35.000	0.005	310
<i>Cecropia peltata</i>												
Flower buds	Y	82.4	12.847	54.779	47.324	25.237	18.008		0.381	1.647		211
Flower buds	Y	79.5	9.196	42.768	37.782	24.930	19.352	9.724	0.512	4.105	0.086	254
Flowers	Y	81.1	6.020	47.820	41.244	24.907	18.133		0.440	7.023		255
Immature fruits	Y	82.8	4.987	54.591	40.769	21.121	17.235		0.423	3.679	0.019	244
Mature fruits	Y	72.3	8.631	55.338	46.797	27.641	10.566	6.977	0.226	7.559	0.128	231

Species/Part	Eaten ²	Water	Ash	NDF	ADF	Lignin	CP	AP	CP:ADF	WSC	Fat ³	ME _{AP}
Mature fruits (including seeds)	Y	68.4	6.245	55.804	47.220	29.904	8.882	6.124	0.188	4.838	0.268	241
Mature fruits (including seeds)	Y	84.1	9.944	47.190	31.292	17.125	14.480	6.204	0.463	4.873	0.018	243
Mature fruits (including seeds)	Y	59.4	4.038	31.231	26.270	16.349	5.962	3.319	0.227	29.453	0.069	308
Mature leaves	R	71.8	12.369	56.722	46.407	19.473	17.863		0.385	2.325	0.026	209
Seeds	S	72.3	5.530	69.633	59.308	39.631	8.536		0.144		0.152	
Young leaves	Y	76.9	9.463	57.552	51.453	34.678	26.337	10.790	0.512	1.483	0.009	215
<i>Cedrela odorata</i>												
Mature leaflets	N	64.8	11.276	44.279	30.256	10.396	22.233	15.085	0.735	3.109	0.045	241
Mature leaflets	N	58.7	12.834	36.915	26.230	10.299	18.889	14.363	0.720	7.828	0.079	254
<i>Ceiba pentandra</i>												
Young leaflets	Y	78.4	6.472	41.304	37.349	22.276	25.584	14.189	0.685	3.569	0.006	265
<i>Diospyros nicaraguensis</i>												
Mature fruits	Y	56.4	2.258	66.100	57.369	36.853	4.619		0.081	5.213		233
<i>Dyphisa robinoides</i>												
Flowers	Y	79.6	7.584	29.221	18.829	6.470	25.416		1.350	16.566		290
<i>Enterolobium cyclocarpum</i>												
Flowers	Y	74.0	5.683	38.449	29.296	17.014	29.054		0.992	6.241		274
Mature leaflets	Y	56.6	6.109	54.761	45.718	33.796	22.497	10.821	0.492	4.596	0.047	237
Raches	N	57.1	2.621	69.669	57.641	24.456	10.560		0.183			
Young compound leaves	Y	67.4	4.537	40.712	30.853	17.348	30.492	25.320	0.988	3.717		272
Epiphytes												
“Dark Green” Mature leaves	Y	72.0	16.736	19.239	12.545	5.010	16.857	11.605	1.344	5.299	0.101	281
“Epiphyte no. 1” Fruits	Y	82.4	9.025	56.651	47.384	24.353	13.993		0.295	4.756		224
<i>Erythrina fusca</i>												
Leaves	Y	67.8	4.032	49.530	36.044	16.352	28.433		0.789	2.228		254

Species/Part	Eaten ²	Water	Ash	NDF	ADF	Lignin	CP	AP	CP:ADF	WSC	Fat ³	ME _{AP}
<i>Eugenia salamensis</i>												
Mature fruits	Y	57.5	3.937	72.342	63.599	27.197	4.878		0.077	3.327		211
Fabaceae sp. 1												
Mature leaflets	Y	48.0	9.382	52.843	35.442	12.332	18.456	14.506	0.521	3.973		230
Leaf buds	Y	73.9	6.262	47.173	36.788	9.289	36.074		0.981			
Young leaflets	Y	78.7	2.670	45.910	35.093	14.178	24.035		0.685	2.995		292
<i>Ficus benjamina</i>												
Young leaves	Y	80.3	5.493	40.341	29.503	15.207	10.847		0.368	4.755		278
<i>Ficus costaricana</i>												
Fruits	Y	60.8	8.058	61.513	49.272	27.261	7.531		0.153	3.254		219
Immature fruits (including seeds)	Y	56.7	9.356	53.280	40.273	20.136	7.700		0.191	2.659	0.025	234
Mature fruits	Y	69.1	10.213	46.285	38.058	20.394	5.777	2.366	0.152	12.081	0.045	248
Mature fruits (including seeds)	Y	72.5	9.980	47.840	39.335	21.651	7.476	2.909	0.190	14.444	0.045	244
Mature leaf petioles	Y	68.8	13.576	46.650	39.232	20.814						
Seeds	N	69.1	9.901	56.588	46.660	24.888	4.829		0.103		0.133	
Leaf buds	Y	82.3	3.522	52.975	45.626	26.600	15.700		0.344	3.705		254
Leaf buds	Y	82.0	9.192	45.104	35.670	19.102	17.429	7.004	0.489	5.215	0.133	250
Leaf buds	Y	81.7	5.635	59.772	52.661	32.657	15.507	3.797	0.294	6.747		230
Young leaves	Y	79.2	11.067	58.589	55.484	34.623	13.518	2.003	0.244	3.077	0.064	212
Young leaves	Y	78.9	11.204	54.831	50.262	33.020	11.190	0.634	0.223	3.017	0.072	221
<i>Ficus obtusifolia</i>												
Mature fruits	Y	74.2	6.089	66.837	58.017	25.713	6.763		0.117	2.250	0.036	215
Mature leaves	N	13.446	60.386	49.671	25.501	12.220		0.246	1.450	0.025	0.025	198
Seeds	N	74.2	5.156				7.675				0.006	
<i>Ficus spp.</i>												
Mature fruits	Y	74.4	6.959	61.843	55.835	31.102	8.470	0.814	0.152	3.585	0.041	223

Species/Part	Eaten ²	Water	Ash	NDF	ADF	Lignin	CP	AP	CP:ADF	WSC	Fat ³	ME _{AP}
Mature fruits	Y	82.5	7.666	58.348	52.763	29.446	9.001		0.171	3.265	0.003	228
Mature leaves	N		11.347	64.217	54.085	27.953	8.712		0.161	1.191	0.112	200
Mature leaves	Y	62.5	7.045	47.641	37.353	14.363	10.862	4.811	0.291	6.261		255
Seeds	N	74.4	6.280	68.441	64.635	39.922	8.616	1.112	0.133		0.019	
Seeds	N	82.5	8.022				10.926					
<i>Gliricidia sepium</i>												
Flowers	Y	89.6	8.303	33.178	25.845	12.364	24.812		0.960	11.634		278
Mature leaflets	Y	69.6	6.237	47.953	33.656	17.877	23.529	20.040	0.699	6.797		252
Mature leaflets	Y	67.2	3.493	35.450	24.268	13.634	22.104		0.911	6.923		293
Mature leaflets	I	54.4	7.368	38.201	29.146	18.162	22.841	13.100	0.784	6.107	0.112	271
Young leaflets	S	74.3	3.313	37.759	28.465	13.244	30.203		1.061			
<i>Guarea glabra</i>												
Mature fruits	N		3.340	82.746	64.025	28.005	4.732		0.074	0.290	0.263	191
Mature leaves	N		10.232	60.229	39.403	18.035	23.046		0.585	0.071		207
<i>Inga sp.</i>												
Mature fruit	N		3.942	47.664	25.934	11.664	13.634		0.526	0.236	0.094	266
<i>Inga vera</i>												
Mature fruit	N		5.166	74.102	55.277	11.689	12.376		0.224	0.450	0.024	199
Mature leaflets	I	44.4	10.409	53.804	45.126	27.177	20.071		0.445			
Mature leaflets	Y	52.8	5.714	54.280	41.808	22.956	27.682	20.921	0.662	4.082		237
Mature leaflets	Y	54.8	4.555	51.025	42.467	20.988	22.977		0.541	3.860		251
Mature leaflets	Y	53.4	8.215	51.740	39.799	19.143	24.110	19.961	0.606	6.939	0.050	235
Young leaflets	Y	71.9	4.199	60.424	49.505	28.009	24.347		0.492	2.286		230
<i>Luebea speciosa</i>												
Mature fruits	N	3.470	84.426	70.623	31.407	8.974		0.127	0.905	0.134	0.134	184
Mature leaves	Y	55.3	8.239	69.084	54.706	21.943	15.184	6.624	0.278	4.541		197
Young leaves	Y	75.4	5.676	54.251	47.129	19.798	15.472		0.328	3.447		242

Species/Part	Eaten ²	Water	Ash	NDF	ADF	Lignin	CP	AP	CP:ADF	WSC	Fat ³	ME _{AP}
<i>Lysiloma aurita</i>												
Flowers	Y	70.4	5.552	39.425	34.577	21.008	19.445		0.562	10.705		276
Young compound leaves	Y	70.7	8.451	50.097	33.029	12.678	34.429	30.032	1.042	4.895		233
Mature compound leaves	Y	53.5	4.543	45.912	41.153	26.445	13.566		0.330			
<i>Manilkara chicle</i>												
Mature fruits	Y	65.4	3.289	45.005	38.528	25.669	4.826	1.888	0.125	25.000	0.177	280
<i>Mastichodendron capiri</i>												
Flowers	Y	46.7	3.999	38.762	27.424	13.086	20.913		0.763	6.887		283
Mature leaf petioles	Y	57.6	12.048	41.289	29.706	9.273	8.666	7.513	0.292	7.893		251
Mature leaves	Y	57.9	5.809	43.941	32.006	12.335	17.128	15.409	0.535	5.460		266
Mature leaves	N	67.6	10.593	50.567	32.298	11.326	17.584	11.928	0.544	9.169	0.135	231
Myrtaceae sp. (“Cafecillo”)												
Mature fruits	Y	73.9	6.095	23.058	15.927	2.562	7.982	5.623	0.501	42.025	0.012	318
<i>Persea americana</i>												
Mature leaves	N		6.113	59.685	50.569	28.162	13.244		0.262	0.356	0.023	229
<i>Pithecellobium saman</i>												
Mature leaflets	Y	42.0	4.532	68.514	63.323	39.927	25.244	19.434	0.399	4.505	0.004	209
Sapindaceae sp.												
Young leaves	Y	64.2	5.193	55.361	46.625	26.773	13.342	4.890	0.286	4.874	0.059	243
<i>Sapium macrocarpum</i>												
Young leaves	Y	79.9	10.053	24.093	16.629	3.275	17.953		1.080	8.043		295
<i>Simarouba glauca</i>												
Mature fruits	Y	65.1	4.832	41.509	42.894	28.583	5.760	1.644	0.134	38.874	0.079	281
<i>Spondias mombin</i>												
Mature fruits	Y	76.8	6.601	25.436	20.175	10.134	9.657	6.670	0.479	29.853	0.024	309
Mature fruits	Y	75.0	6.899	26.327	21.179	9.905	7.623	5.062	0.360	32.583	0.019	307
Young leaves	Y	66.4	7.505	41.679	43.399	27.785	22.184		0.511	2.025		262

Species/Part	Eaten ²	Water	Ash	NDF	ADF	Lignin	CP	AP	CP:ADF	WSC	Fat ³	ME _{AP}
<i>Spondias purpurea</i>												
Mature fruits	Y	66.8	5.128	38.974	30.434	14.048	5.956	3.929	0.196	29.026	0.009	285
Young leaves	Y	72.8	5.757	33.797	34.822	23.916	16.678		0.479			
<i>Terminalia oblonga</i>												
Mature leaves	Y	72.9	13.183	27.852	19.221	5.417	15.708	7.275	0.817	5.778	0.112	275
<i>Trichilia sp.</i>												
Mature leaves	N		10.994	61.508	44.969	22.948	15.203		0.338			
Unknown												
Mature leaves	Y	60.6	8.209	51.977	34.175	21.441	21.918	17.098	0.641	2.891		235

¹NDF = neutral detergent fiber, ADF = acid detergent fiber (hemicellulose + lignin), BP = bound protein, AP = available protein, WSC = water soluble carbohydrate. Water reported as percentage of fresh weight, ME_{AP} reported as kcal/100 g dry matter; all other values are reported as percent of dry matter.

²Y = Regularly eaten; R = Rarely eaten; N = Never eaten; I = Ignored by howlers from tree collected but known to eat phenophase in other conspecifics; S = seeds that are eaten with fruit but defecated whole.

³Missing values for crude fat assumed to be zero for calculation of energy content.

APPENDIX III. Micronutrient Content of Plant Samples Analyzed.¹

Species/Part	Eaten	Ca	Co	Cr	Cu	Fe	K	Mg	Mn	Na	P	Zn	Ca:P
<i>Albizia guachapele</i>													
Mature leaflets	Y	0.69	13.2	2.41	8.1	138.0	1.46	0.181	25.5	0.0310	0.167	22.1	4.13
Young compound leaves	Y	0.18	35.2	2.25	17.9	70.5	2.62	0.183	26.6	0.0169	0.398	41.9	0.45
<i>Annona purpurea</i>													
Immature fruits	Y	0.19	6.1	1.85	18.9	26.1	1.7	0.149	4.9	0.0101	0.148	20.5	1.28
Mature fruits	Y	0.22	6.8	2.29	15.3	35.8	2.71	0.128	6.5	0.0073	0.192	18.0	1.15
<i>Astronium graveolens</i>													
Mature leaflets	Y	0.93	6.3	2.14	8.5	94.1	1.43	0.294	20.1	0.0270	0.216	19.8	4.31
Young compound leaves	Y	0.37	45.7	2.13	24.2	93.2	2.78	0.202	25.6	0.0090	0.463	45.5	0.80
<i>Bursera simarouba</i>													
Immature fruits	N	0.62	4.7	1.73	13.0	47.5	1.51	0.347	9.1	0.0077	0.205	59.7	3.02
Mature leaflet bases	N	1.19	107.0	1.86	6.5	102.0	1.39	0.359	18.5	0.0190	0.112	23.1	10.63
Mature leaves	Y	1.09	82.3	2.13	7.0	102.0	1.39	0.364	16.0	0.0142	0.125	19.5	8.72
<i>Carica papaya</i>													
Mature fruits	Y	0.42	32.0	1.55	3.9	40.6	5.23	0.480	8.3	0.0156	0.372	9.9	1.13
<i>Cecropia peltata</i>													
Flower buds	Y	1.69	19.3	1.57	15.7	123.0	1.96	0.526	41.4	0.0036	0.316	38.3	5.35
Flower buds	Y	1.08	4.9	2.05	13.2	94.3	1.78	0.424	24.4	0.0025	0.309	32.2	3.50
Flowers	Y	1.03	13.8	1.90	14.0	104.0	2.15	0.451	20.1	0.0038	0.260	32.2	3.96
Immature fruits	Y	1.39	35.3	2.01	13.0	109.0	1.43	0.455	35.7	0.0078	0.282	30.6	4.93
Mature fruits	Y	1.16	8.0	2.35	83.1	105.0	2.16	0.439	20.0	0.0402	0.218	42.4	5.32
Mature fruits (including seeds)	Y	0.89	4.0	2.14	10.2	74.9	1.36	0.365	16.2	0.0050	0.164	24.4	5.43
Mature fruits (including seeds)	Y	1.36	31.7	1.81	13.4	105.0	1.54	0.439	31.4	0.0086	0.266	29.8	5.11
Mature fruits (including seeds)	Y	0.60	8.4	1.96	7.4	63.0	0.79	0.226	16.2	0.0034	0.141	19.2	4.26

Species/Part	Eaten	Ca	Co	Cr	Cu	Fe	K	Mg	Mn	Na	P	Zn	Ca:P
Mature leaves	N	1.47	18.4	1.90	12.8	133.0	2.29	0.450	40.0	0.0297	0.151	18.9	9.74
Seeds	N	0.99	3.4	2.73	19.8	83.1	1.13	0.295	25.9	0.0232	0.205	30.9	4.83
Young leaves	Y	1.24	10.5	2.29	15.5	145.0	2.48	0.484	40.9	0.0087	0.446	37.8	2.78
<i>Cedrela odorata</i>													
Mature leaflets	N	1.47	15.6	1.88	7.2	137.0	1.89	0.263	24.7	0.0441	0.146	19.4	10.07
Mature leaflets	N	2.04	10.2	1.93	7.7	159.0	1.07	0.237	20.0	0.0451	0.141	28.3	14.47
<i>Ceiba pentandra</i>													
Young leaflets	Y	0.355	6.5	1.81	22.8	49.9	2.27	0.337	15.9	0.0090	0.436	38.1	0.81
"Dark Green Epiphyte"													
Mature leaves	Y	2.14	22.6	1.95	1.7	192.0	4.86	0.205	11.2	0.0874	0.091	15.3	23.52
<i>Diospyros nicaraguensis</i>													
Mature fruits	Y	0.445	15.9	1.98	3.2	41.6	2.4	0.146	6.2	0.0157	0.126	12.9	3.53
<i>Enterolobium cyclocarpum</i>													
Flowers	Y	0.173	43.3	2.05	39.3	76.4	2.81	0.390	31.1	0.0468	0.391	48.7	0.44
Mature leaflets	Y	0.334	7.9	2.02	6.8	108.0	1.43	0.638	29.4	0.0124	0.138	15.5	2.42
Young compound leaves	Y	0.272	81.2	2.06	8.9	99.1	2.99	0.383	25.6	0.0184	0.307	24.1	0.89
<i>Eugenia salamensis</i>													
Mature fruits	Y	0.534	10.3	1.6	7.8	53.6	1.18	0.146	8.0	0.0054	0.057	10.5	9.37
Fabaceae sp. 1													
Mature leaflets	Y	3.17	38.7	1.7	5.9	187.0	0.52	0.245	37.0	0.1150	0.105	7.3	30.19
<i>Ficus benjamina</i>													
Young leaves	Y	1.36	47.4	1.74	7.7	119.0	3.28	0.311	14.3	0.0924	0.176	13.3	7.73
<i>Ficus costaricana</i>													
Fruits	Y	1.79	14.7	1.52	9.1	118.0	1.38	0.366	28.6	0.0113	0.134	20.4	13.36
Mature fruits	Y	2.7	7.4	2.05	29.2	150.0	1.22	0.455	24.3	0.0268	0.101	26.8	26.73
Mature fruits (including seeds)	Y	2.03	11.8	1.49	11.2	134.0	1.13	0.393	17.7	0.0234	0.114	15.5	17.81

Species/Part	Eaten	Ca	Co	Cr	Cu	Fe	K	Mg	Mn	Na	P	Zn	Ca:P
Seeds	N	2.45	7.4	2.12	15.8	140.0	0.896	0.335	23.4	0.0187	0.106	20.7	23.11
Leaf buds	Y	0.642	114.0	1.75	19.2	78.4	3.29	0.403	12.8	0.0145	0.34	34.1	1.89
Leaf buds	Y	0.692	22.6	1.7	17.5	74.7	2.91	0.489	18.9	0.0161	0.317	44.2	2.18
Leaf buds	Y	0.77	38.1	1.73	16.6	128.0	3.33	0.450	19.1	0.0164	0.302	40.7	2.55
Young leaves	Y	0.999	57.5	2.03	15.8	81.1	3.69	0.518	20.2	0.0278	0.314	35.4	3.18
Young leaves	Y	1.35	46.6	1.91	11.3	109.0	3.15	0.578	14.8	0.0374	0.183	25.0	7.38
<i>Ficus sp.</i>													
Mature fruits	Y	0.975	11.2	2.16	15.7	103.0	2.88	0.255	20.6	0.0130	0.223	20.9	4.37
Mature leaves	Y	0.796	12.8	1.95	5.8	75.8	2.4	0.289	13.6	0.0509	0.128	13.8	6.22
Seeds	N	0.839	7.1	2.49	14.4	92.4	2.46	0.159	16.0	0.0103	0.223	27.3	3.76
<i>Gliricidia sepium</i>													
Mature leaflets	Y	1.38	49.7	2.28	7.4	173.0	2.29	0.337	22.5	0.0242	0.190	16.0	7.26
Mature leaflets	Y	1.70	11.5	2.09	4.2	205.0	1.69	0.578	50.9	0.0175	0.165	11.6	10.30
Mature leaflets	N	1.15	13.7	1.85	2.8	99.1	2.00	0.305	55.1	0.0058	0.217	14.2	5.30
<i>Inga vera</i>													
Mature leaflets	Y	0.98	17.1	2.01	15.0	110.0	1.53	0.212	59.3	0.0722	0.191	18.6	5.13
Mature leaflets	Y	1.36	10.6	1.97	14.1	110.0	1.22	0.261	34.8	0.0245	0.150	9.5	9.07
Mature leaflets	Y	1.14	35.5	1.80	16.6	104.0	1.25	0.14	89.0	0.0391	0.150	11.0	7.60
Young leaflets	Y	0.18	15.4	1.86	22.0	76.3	1.38	0.165	26.5	0.0123	0.315	34.3	0.57
<i>Luebea speciosa</i>													
Mature leaves	Y	1.87	7.9	1.88	9.2	136.0	1.26	0.339	68.6	0.0135	0.158	7.3	11.84
<i>Lysiloma aurita</i>													
Flowers	Y	0.34	33.3	2.83	10.4	111.0	1.98	0.214	20.2	0.0265	0.293	26.0	1.16
Young compound leaves	Y	1.01	7.8	1.82	8.0	87.3	2.69	0.326	23.9	0.0105	0.249	12.2	4.06
<i>Manilkara chicle</i>													
Mature fruits	Y	0.24	14.4	1.71	2.0	84.7	1.05	0.0916	4.7	0.0292	0.0339	0.5	7.08

Species/Part	Eaten	Ca	Co	Cr	Cu	Fe	K	Mg	Mn	Na	P	Zn	Ca:P
<i>Mastichodendron capiri</i>													
Flowers	Y	1.08	10.4	1.88	5.2	65.5	2.07	0.273	12.9	0.0552	0.228	11.9	4.74
Mature leaf petioles	Y	3.13	3.0	1.81	2.8	161.0	2.47	0.427	32.0	0.0328	0.0619	0.5	50.57
Mature leaves	Y	2.06	11.1	1.99	5.2	148.0	1.35	0.186	15.8	0.0400	0.0912	0.7	22.59
Mature leaves	N	2.53	142.0	2.04	5.3	178.0	1.42	0.303	17.4	0.0818	0.0964	2.2	26.24
Myrtaceae sp. (“Cafecillo”)													
Mature fruits	Y	0.15	2.9	1.58	11.6	35.2	2.05	0.173	10.7	0.0117	0.124	15.9	1.21
<i>Pithecellobium saman</i>													
Mature leaflets	Y	0.74	219.0	1.91	16.3	71.4	1.22	0.0755	17.3	0.0159	0.161	0.5	4.60
Sapindaceae sp.													
Young leaves	Y	0.34	48.7	1.55	17.7	43.5	2.16	0.228	9.2	0.0309	0.239	21.2	1.42
<i>Sapium macrocarpum</i>													
Young leaves	Y	0.80	36.0	1.52	12.3	115.0	3.14	0.375	25.6	0.0192	0.303	45.6	2.64
<i>Simarouba glauca</i>													
Mature fruits	Y	0.21	11.4	1.45	5.3	20.5	1.62	0.183	4.0	0.0044	0.0585	0.5	3.59
<i>Spondias mombin</i>													
Mature fruits	Y	0.25	6.1	1.32	12.7	29.5	2.21	0.131	6.7	0.0050	0.181	0.6	1.38
Mature fruits	Y	0.27	5.1	1.32	11.9	40.4	2.01	0.116	6.6	0.0024	0.135	0.5	2.00
Young leaves	Y	0.79	117.0	1.51	23.0	76.7	5.5	2.76	34.2	0.0333	0.549	25.6	1.44
<i>Spondias purpurea</i>													
Mature fruits	Y	0.14	2.2	1.29	6.6	24.8	2.17	0.144	4.2	0.0037	0.173	2.4	0.81
<i>Terminalia oblonga</i>													
Mature leaves	Y	2.9	40.2	2.01	11.0	179.0	1.92	0.283	49.5	0.0916	0.156	8.5	18.59
Unknown													
Mature leaves	Y	0.78	117.0	2.05	12.2	72.9	3.45	0.679	11.9	0.0525	0.454	17.1	1.72

¹ Ca, K, Mg, Na, and P reported as % dry matter; Co, Cr, Cu, Fe, Mn, and Zn reported as mg/kg.