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Diet, Activity and Ranging Behavior of *Alouatta pigra* in Monkey River, Belize

by

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ABSTRACT

Three groups of black howler monkeys (*Alouatta pigra*) were observed in Monkey River, Belize from June 1999 to August 1999, with the objective of determining diet, ranging, and activity patterns. The results revealed variations in all three aspects of behavior between age-sex classes and groups. In comparison to published accounts, the results fit roughly into the parameters for *Alouatta*, a genus known for its large degree of variability on the interspecific and intraspecific level. The small home ranges, low level of diversity in diet, and high levels of frugivory may be products of the short period of time each group was studied.

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INTRODUCTION

The primary goal of this thesis is to provide a detailed description of the group size and composition, home range, diet, and activity budgets of three groups of black howler (*Alouatta pigra*) monkeys from Monkey River, Belize. This *Alouatta pigra* population will be compared to published accounts of other species of the genus *Alouatta* for these variables.

In this chapter, a brief overview of the group size and composition, home range size, diet, and activity budgets of other species of the genus *Alouatta* will be provided. At present, few publications specifically focus on *Alouatta pigra*. Therefore, the majority of the published data that is presented refers to other species in this genus.

The following chapter, Chapter 2 (Methods and Materials), focuses on the methods applied throughout this study, the geographic location of the site, and the time period in which the study was performed.

In Chapter 3 (Results) I report the results of the study. Specifically I provide a quantitative description of the group size and composition, home range size, diet, and activity budgets for each of the three study groups, for each age-sex class, and for the total sample of animals from Monkey River. Chapter 4 (Discussion) compares these results to what is known about the other howler monkey populations in the genus *Alouatta*.

LITERATURE REVIEW

Overview of the Genus *Alouatta*

The genus *Alouatta* contains six species with the largest geographic distribution, in the New World, ranging from Southern Mexico to Northern Argentina (Rosenberg & Strier 1989). The common name, the scientific name, and the geographic distribution for each species are as follows:

Alouatta pigra: The Guatemalan or Belizean black howler monkey; southeastern Mexico, Belize, and Guatemala.

Alouatta palliata: The mantled howler monkey; southern Mexico, throughout Central America, and the west coast of Colombia and Ecuador.

Alouatta belzebul: The red-handed howler monkey; northeastern Brazil, south of the Amazon River.

Alouatta seniculus: The red howler monkey; northern South America, north of the Amazon River in the in the east and south in to Bolivia in the west.

Alouatta fusca: The brown howler monkey; southeastern Brazil to northeastern Argentina.

Alouatta caraya: The black howler monkey is found in southern Brazil, eastern Bolivia, Paraguay, and northern Argentina.

Due to the genus' lack of specialization, howler monkeys can exist in a wide variety of habitats including most types of forests, salt-water mangrove swamps, and savannahs (Neville et al. 1988). Howler monkeys have been reported existing in habitats at sea level and elevations exceeding 2,300 meters (Crockett & Eisenberg 1987). This variability allows the members of the genus to thrive in most neotropical habitats but it is complicated for researchers to make cross species comparisons.

Members of the genus *Alouatta* are among some of the largest of the New World Monkeys. Of the Neotropical primates, only animals from the genera *Ateles*, *Brachyteles*, and *Lagothrix* are of the approximate size or larger (Crockett and Eisenberg 1987). All six species are diurnal and the most noticeable morphological feature of the genus *Alouatta* is the enlarged hyoid, allowing members of the genus to "howl". The function of howling perhaps serves as a low energetic approach to spacing between two or more groups. Howling announces a group's location and eliminates the need for physical confrontations (Horwich & Gebhard 1983). In addition to a specialized vocal apparatus, howler monkeys possess a prehensile tail. The tail functions primarily as support mechanism during foraging bouts or locomotion throughout the forest canopy (Neville et al. 1988). The length of the tail is approximately the length of the body with a naked portion that enhances tactile stimulation (Rosenberg & Strier 1989).

All species of howler monkeys are sexually dimorphic. The degree of sexual dimorphism varies among each species (Neville et al. 1988). Adult female black howler monkeys (*Alouatta caraya*) weigh approximately 69% of adult males while adult female mantled howler monkeys (*Alouatta palliata*) weigh approximately 84% of the adult male's weight (Neville et al. 1988). Males and females in the genus both display external genitalia.

The large portion of leaves that are consumed by howler monkeys, has given rise to dental morphology that assists in masticating large amounts of leafy material. The stomachs of howler monkeys are elongated and globular allowing large amounts of vegetation to be processed (Rosenberg & Strier 1989).

Social Structure of *Alouatta*

Glander (1992) describes howler monkeys as living in multi-male multi-female groups, uni-male multi-female groups, or as solitary individuals. Unlike most primate species, both males and females emigrate at the juvenile stage of life. Recent emigrants have three alternatives: join up with another solitary individual, thus creating a new group, join an existing a group, or remain solitary. Due to the dispersal of both sexes, the adults of most groups consist of unrelated individuals. Joining another group eliminates competition for food and other limited resources among related kin and increases inclusive fitness of the emigrant's parents.

The result of bi-sexual dispersal is a linear dominance hierarchy that is inversely linked to age (Glander 1992). In order to join an existing group, a female emigrant must systematically supplant the other individuals. New females start supplanting infants and juveniles of both sex, and ultimately, the adult females. After this succession is accomplished she becomes the alpha female. If she fails to supplant the other females in the groups she leaves and attempts to join another group or remains solitary. Emigrant males on the other hand directly challenge the alpha male to join an existing group. If successful, the new male assumes the alpha position. In both strategies, the younger emigrant displaces the older members of an existing group which gives rise to the inversely age linked linear dominance hierarchy. Ken Glander's observations are based primarily on studies of mantled howler monkeys, *Alouatta palliata.*

Group Size and Composition

Many theories have been developed to explain the existence of primate social groups. Wrangham (1979) suggested that groups formed on the basis of food resources. Furthermore, the size and distribution of food resources will determine the size of the primate groups that feeds on the particular resource. Those species that feed primarily on widely distributed food resources can live in large groups with low levels of intragroup competition for food. Species that exploit small, patchy food resources, live in smaller groups with increased levels of intragroup competition for food.

Van Schaik (1983) has suggested that predator pressures have forced primates to exist in groups. This concept suggests that a high number of individuals will have a increased probability of detecting a predator and larger groups may play an effective role in predator defense. Van Schaik and Dunbar (1990) have hypothesized that group living may have evolved to resist infanticide by unrelated males. It is proposed that females band together and seek out males that can protect infants within a group from outside males.

Alouatta Group Size

The genus *Alouatta* poses interesting questions to the above hypotheses. Each hypothesis may play a role in howler monkey group living for the following reasons. First, most howler monkey troops are vulnerable to predation (Peetz et al. 1992). Secondly, howlers compete for food resources both within a group and between groups (Glander 1992, Sekulic 1982). Lastly, researchers in the field have observed outside males committing infanticide to unrelated infants (Agoramoorthy & Rudran 1995, Rudran 1979).

When reviewing published accounts, it becomes obvious that within the genus *Alouatta*, there exists an extreme amount of variation in group size and composition. The adaptability of the species and the members of the genus to thrive in habitats not suitable for other Neotropical primates, perhaps best explain this variation. Howler monkeys have been observed living alone or in groups that numbering two to forty individuals (Glander 1992, Chapman 1990). Variations of group size can change within the same

location throughout time due to a host of environmental factors. Crockett and Eisenberg (1987) mention the following influences that increase or reduce the mean group size in a specific location: epidemics, natural disasters, predations, abnormal seasonality, human habitat destruction or preservation, and human hunting. The numerous factors that can drastically influence group size in one site make it difficult to make accurate comparisons from site to site.

The ability of howler monkeys to inhabit marginal environments is probably responsible for such wide reports on group sizes. Rumiz (1990) compared two populations of black howler monkeys (*Alouatta caraya*) in Argentina. One population inhabited a small flooded island. The second population inhabited the forests near the riverbeds. The island population had an overall higher mean group size (10.2 animals) and population density (27.5 groups per square kilometer) in comparison to the forest population; mean group size of 6.4-8.4 animals and a population density of 5.7 individuals per square kilometer.

Some howler troops are found in sympatric associations with other primates (Chapman 1990, Simmen 1992). At such sites, howlers must share resources among other groups of Neotropical primate species. Simmen (1992) found that howler monkeys won and lost agonistic interactions between spider monkeys over *Bagassa* fruits. Constant loses at a preferred site may push a troop into a marginal habitat with reduced nutritional benefits. Furthermore, higher population densities would deplete resources rapidly. Glander (1992) reported red howlers living in secondary growth forest. The fact

that howlers obtain sufficient water from their diet may also increase their ability to colonize newly regenerating forests and poor environments (Bicca-Marques 1992). Troops inhabiting habitats with low carrying capacities should have reduced numbers. The ecological variability lends itself to group size variability among members of the same species and between species of howler monkeys.

The following chart illustrates the variations among group size between five of the currently recognized species of howler monkeys.

TABLE 1.1 Variations of Group Sizes

Author	Year	Species	Location	Mean Group Size
*Ostro et al.	1999	*A. pigra*	Community Baboon Sanctuary, Belize	7 10 6 4 4 3 8
Zucker & Clarke	1998	*A. palliata*	La Pacifica, Costa Rica	18
Julliot	1996	*A. seniculus*	Noraque Station, French Guiana	6
Bicca-Marques & Calegaro-Marques	1994	*A. caraya*	Santa Genera Reserve, Brazil	4.9
Simmen	1992	*A. seniculus*	Les Noragues, French Guiana	8
Glander	1992	*A. palliata*	La Pacifica, Costa Rica	15.5
Da Silvia Jr.	1981	*A. fusca*	Cantarirera Reserve, Brazil	5.8

*Ostro provides the mean group size for seven different groups that inhabit the Community Baboon Sanctuary in Belize.

Alouatta Group Composition

Howler monkeys are found living in; unimale multi female groups, multi male multi female groups, or as solitary individuals. Group compositions also vary within and between study sites. Neville et al. (1988), criticized the lack of a reliable methodology which contributes to this dilemma. Workers in the field define juveniles, sub adults, and adult individuals without a agreeable methodology, resulting in potentially unreliable results for group compositions.

Bisexual transfer in the genus *Alouatta* influences sex ratios and group composition. Males in howler monkey troops may transfer into new groups alone or with another individual (Agoramoorthy & Rudran 1995). New males may or may not evict the alpha male of the group. On rare occasions natal males will remain in their natal group (Clarke et. al 1994). Females may or may not remain in their natal group. Glander (1992) suggests that females leave their natal group to increase their foraging efficiency and to eliminate competition for food among kin. Females may also join a group alone or with another female. Glander (1992) found that males remain solitary for a longer period of time when compared to females. Longer periods of a solitary lifestyle increased the probability of falling prey to a predator, fighting or avoiding an established group, and consuming a lower quality of food. These factors increase the likelihood of death for a solitary male individual and may account for the fact increased number of female in groups.

Rumiz (1990) notes many social influences on group sizes are outcomes of the social structure of black howler monkeys. The dispersal of both sexes constantly changes the number of individuals in the group, the social composition, and the sex ratio. Recently transferred animals or infanticide change the group's dynamics in a similar fashion. These influences are characteristics of howler monkey social organization and do not take into account ecological factors.

Table 1.2 summarizes some published data on the age sex composition of howler groups. The chart provides data from three of the six species in the genus *Alouatta*. Among the groups in the same location there are differences in composition, as well as a large degree of variation between the three howler monkey species listed below.

TABLE 1.2 Howler Monkey Group Sizes and Compositions

Author	Year	Species	Mean Group Size	# of Adult Males	# of Adult Females	# of Juvenile Males	# of Juvenile Females	# of Infant Males	# of Infant Females
Agoora-moorthy & Rudran	1995	*A. seniculus*	12 13 11 9 9	1 1 1 1 1	4 4 3 3 4	4 2 3 1 2	2 4 1 2 1	1 2 3 2 0	0 0 0 0 1
Bica-Marque & Calegaro-Marque	1994	*A. caraya*	17	1	4	3	6	2	1
Julliot & Sabatier	1993	*A. seniculus*	6	1	2	2	0	0	1
Neves & Ryland	1991	*A. seniculus*	10	3	2	1	1	0	3
Bolin	1981	*A. pigra*	6 4 4 6 4 7	2 1 1 1 1 1	2 1 1 1 1 2	0 0 0 1 0 0	0 1 0 2 1 2	1 0 2 1 1 2	1 1 0 0 0 0

*The above chart serves only as an example to illustrate the variation in group compositions among groups of *Alouatta*.

Home Range

Home range and ranging behavior from location to location also varies tremendously among the members of the genus *Alouatta*. Differences in habitat quality, group sizes, and population densities all influence home ranges and ranging behavior (Neville et al. 1988).

Differences in home range are attributed to population densities and the quality of habitat. Ostro et al. (1999), found that *Alouatta pigra* use their home ranges in a seasonal manner. The troops used only 28% of their range in the month of April and traveled between feeding sites distributed within the home range. Ostro et al. compared ranging behavior in troops existing in two nature reserves in Belize. The first study group had smaller home ranges in comparison to the second population. The first study group inhabited a region with higher densities. The second population had a lower population density; this resulted in overall larger home ranges and fewer intergroup interactions. The second population inhabited an area with lower abundance and diversity of food resources. Ostro et al. (1999), found that the first population had a significantly larger day range pattern and smaller home ranges when compared to groups from the second population. Longer day ranges are attributed to the larger group sizes. The larger groups depleted the food at one site in a rapid manner when compared to the second population. In this case, ranging behavior is linked to group size (and food density and quality) and

not to the size of a group's home range. Ostro et al. (1999) findings agree with Crockett and Eisenberg (1987). Crockett and Eisenberg (1987) analyzed the home ranges of howlers in a variety of locations and found that home range is inversely related to howler population densities.

A high degree of home range overlap suggests that the troops are less territorial than once thought. Neville et al. (1988), propose that howler monkey troops maybe defensive if another troop is seen approaching their group and less defensive if a troop enters their range. Sekulic's (1982) work at Hato Masaguaral, Venezuela, noted that troops howled when another group was in sight. Sekulic's study site is densely populated with monkeys. Horwich and Gebhard (1983), indicated troops of *Alouatta pigra* howled due to territorial defense.

Howler monkeys may inhabit sympatric environments with other neotropical primates (Chapman 1990, Simmen 1992, Fedigan et al. 1985, Fedigan 1986, Cant 1986, Estrada & Estrada-Coates 1984). Howlers appear to act neutral in interspecific encounters (Neville et al. 1988). Simultaneous consumption or range overlap of specific trees quickly depletes resources and may increase home range and ranging behavior. Most dietary overlap occurs at large fruiting trees (Simmen 1992).

The table below serves as an overview of reported home ranges by the members of the genus *Alouatta*. Variations in home range (ha) size occur between sites and species.

TABLE 1.3 Howler Monkey Home Ranges between Sites

Author	Year	Species	Location	Home Range (ha)
* Ostro et al.	1999	*A. pigra*	CBS, Belize CBWS, Belize	9.6 18.7
** Stoner	1994	*A. palliata*	La Selva, Costa Rica	5-29
Chiapello	1994	*A. fusca*	Estancia Casa Branca, Brazil	4.13
Bicca-Marques & Calegaro-Marques	1994	*A. caraya*	Santa Genebra, Brazil	2
Julliot & Sabatier	1993	*A. fusca*	Nouragues, French Guiana	45
Simmen	1992	*A. seniculus*	Les Nouragues, French Guiana	22
Neves & Rylands	1991	*A. seniculus*	Reserve #1202, Brazil	13
Estrada & Estrada-Coates	1984	*A. palliata*	Los Tuxtlas, Mexico	60

* Ostro et al. compared two populations at two different locations in Belize.
** Stoner averaged the home range of multiple groups in La Selva, Costa Rica.

Activity Budgets

In general, diurnal primates engage in the same behaviors throughout the day. Differences become apparent in the total amount of time engaged in certain activities. Most primates are quite active during the dawn and dusk hours (Fleagle 1988). For most primates each day can be divided into three basic categories: resting, moving, and feeding. The number of behaviors a primate may engage in is plentiful, but in the large picture most behaviors occupy a small amount of time (Fleagle 1988). For example grooming or sex may occur numerous times in one day but the overall time engaged in

these behaviors is small. A concise activity budget uncovers differences or similarities among different ages, sexes, groups, or species. For example, in most primate groups, traveling occurs in the early morning hours of a day. Comparisons between the activities of different ages will uncover differences in time spent feeding, playing, and resting. By constructing activity budgets, researchers can understand how primates interact with their environment. For example, extended periods of resting may be due to a large folivorous diet or merely an emergent factor of an abundant food source that reduces the need to move about. An accurate activity budget and study of ecological variables are critical in understanding primate social behavior.

Activity Budgets for *Alouatta*

Neves and Rylands (1991) comprised activity budgets for a group red howler monkeys at the Colosso Reserve (Reserve 1202) in Brazil. The groups spent 67% of their time resting, 22% of their time feeding, and 11% of their time moving throughout their home range (Neves & Rylands 1991). The long periods of resting are perhaps related to the large amounts of leafy material consumed.

Bicca-Marques and Calegaro-Marques (1994) constructed activity budgets for a group of black howler monkeys (*Alouatta caraya*) inhabiting the Estancia Casa Branca site in Brazil. Behavioral data was collected for 60 days from dawn to dusk. The researchers found that with age, animals tend to move less and rest more. Significant differences were found between age-sex classes in feeding, resting, locomotion, and

social behavior. The results of the study suggest that different ages and sexes use their time in a different manner. Differences can be the result of priority of resources, gestations and lactation, and an overall need for energy for smaller individuals (Bicca-Marques & Calegaro-Marques 1994).

Braza et al. (1981) analyzed the activities of red howler monkeys at Hato del Frio, Brazil. The researchers extracted eight complete days of data. Rainy and dry season results showed that howlers spent 18 and 15% of their time engaged in locomotion behaviors, 20 and 24% of their time in feeding behaviors, 38 and 43% of their time in sleeping behaviors, and 24 and 18% of their time in resting and other activities.

Crockett (1987) compared the activity budgets from two populations of red howler monkeys at Hato Masaguaral, Venezuela. One population inhabits a gallery forest, while the other inhabits an open shrub woodland forest. Differences in the habitats were reflected through the activity budgets of the two populations. Those troops inhabiting the gallery forest spent more time resting, and traveling. Troops inhabiting the woodland forests spent more time in mixed activities and feeding. Crockett neglects to provide percentages of time spent in each behavior, but offers a comparative example of the activities of two populations living in different habitats.

Silver et al. (1998), constructed activity budgets for six troops, of *Alouatta pigra* inhabiting the banks of the Belize River. The study groups spent an average of 24.4% of their time each month feeding, 61.9% of their time each month resting, 9.8% of their time

each month traveling, 2.3% of their time each month engaged in social play, and 1.5% of their time each month vocalizing.

Each of the above studies report a variation in the in the amount of time each group, population, or sex-class spends in different behaviors.

Diet

Howler monkeys have been classified as folivore-frugivores (Crocket & Eisenberg 1987). Howler monkeys eat a wide range of vegetative matter including: mature and immature leaves, ripe and unripe fruits, buds, flowers, bark, seeds and nuts, and twigs (Neville et al. 1988). The ability of howler monkeys to exploit large amounts of leaves has probably allowed the members of the species to thrive in marginal habitats. In addition, the large intake of leafy matter has probably reduced daily ranging patterns. Milton (1980) suggests that the relatively low energetic consumption of leaves by howler monkeys has perhaps led to their lack of movement. This suggestion is debatable, for some groups of howler monkeys subsist largely on fruits as opposed to leaves. Those groups exploiting a large biomass of fruits do not necessarily range farther in a day. The percentage of time each group eats a food type may depend on the season thus, long-term studies best describe howler monkey diets.

Julliot (1996) observed a group of red howler monkeys for two years at the Norague Station in French Guiana. From a pool of 1,540 hours of behavioral data, she constructed feeding budgets for the troop. The study group's diet was composed of 57%

leaves, 25.5 % fruits, and 12.5% flowers. The troop consumed a total of 195 plant species representing, 47 families (Julliot 1996). Dietary compositions were obtained by direct observations and fecal analysis. The troop's diet reflected seasonal variations throughout the year. In a previous paper, Julliot and Sabatier (1993) observed the same troop. A total of 9,256 observational feeding units were collected in 19 months. The overall dietary budget was as follows: leaves 54%, fruits 21.5%, and flowers 12.6%. Additional foods included immature fruits (0.4%), mature leaves (3%), termitaria (1.5%), and bark (0.4%). The authors occasionally observed the monkeys eating mosses and other food sources but theses food sources, contributed very little to the overall diet and no percentages were reported. Consumption of food types seemed opportunistic and seasonal. The monkeys ate what food was available throughout the year.

Neves and Rylands (1991), observed red howlers in a isolated forest patch in Central Amazonia (Brazil). The total observation time was 491 hours and spanned over a five-month period (September to January). During the study, the troop's dietary budget was comprised of 56% leaves, 13.5% fruits, 4% flowers, and 27% seeds. The authors noted seasonal fluctuations in the troop's diet. Leaves were consistently eaten throughout the study but flowers became the second most important food item in the month of September. Seeds were the second most important food source throughout the rest of the study. The researchers recorded over 130 plant species that were consumed by the monkeys. What is unusual is the high degree of seed consumption. Neves and Rylands (1991) suggest that the high rates of seed intake are due to the restricted home range the troop inhabits with few fruit trees.

Braza et al. (1983) analyzed the diet of red howler monkeys on the Venezuelan plains. The team of researchers observed the feeding behavior via direct observation, analyzed fecal matter, and dissected monkeys and analyzed gut contents. A dietary budget was not provided. However, over 63 different food species were identified. The food types consisted of fruits, flowers, leaves, grasses, legumes, bark, and woody stalks. Braza et al. (1983) concluded that the troop ate specific fruits at specific time periods dependent on the season.

Galletti et al. (1994) observed the feeding behavior of red howler monkeys along forest fragment edges at the Santa Genebra Reserve in Brazil. The study was conducted from the months of April 1988 to October 1991. The researchers recorded 366 feeding bouts and 56 food items were identified. The diet of the howlers based on the feeding bouts comprised of 75% leaves, 15% fruits, and 10% flowers (Galletti et al. 1994). The diet composition varied monthly. Leaves were consumed at high levels year round. Eighteen species of flowers were consumed after blooming. The howlers appeared to prefer those flowers rich in nectar. Fruits were consumed on a seasonal basis and varied with availability.

Chiarello (1994), observed the diet of a troop of howler monkeys for 718 hours at the Santa Genebra Reserve as well. Chiarello focused on one group as opposed to numerous groups by Galletti et al. The results of Chiarallo's study are as follows: leaves comprised 73% of the diet, fruits made up 5%, flowers 12%, petioles and twigs 3%, and

unidentifiable food items 8%. Chiarello's results agree largely with Galletti et al. Seasonal shifts in the winter led to more flower consumption. Leaves were always predominant and fruit was eaten when available.

Chapman (1987) studied mantled howler monkeys at Santa Rosa National Park, Costa Rica during four field seasons from July 1983 to August 1986. Observations were focused on three species of New World Monkeys. A total of 394 hours were gathered on the howler monkeys. The percentage of total feeding time spent eating different food parts are as follows; fruits 28.5%, flowers 22.5 %, and leaves 49%.

Estrada and Estrada-Coates (1986) found that mantled howler monkeys in Los Tuxtlas, Mexico spent 46% of the time feeding on leaves and 53% of their time eating fruits. The leafy portion of their diet represented 34 species from 21 plant families.

Milton (1979) began a long-term study of the feeding ecology of mantled howler monkeys of Barro Colorado Island. Over five years, the animals spent 48.2% of feeding time on leaves, 42.1% on fruit, and 9.6% of their time feeding on flowers. Of the time spent on leaves, 82% of the time was devoted to immature leaves. Younger leaves contain more protein, less toxins, and less fibrous materials than mature leaves (Milton 1979). Immature leaves are probably more difficult to procure but easier to process.

Silver et al. (1998) observed six troops of black howler monkeys (*Alouatta pigra*) on the banks of the Belize River. A total of 1,160 hours of behavioral data was collected

via focal animal sessions lasting 25 minutes. The diet of the howlers consisted primarily on foliage and fruits. Young leaves comprised 37.2% of the diet, mature leaves 7.9%, fruits 40.8%, flowers 10.6% and other food sources 3.4%. The researchers identified 551 plants species that the howlers fed on. Ripe fruit was eaten 91% of the time, some species of fruit were eaten whole and some species the seeds were spit out. Leaves were eaten year round and fruits and flowers had seasonal peaks. The researchers did not observe the howlers eating any animal matter.

Conclusion

This objective of this study is to compare the group size and composition, home range, dietary behavior, and daily activities of three troops of black howler monkeys (*Alouatta pigra*) to what is known of the larger genus.

The variation within this genus is probably the product of environmental factors. By understanding each group's environment and the variables within that environment, comparisons can perhaps be made in a clear manner. Because of the tremendous variation within the genus *Alouatta*, behavioral dichotomies that are created by researchers are challenged such as folivore or frugivore, unimale or multi-male groups, or territorial vs. non-territorial species (Crocket & Eisenberg 1987). With such a extreme degree of variation within the genus *Alouatta*, only one property of howler monkey life is dependable and that is variation itself.

Chapter Two- MEHTODS AND MATERIALS

Study Site and Study Groups

The study site is located approximately one kilometer inland on the northern shore of Monkey River, Belize. The site is best characterized as a broadleaf, riparian forest belt that lies between the river to the south, and a road to the north. The approximate elevation of the field site is sea level meters. The average annual rainfall ranges from 200-250 cm and the average temperature during the study ranged from 28-34 degrees Celsius (Beletsky 1999). The road runs parallel to the river creating the forest belt and isolating the inhabitants thereof. The forest belt is divided into two parts by a large field, which is cleared annually.

Data collection started Wednesday, June 3 and terminated Saturday, August 14 of 1999. A group of three researchers collected data. In the first month James Loudon, Brad McVittie, and Katie Kaput collected the data. For the remainder or the study, two researchers (James Loudon, and Brad McVittie) collected data. Data were collected six days a week with the remaining day to rest and analyze data. If possible, the researchers collected data on a different group each day. The time of day when data collection began was staggered for each group to obtain a accurate description of the activities the groups engaged in each hour. Troops were located via vocalizations or movement within the trees. In many instances the monkeys were silent and completely still. In such an

instance the researcher walked the trails in search of a focal troop. Upon locating a group each member was counted and recorded to determine the age and sex composition.

The project focused on three groups living in the forest. Of the three, Group #1 inhabited the eastern most forest patch, separated from the remaining forest by the field and geographically isolated to the south by the river and north by the road. The second group (Group #2), inhabited a large portion of the western forest and a small region in the eastern forest patch, across from the field. The second group's border included the river to the south and Group #3 to the north. The final group, inhabited an area in the western forest belt, bordered south by Group #2 and north by the road. Initial observations led the researchers to believe four groups inhabited the forest belt. After further investigation, Group #3 was observed in two sub groups.

To determine the home range and of each group, the researchers marked the forest with fluorescent flagging tape. Trails were labeled with a letter and a number was issued to each flag to determine a sequence. Each flag had the trail letter and number; allowed the researcher to record the location of the focal animal for each session.

The researchers then copied all the information on data sheets. Each data sheet contained the flag coordinate, the distance between the flag and the previous and following flag. This enabled the researchers to easily locate where they were in the forest and to record the flag that a troop was nearest. The distance between each flag was measured by an electronic range finder. The location of each flag was measured with a

handheld compass. The same researcher measured the distance between each flag, and compass bearing, to reduce human error. The first researcher (using the compass and range finder) took a compass reading and distance from the flag he was at to the next flag and called out to the two other researchers. One researcher recorded the information on a data sheet and the third researcher cleared the trails of any debris and brush. It should be noted that local people of Monkey River Town cleared the major trails. The researchers mainly kept the trails from becoming overgrown with brush and saplings. However, on several occasions, the researchers cleared auxiliary trails to avoid the flooding, to collect data where remote trees were fruiting, or to make a more efficient route between various locations.

In addition to flagging trails, the researchers entered geographical locations with a handheld global positioning system (GPS). GPS points were entered at the end of any trail that ultimately joined up to the road, at various locations on the river, and at the field where the researchers took breaks.

Home ranges were determined by viewing all the data and all the locations of each troop. If possible during each focal session, the researcher recorded the location of the troop. Wherever the troop was observed is considered part of that troop's home range.

Diet

The researchers recorded all food items consumed by the monkeys. The researcher recorded: each species consumed, what part of the species that was consumed,

and if possible, the state of the food. The parts of each species include: leaves, fruits, flowers, or shoots. The state of each food was merely ripe or unripe fruits or mature or immature leaves. All data recorded regarding the part and state of the food was included in ad libitum notes.

Activity Budget and Feeding Budget

Data on activity and feeding budgets were collected using ten-minute focal animal sessions (Altmann 1974). A minimum of twelve sessions were collected daily on each age and sex class (individual identification of animals was not possible). Sex was determined by each animal's external genitalia and with the aid of binoculars. The researchers determined the age class of each animal by size. The researchers established the following categories: adults, juveniles, and infants. If a focal animal was lost during the sample for a time period exceeding 1.5 minutes, the session was discarded. Each focal animal session included the date, time of day, group, the sex and age class of the focal animal, the location of the focal animal, the temperature, and a description of the weather.

Two classes of behaviors were recorded: event and states. The three researchers constructed an ethogram, after a three-week period of preliminary observations. The preliminary observations allowed the researchers to distinguish each sex, establish categories for age classes and develop accurate descriptions of distinct behaviors that were observed. For the purpose of this study, an event is defined as a behavior of short

duration, not exceeding one second. Events were totaled and measured in terms of their frequency. States can be defined as behavioral patterns of relatively long duration (Martin and Bateson 1996). The total amount of time engaged in a "state" behavior was measured. The precise time was noted when the focal animal engaged in a new behavior. This provided the researchers with a start and ending time of every behavior and allowed time budgets to be calculated. While collecting focal data, the researchers recorded ad libitum notes to provide a qualitative "context" when the data were transcribed at a later time period.

When recording feeding, observers noted the species and plant part being consumed. The researchers constructed an ethogram, which accurately described all behaviors and who initiated or received each behavior. Increased attention was focused on feeding behaviors (see below) and inter-group interactions. At the occurrence of an inter-group interaction, the researchers would terminate focal samples and go directly to the interaction and take ad libitum notes. This provided the researchers with an idea of each group's range, how each troop defends its range, and the behaviors the individuals are engaged in during the interaction.

Data Analysis

Group size and composition and home range was calculated for each group. Activity and feeding budgets were calculated for each of the three study groups, as well

as for each age-sex class within each group, each age-sex class regardless of group membership, and for the total sample of 32 animals.

By using Lehner's Minimum Polygon Method (1996), we determined the home range of each of the three groups. This technique uses all locations where the troop was observed to form a polygon representative of the home range. Each diet and feeding budget was extracted from focal animal data.

ETHOGRAM

States

Inactive (I)- This is a default behavioral category which is used if an individual is not engaged in any activity. Behaviors include sitting, lying with eyes open, sleeping, or sun bathing.

Feed On (FO)- This behavior is the act of masticating, consuming, foraging among food sites, or drinking water. This broad category also includes the act of obtaining food such as reaching for a food item with the hands, feet or, mouth.

Locomotion (LO)- The state includes every form of moving from one location to another. Such behaviors include: quadrupedal walking and running, bipedal walking and running, bridging, aided brachiating, leaping, and climbing upon a substrate.

Hang (H)- An individual engaged in a behavior in which it is under the substrate to which it is supported by. This includes; using one to all four limbs and the prehensile tail.

Out of Sight (OS)- If the observer can no longer observe his or her focal animal this behavior is recorded. Samples in which the focal animal is not observable for a period of time exceeding one and a half minutes will be discarded.

Sit Near (SN)- Individuals that are within meter radius to the focal animal are recorded in this behavior.

Sit in Body Contact (SIB)- This behavior includes inactive activities in which the focal is in body contact with another animal. The following behaviors are encompassed; huddling, holding, licking, touching, lying in contact, and sitting in contact with another individual.

Ventral Cling (VCL)- Infants that are clinging to a larger animal's (usually adults) ventrum for support. This behavior is intended for sessions when an infant is the focal animal. It doesn't take into account what behavior the larger animal is engaged in. For example, infants may cling to a moving or an inactive female. The behavior recorded remains "ventral cling". The moving female's behavior maybe recorded in the ad libitum notes

Dorsal Cling (DCL)- This behavior uses the same pretence as the behavior above. An infant clinging to a larger animal's dorsal side for support is the requirement for this behavior.

Ventral Carry (VCA)- This behavior focuses on the larger animal that is carrying a smaller infant on its ventral side. This behavior is intended when the focal animal is an adult or juvenile.

Dorsal Carry (DCA)- Larger individuals who are carrying smaller infant on their dorsal side are engaged in the dorsal carry behavior. As above, this behavior is intended for adult or juvenile focal scans.

Copulation (CO)- This behavior is strictly focused on the act of sex. That is, the males penetration into a female's labia. It does not include dominant and submissive mounts.

Vocalization (VO)- Vocalizations can be categorized as either states or events. Any focal animal engaging in vocalizations that exceed 2 seconds are included in the state vocalization category. Such vocalizations include, grunts, and roars. This criteria, excludes alarm calls and barks.

Social Play (SP)- Individuals that engage in any play activity with another individual. Play behaviors include; wrestling, slapping, chasing others, play bites, pulling hair, and grabbing. Play behavior is a non-aggressive behavior and may include play faces and vocalizations.

Non-Social Play (NSP)- Non-social play occurs when an individual is engaged in play behaviors alone. It is directed at infants, which constantly approach and leave another individual. This category includes behaviors such as playing with inanimate objects, or crawling upon other individuals who are inactive.

Scanning (SC)- Individuals who engage in this behavior are visually inspecting their environment. Scanning includes looking intensely at a particular object or looking to and for in a general direction at a number of objects.

Vigilance (VG)- Vigilance is much like scanning, differing only intensity and duration of the scan. Vigilance is characterized by an individual engaging in many short scans. Such behavior is observed when another group is near, a predator is near, or the individual is observing its group from afar. This behavior differs from scanning in intensity and context. Vigilance in this context is used as an alerted or cautious state.

Mount (M)- Includes both males and females which mount the ano-genital area of another animal. Mounts are submissive and dominant in context. Both dorsal and ventral mounting may be recorded.

Embrace (EM)- This behavior is simply defined by an animal wrapping one or all four limps around another animal's dorsal or ventral side.

Allogroom (AL)- Any behavior in which the focal animal receives of initiates the following; inspect or combing through the hair of another individual, removing dead skin or parasites from another individual. Manipulation of hair may be preformed with the forelimbs and/or hind limbs.

Autogroom (AU)- All of the above behaviors, in which the individual directs its attention to itself as opposed to another individual.

Events

Approach (A)- This behavior may be initiated by the focal or received by another animal(s). It includes locomotion to another individual (initiated) within a one-meter radius in any direction or being the recipient thereof.

Leave (L)- This behavior may be initiated or received by the focal animals. It includes locomotion to away from another animal (initiated) within a one-meter radius in any direction or being the recipient thereof.

Muzzle (MZ)- A behavior in which the focal animal rubs its face upon another animals face. Muzzling may also include kisses. The focal animal can be the initiator or recipient of this behavior.

Lunge (LU)- Lunging occurs when an individual leaps or rapidly advances toward another monkey or animal. Lunges are agonistic behaviors, which are initiated and received by the focal animal.

Slap (SL)- Slapping is an agonistic behavior in which an animal strikes another animal with its' forelimb. The focal subject may be either the initiator or receiver.

Branch Shake (BS)- Behavior in which the focal animal shakes a tree limb or branch. This agonistic behavior is usually one component of an aggressive display directed toward another individual, another troop, or a researcher. Often branch shaking is accompanied with pilo erect hair.

Branch Throw (BT)- Behavior in which the focal animal breaks off a portion of a tree limb or branch and throws it at another individual. The recipient of the throw includes; another monkey from the same group, a monkey form a neighboring group, a potential predator, or a researcher.

Scratch (S)- This category is characterized by the focal animal repeatedly rubbing or raking a portion of the body with its fingers. Scratching maybe preformed with the forelimbs, hind limbs, or tail. Scratching may relieve a skin irritation or remove invertebrates from a specific area. Excessive scratching in some cases is an abnormal behavior and may indicate an individual under a high degree of stress.

Elimination (E)- A animal that is urinating or defecating. This behavior maybe classified as either a state or event.

Bridge (BR)- This event is characterized when a individual is between two substrates, holding both with hind limbs, fore limbs, and tail, in the process of crossing.

Quick Vocalization (QV)- A vocalization produced by an individual no longer than 2 seconds in duration. Quick vocalizations include; alarm calls, contact calls, and barks.

Unknown (?)- This default category includes all behaviors that do not exist in the ethogram or cannot be identified by the researcher.

Chapter Three - RESULTS

Group size and Composition

The entire study population consisted of 32 animals. Group 1 consists of 2 adult males, 2 adult females, 2 juvenile males, 2 juvenile female, 1 infant male, and 1 infant female. The total group membership of Group 1 is 10.

The total number of animals of Group 2 is 12. Group 2 included 3 adult males, 2 adult females, 4 juvenile males, 1 juvenile female, and 2 infant males.

Group 3 is comprised of 10 animals. The composition of the group is as follows: 2 adult males, 1 adult females, 3 juvenile males, 2 juvenile females, 1 infant male, and 1 infant female.

Of the 32 subjects, 7 animals are adult males. Adult females consisted of 5 animals. The remaining number for each age and sex class is as follows: 9 juvenile males, 4 juvenile females, 4 infant males, and 2 infant females.

Table 3.1 Group Size and Composition of the Study Groups

	GROUP 1	GROUP 2	GROUP 3	Total # of each age-sex class
# of Adult Males	2	3	2	7
# of Adult Females	2	2	1	5
# of Juvenile Males	2	4	3	9
# of Juvenile Females	2	1	2	5
# of Infant Males	1	2	1	4
# of Infant Females	1	0	1	2
Total Group Membership	10	12	10	32

Home Range

Each Groups home range is listed below in Table 3.2..

Table 3.2 Home Range in Hectares for Each Study Group

Group	Home range in hectares
1	0.41
2	0.89
3	1.2

Activity Budgets

Activity Budgets were constructed for each age-sex class in each group, for each group as a whole, and for each age-sex class as a whole. The behavioral categories are as follows: feeding, inactive, locomote, out of sight, social behavior, and other.

The "social" behavioral category includes: allogroom, dorsal carry, dorsal cling, embrace, muzzle, sit in proximity, sit in body contact, social play, ventral carry, and ventral cling. The social behavioral category was designed to represent each social category as a whole. The social category combines are behaviors that are social in nature and are under represented on their own.

The "other" category includes: bridging, branch throw, branch shake, eliminate, hang, non-social play, scan, vigilance, vocal inactive, and vocal other. This category combined many behaviors that were observed rarely in comparison to other behaviors.

The pages following will display figures that illustrate the activity budgets for each age-sex class in each group, each group's activity budget, the activity budget for all members of each age-sex class, and the activity budget all the animals sampled.

Figures 1 through 6 display the activity budgets for Group 1 individuals, broken down by age and sex classes.

Figure 1 illustrates the activity budget of the two adult males of Group 1. These two males were observed for a total of 1,153 minutes, 39 seconds. Group 1 adult males spent the majority of their time (52%) inactive. Group 1 males engaged in social behaviors 19% of their time, followed by feeding (15%), locomoting (8%), in "other" behaviors (5%), and out of sight approximately 1% of the total time observed.

Figure 2 demonstrates the activity budget of the two adult females of Group 1. These females were observed a total of 467 minutes, 36 seconds. The Group 1 adult females spent 39% of their time inactive, followed by 38% of their time in social behaviors. The large proportion of social behavior is due to extended periods of time in spatial proximity or in physical contact to infants in the group. Group 1 adult females were observed spending the remainder of their time in feeding (8%) and in other behaviors 4% of their observed time.

Figure 3 shows the activity budget of the two juvenile males of Group 1. These juvenile males were observed for a total of 255 minutes, 28 seconds. The largest portion of the juvenile males time was spent inactive (34%), followed by feeding 24% and social behaviors 26% of their time. Group one juvenile males engaged in locomoting behaviors 10% of their time, in "other" behaviors 5% of their time, and out of sight approximately 1% of their total time observed.

Figure 4 displays the activity budget for the two juvenile females of Group 1. These juvenile females were observed for a total of 163 minutes, 35 seconds. Group 1

Figure 1
Activity Budget of Adult Males in Group 1
N=2

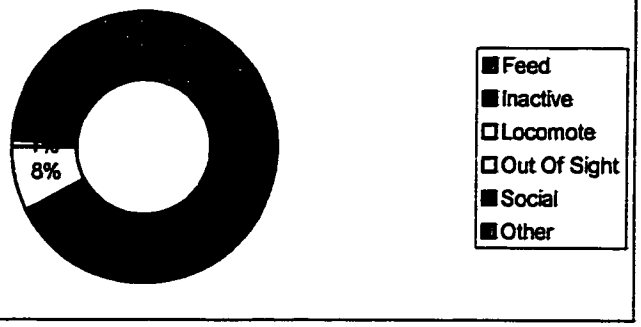
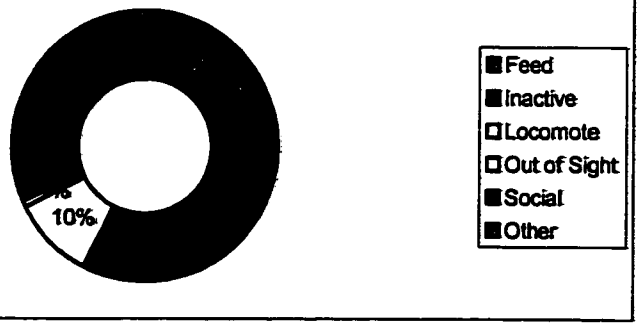


Figure 2
Activity Budget of Adult Females in Group 1
N=2

Figure 3
Activity Budget of Juvenile Males in Group 1
N=2



juvenile females spent 15% of the observed time feeding, 42% of the observed time inactive, 9% of the observed time locomoting, 26% of the in social behaviors, 8% of the observed time in "other" behaviors, and 0% of the observed time out of sight.

Figure 5 illustrates the activity budget for the infant male of Group 1. This infant male was observed for a total of 108 minutes, 31 seconds. The infant male from Group 1 was observed feeding 24% time, in inactivity 46% of the time, locomoting 5% of the time, engaged in social behavior 22%, and in other behaviors 2% of the time. Researchers were unable to observe the infant male approximately 1% of the total time.

Figure 6 depicts the activity budget of the infant female in Group 1. This infant females was observed for a total of 191 minutes, 56 seconds. The Group 1 infant female spent the majority of her time feeding (44%). This was followed by inactivity 41% of the time, locomoting 7% of the time, in social behaviors 6% of the time, and engaged in "other" behaviors 6% of the total observed time. A zero percent value was calculated for the total time out of sight.

Figure 7 demonstrates the total activity budget for the ten individuals in Group 1. Group 1 individuals were observed for a total of 2,340 minutes, 45 seconds. The overall group activity budget is as follows: feeding 16%, inactive 54%, locomoting 11%, out of sight 1%, social behavior 11%, and engaging in "other" behaviors 5% of the time. The percentage of inactivity for Group 1 exceeds the percentage of inactivity for each age-sex class within Group 1.

Figure 4
Activity Budget of Juvenile Females in Group 1
N=2

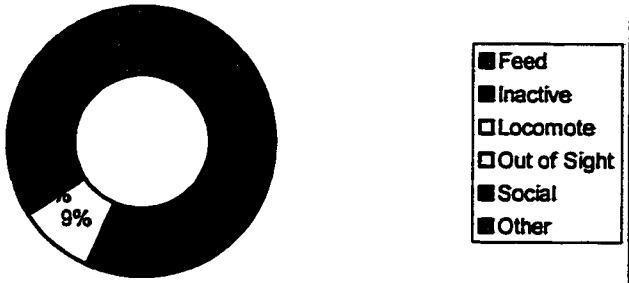


Figure 5
Activity Budget of Infant Males in Group 1
N=1

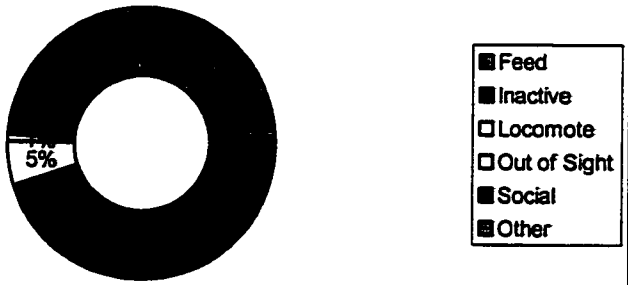
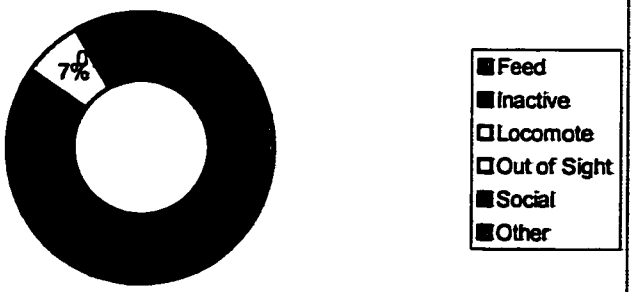


Figure 6
Activity Budget of Infant Females in Group 1
N=6



Figures 8 through 12 depicts the activity budgets of age and sex classes for members of Group 2.

Figure 8 shows the activity budget of the three adult males in Group 2. These three males were observed for a total of 1,595 minutes, 8 seconds. The largest proportion of time that adult males of Group 2 spent was engaging in inactivity, at 54%. This is followed by feeding at 16% of the time, locomoting 11% of the time, social behaviors 11%, out of sight 1% of the time, and lastly, "other" behaviors 7% of the total observed time.

Figure 9 displays the activity budget for two adult females in Group 2. These two individuals were observed for a total of 499 minutes, 47 seconds. The two adult females of Group 2 spent 21% of the total observed time feeding, 40% of the total observed time inactive, 11% of the total time locomoting, 1% of the time out of sight, 22% of the total observed time engaged in social behaviors, and 5% of the total observed time in "other" behaviors.

Figure 10 depicts the activity budget of the four juvenile males of Group 2. These two juvenile males were observed for a total of 195 minutes, 49 seconds. The largest proportion of time the juvenile males were engaged in was the inactive behavior (42%). This was followed by feeding at 19% of the observed time, locomoting 18% of the observed time, social behaviors 12% of the observed time, "other" behaviors 6% of the observed time, and out of sight 3% of the total observed time.

Figure 7
Overall Activity Budget For Group One

Figure 8
Activity Budget of Adult Males in Group 2
N=3

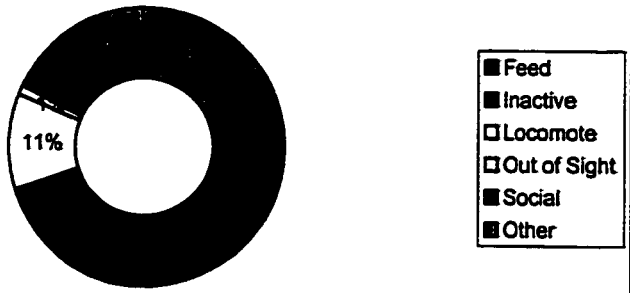


Figure 9
Activity Budget of Adult Females in Group 2
N=2

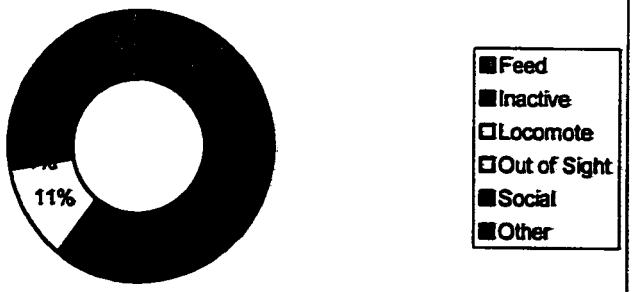


Figure 11 illustrates the activity budget of the one juvenile female of Group 2. This females was observed for a total of 80 minutes, 9 seconds. The calculated activity budget of the juvenile of Group 2 is as follows: 15% feeding, 53% inactive, 12% locomoting, 18% social, 2% in the "other" behavioral category, and 0% of her time out of sight.

Figure 12 shows the activity budget of the two infant males of Group 2. These two infants were observed for a total of 310 minutes, 2 seconds. Infant males of Group 2 spent 17% of the time feeding, 17% of the time inactive, 13% of the time locomoting, were out of sight 1% of the time, engaged in social behaviors 42% of the time, and spent 10% of the time in the "other" behavioral category. The large percentage of time spent in social behavior is due to extended periods of time of physical contact, social playing, or in close spatial proximity to other monkeys. The large number of juveniles in Group 2 (which engaged in social behaviors with the infants) increased the proportion of time spent in the social behavior

Figure 13 demonstrates the overall activity budget for all the members in Group 2. The individuals of Group 2 were observed for a total of 2,681 minutes, 5 seconds. Group 2 as a whole spent 46 percent of the time inactive, 17 percent of the total time feeding, 12 percent of the time locomoting, 17 percent of the total time in social behavior, 7 percent of the total time engaged in "other" behaviors, and approximately 1 percent of the time out of sight. Group 2 and Group 1 have the exact same percentage value for feeding and

Figure 10
Activity Budget of Juvenile Males in Group 2
N=4

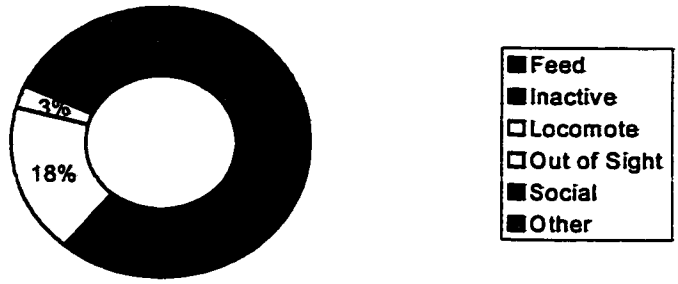


Figure 11
Activity Budget of Juvenile Females in Group 2
N=1

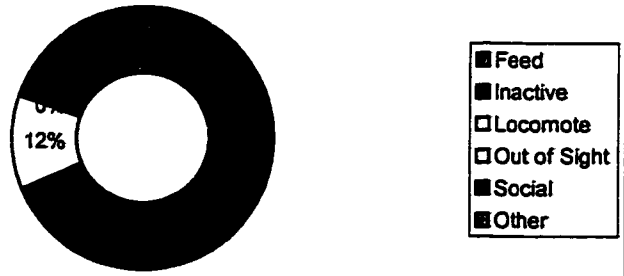
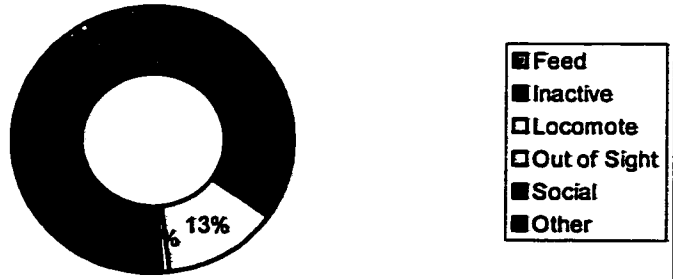


Figure 12
Activity Budget of Infant Males in Group 2
N=2



there is a 1% percent discrepancy for inactive behaviors between each group. The largest difference in percentage values (6%) exists in social behavior between the two groups.

Figures 14 through 19 represent the activity budgets of age and sex classes of Group 3 individuals.

Figure 14 illustrates the activity budget of the two adult males of Group 3. These two males were observed for a total of 952 minutes, 15 seconds. The adult males of Group 3 spent a large portion of their time inactive (56%). This was followed by feeding at 16%, social behavior 15%, locomoting 10%, engaged in "other" behaviors 2%, and out of sight 1% of the total observed time. The activity budget of Group 3 adult males are quite similar to the activity budgets of adult males from the other two groups. The largest difference in percentage value is only 4%, which is found in the social behavior category.

Figure 15 displays the activity budget of the adult female in Group 3. These adult females were observed for a total of 708 minutes, 8 seconds. The activity budget of the adult female of Group 3 is as follows: feeding 20%, inactive 45%, 11% locomoting, 1% out of sight, 16% social, and 7% of the total time engaged in "other" behaviors. A larger degree of difference is found between the adult females of each group. For example, differences in social behavior varied 16%, followed by a 15% discrepancy in the inactive behavior category.

Figure 13
Overall Activity Budget For GROUP TWO
N=12

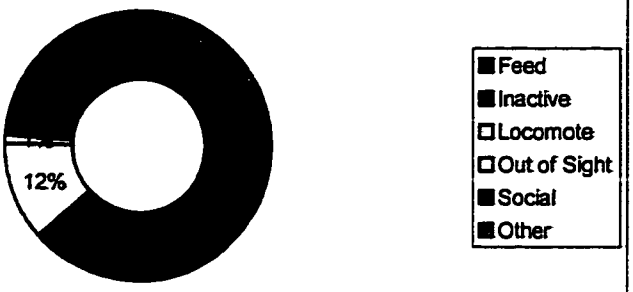


Figure 14
Activity Budget of Adult Males of Group 3
N=2

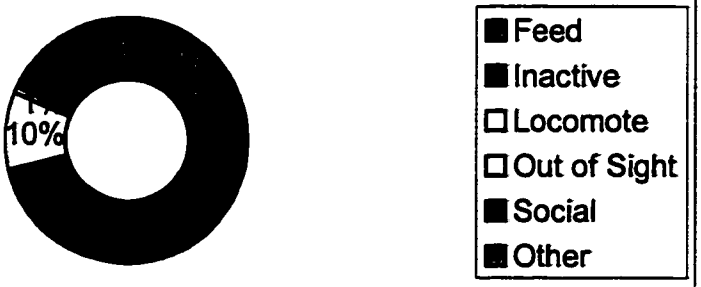


Figure 15
Activity Budget of Adult Females in Group 3
N=1

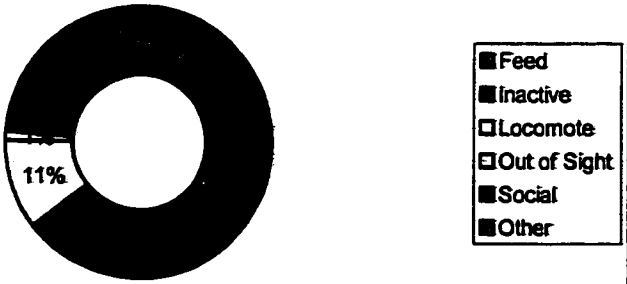


Figure 16 shows the activity budget of three juvenile males of Group 3. These individuals were observed for a total of 357 minutes, 55 seconds. The Group 3 juvenile males spent a total of 50% of their time inactive, followed by 29% of the time inactive, 12% of their time feeding, 5% of the time in the "other" category, 3% of the time locomoting, and 1% of the time out of sight. A large degree of variation is apparent when compared to the juvenile males of Group 1 and Group 2. Variations ranged from 2% (out of sight) to 17% in the social behavior.

Figure 17 demonstrates the activity budget for the two juvenile females of Group 3. These two females were observed for a total of 193 minutes, 20 seconds. The activity budget of Group 3 juvenile females is as follows: 22% of the observed time was spent feeding, 32% of the observed time was spent inactive, 3% of the observed time was spent locomoting, 35% of the observed time was spent in social behavior, and 8% of the observed time the juvenile females were engaged in "other" behaviors. The largest degree of variation from the other juvenile females is in the inactive behavioral category, in which an 11 percentage spread was observed, in contrast to no variation in the out of sight category.

Figure 18 depicts the activity budget of the infant male of Group 3. This male was observed for a total of 224 minutes, 35 seconds. The infant male spent 35% of his time in the "other" behavioral category. This is followed by 26% of observed time spent in social behaviors, 16% of observed time spent in locomoting, 15% of observed time as inactive, 8% of the observed time feeding, and 0% of the observed time out of sight. The

Figure 16
Activity Budget of Juvenile Males in Group 3
N=2

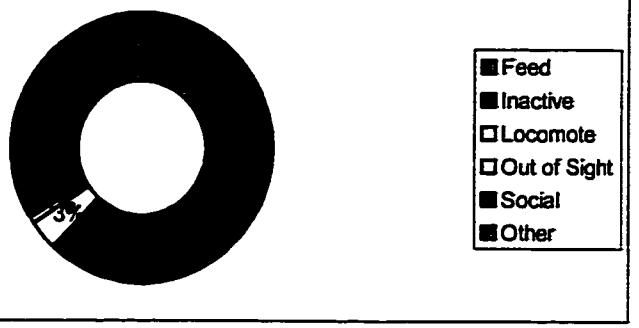


Figure 17
Activity Budget of Juvenile Females in Group 3
N=2

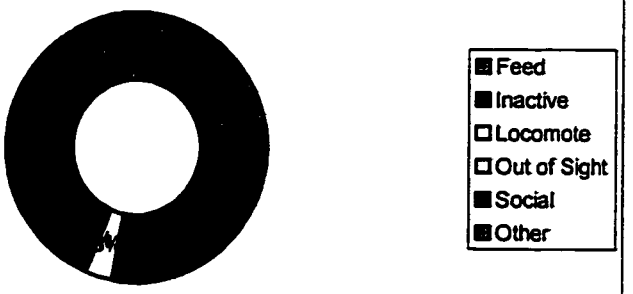
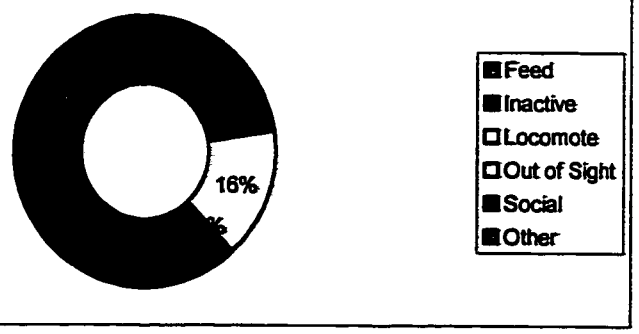


Figure 18
Activity Budget of Infant Males in Group 3
N=1



largest discrepancy between the behaviors of the infant male in the group and the other infant males is apparent in the inactive behavioral category (29%).

Figure 19 illustrates the activity budget for the infant female of Group 3. This female was observed for a total of 85 minutes, 55 seconds. The infant female was observed in social behavior 100% of the time. Needless to say, these results do not compare well with the results of infant females in the other two groups.

Figure 20 displays the overall activity budget for the 10 individuals in Group 3. Individuals of Group 3 were observed for a total of 2, 520 minutes, 8 seconds. The Group 3 animals spent the largest proportion of their time inactive (44%), followed by social behavior at 23%, and feeding at 16%. They locomoted for 9% of the observed time, and engaged in "other" behaviors for 7%.

Figures 21 through 26 represent the activity budgets of pooled age and sex classes across all three groups.

Figure 21 depicts the activity budget of all seven adult males, from all three groups. The largest portion of their time was spent inactive, at 55%, followed by feeding at 15%, social behaviors at 14%, locomoting at 10%, "other" behavior at 5%, and they were out of sight for 1% of the observed time.

Figure 19
Activity Budget of Infant Females in Group 3
N=1

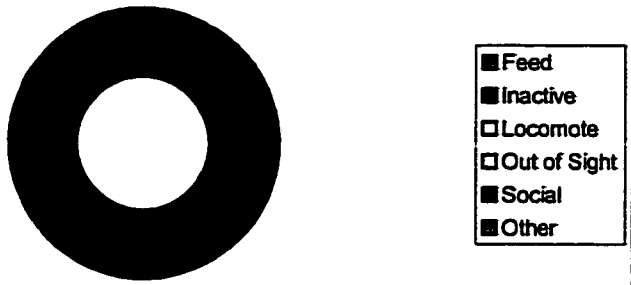


Figure 20
Overall Activity Budget For GROUP THREE
N=10

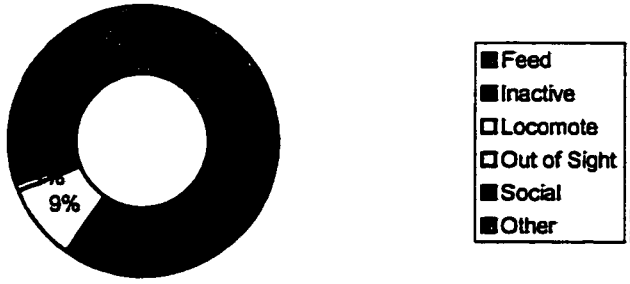


Figure 21
Activty Budget For All Adult Males
N=7

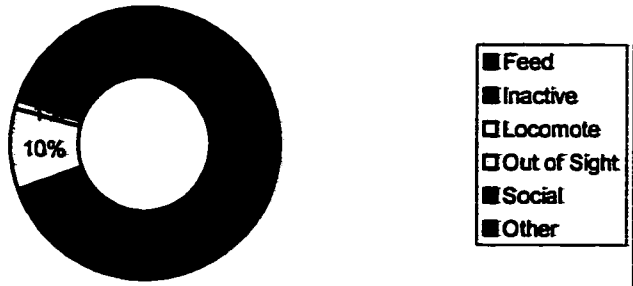


Figure 22 demonstrates the activity budget of all five adult females, from all three groups. They collectively spent 41% of their time inactive, 24% in social behaviors, 17% in feeding, 11% in locomoting, 6% engaging in "other" behaviors, and 1% of the observed time they were out of sight.

Figure 23 summarizes the activity budget of all nine juvenile males, from all three groups. They spent 42% of their observed time inactive, 24% of the time was spent in social behavior, 17% of the time in feeding, 9% of the time locomoting, 5% in the "other" behavioral category, and they were out of sight for 3% of the observed time.

Figure 24 shows the activity budget of all five juvenile females, from all three groups. Juvenile females were inactive 40% of the time, and were observed in social behaviors 28% of the time. They spent 18% of the time feeding, followed by locomoting and "other" behaviors, which were each 7% of the time.

Figure 25 displays the activity budget of all four infant males, from all three groups. Infant males engaged in social behaviors 32% of the time, were inactive 21% of the time, and were engaged in "other" behaviors 18% of the time. They were observed feeding for 15% of the time, locomoting 13% of the time, and were out of sight 1% of the time.

Figure 22
Activity Budget For All Adult Females
N=5

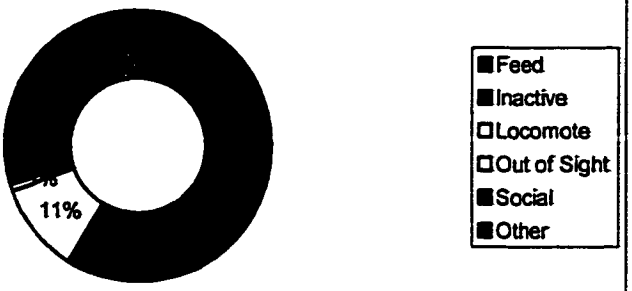


Figure 23
Activity Budget For All Juvenile Males
N=9

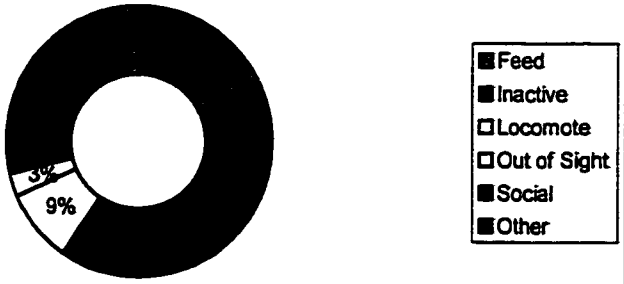


Figure 24
Activity Budget of All Juvenile Females
N=5

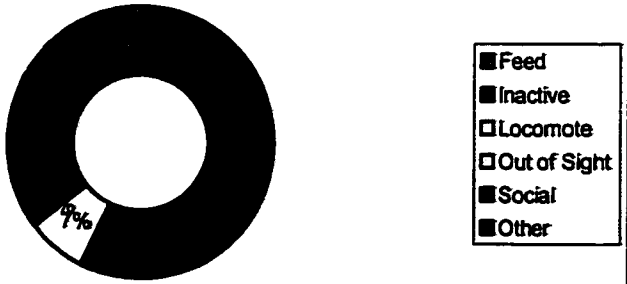


Figure 26 demonstrates the activity budget of all four infant females, from all three groups. The activity budget is as follows: 35% social behaviors, 31% feeding, 28% inactive, 5% locomoting, and 1% engaged in "other" behaviors.

Figure 27 summarizes the overall activity budgets of all animals sampled, in all three groups, across all age and sex classes. In total, these howler monkeys spent 45% of the observed time inactive, 21% of the time in social behaviors, 17% of the time feeding, 10% of the time locomoting, 6% of the time engaged in "other" behaviors, and were out of sight for 1% of the time.

Figure 25
Activity Budget of All Infant Males
N=4

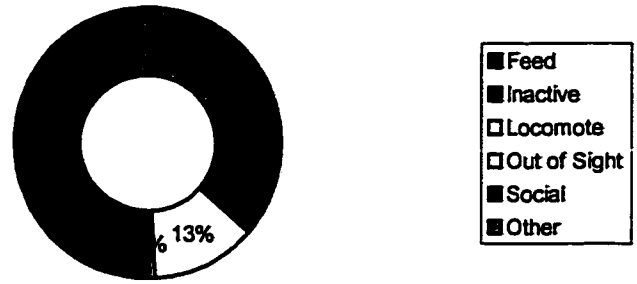


Figure 26
Activity Budget of All Infant Females
N=2

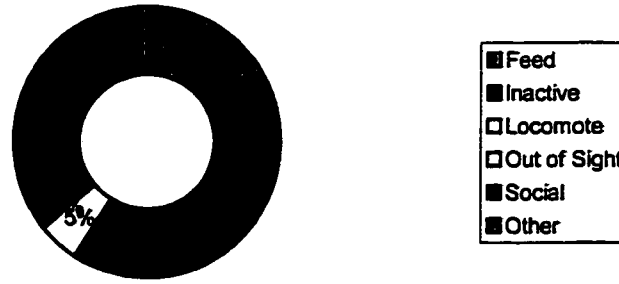
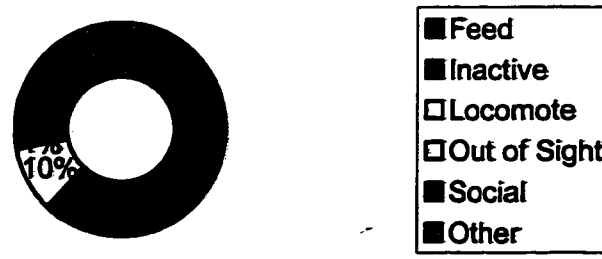


Figure 27
Overall Activity Budget For All Animals Sampled
N=32



Diet

Howler monkeys were observed feeding on 21 different species from 12 different families. All unidentifiable plants are listed as unknown. Howler monkeys were observed feeding on leaves, fruits, and flowers. The howler monkeys did not engage in carnivory or consume barks, buds, grasses, nuts, seeds, or shoots during the three-month study.

Table 3.3 lists the species name, the family name, the common name, and the part of the plant consumed by any monkey during this study period.

Table 3.3 All Foods Consumed by Focal Animals During the Study

Scientific Name	Family Name	Common Name	Part Consumed
Virolia kosechnye	Myristucaceae	Banac	Leaf, Fruit
Gauzuma ulmifolia	Sterculiaceae	Black Bay Cedar	Leaf
Simarouba glauca	Simarubaceae	Cochito	Leaf, Fruit
Vitexi gaumeri greenm	Verbenaceae	Fiddle Wood	Fruit
Ficus sp.	Moraceae	Common Fig	Leaf, Fruit
Spondias mombin	Anacardiceae	Hog Plum	Leaf
Inga edulis	Leguminosae	Inga (Bri-Bri)	Leaf
Pterocarpus belizensis	Leguminosae	Kaway (Jesus Christ Tree)	Leaf
Eugenia malaccensis	Myrtaceae	Malay Apple	Fruit
Mangifera indica	Anacardiaceae	Mango	Fruit
Stemmadenia donnelli-smithii	Acocynaceae	Paper Glue Tree (Cojoton)	Leaf, Fruit

Pachira aquatica	Bombacaceae	Provision Tree	Leaf
Miconia argentea	Melastomaceae	Sering Tree	Fruit
Ximenia americana	Anacardiacea	Sour Plum	Leaf
Ficus crassiuscula	Moraceae	Strangler Fig	Fruit
Cecropia obtusifolia	Moraceae	Trumpet Tree	Leaf
Mouriri myrtilloides	Moraceae	Turtle Bone	Leaf
		Unknown	Leaf, Fruit, Flower
Vitis tiliifolia	Polygonaceae	Wild Grape	Fruit
Dioscorea sp.	Dioscoraeceae	Wild Yam	Leaf
Cedrela mexicana	Meliaceae	Yellow Bay Cedar	Leaf

Feeding Budget

Species and Plant Part feeding budgets were constructed for: each age-sex class within each group, for each group as a whole, for each age-sex class as a whole, and for all animals sampled.

Figure 28 illustrates the feeding budget by plant species for the two adult males in Group 1. The two adult males of Group 1 were observed feeding a total of 168 minutes and 16 seconds. Cochito berries were eaten 42% of the time, followed by Fiddle Wood *(Vitexi gaumeri greenm)* fruits, at 24%. The remainder of the diet is as follows: Common Figs *(Ficus sp.)* 1%, Hog plum *(Spondias mombin)* 3%, Inga *(Inga edulis)* 1%,

Figure 28
Feeding Budget by Plant Species for Adult Males in Group 1 N=2

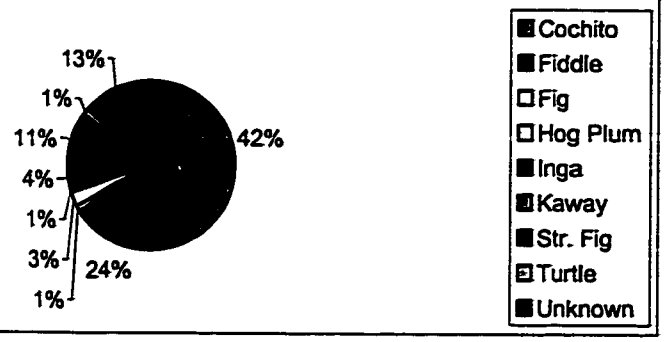


Figure 29
Feeding Budget by Plant Species for Adult Females in Group 1
N=2

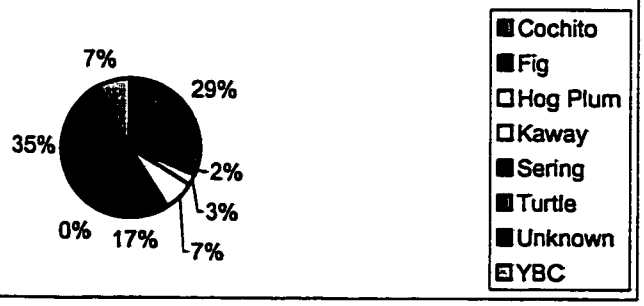
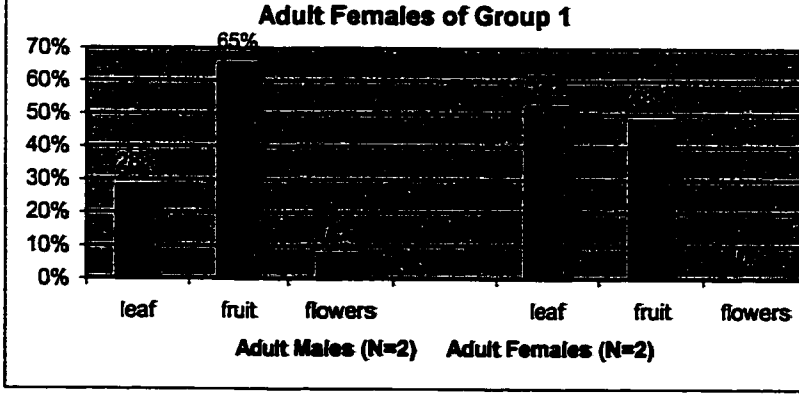


Figure 30
Feeding Budgets by Plant Part for Adult Males and Adult Females of Group 1



Kaway *(Pterocarpus belizensis)* 4%, Strangler Fig (*Ficus crassiuscula)* 11%, Turtlebone *(Mouriri myrtilloides)* 1%, and various unknown species 13%.

Figure 29 demonstrates the feeding budget by plant species for the two adult females in Group 1. The Group 1 adult females were observed feeding for 37 minute and 54 seconds. Unknown species comprised the largest part of the diet at 35%, and the remainder of the diet is as follows: Cochito 29%, Common Fig 2%, Hog Plum 3%, Kaway 7%, Sering *(Miconia argentea)* 35%, and Yellow Bay Cedar 7%.

Figure 30 displays the feeding budget by plant part for adult males (N=2) and adult females (N=2) for Group 1. 65% of the males diet was comprised of fruits, 28% leaves, and 7% flowers. Adult females were observed feeding on leaves 52% of their total feeding time and fruits 48% of their feeding time. Although females were observed eating flowers, their contribution was minimal and is not represented here.

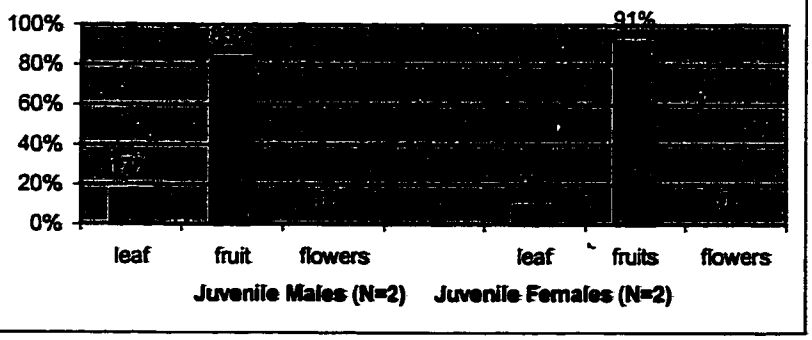
Figure 31 shows the feeding budget for two juvenile males of Group 1. Juvenile males from Group 1 were observed feeding 60 minutes and 8 seconds. Common Figs were the largest food source in their diet at 63% followed by Fiddle Wood (20%), and Kaway (17%).

Figure 32 illustrates the feeding budget by species for two juvenile females of Group 1. The total time the juvenile females were observed feeding was 24 minutes and 9 seconds. The diet of juvenile females of Group 1 was made up of Banac berries

Figure 31
Feeding Budget by Plant Species for Juvenile Males in Group 1
N=2

Figure 32
Feeding Budget by Plant Species for Juvenile Females in Group 1
N=2

Figure 33
Feeding Budgets by Plant Part for Juvenile Males and Juvenile Females in Group 1



(Virolia kosechnye) 4%, Cochito berries 4%, Fiddle Wood fruits 57%, Common Figs 34%, and Hog Plum leaves or fruits at 1%.

Figure 33 shows the feeding budget by plant part for juvenile males (N=2) and juvenile females (N=2) of Group 1. Juvenile males consumed fruits 83% of the time, and leaves 17% of the time. Juvenile females consumed fruits 91% of their time, followed by leaves 9% of their time. The dietary contribution of flowers was extremely small and is not represented by Figure 33.

Figure 34 displays the feeding budget by species of the infant male of Group 1. The total amount of time Group 1 infant male was observed feeding was 26 minutes and 18 seconds. Trumpet Tree leaves (*Cecropia obtusifolia)* were the largest contributor to his diet at 37%, succeeded by various unknown species (35%) and finally Fiddle Wood fruits at 28%. This graph may inaccurately demonstrate the overall feeding budget of the infant male. Trumpet Tree leaves in general were rarely consumed. Unfortunately most of the data on the infant male's feeding behavior occurred on days when the troop fed on these leaves.

Figure 35 depicts the feeding budget by plant species for the infant female of Group 1. This infant was observed feeding for a total of 37 minutes and 55 seconds. Of this time, Fiddle Woods were consumed at 86%, Kaway at 3%, unknown species 6%, and Provision Tree leaves (*Pachira aquatica)* at 5%.

Figure 34
Feeding Budget by Plant Species for Infant Males in Group 1
N=1

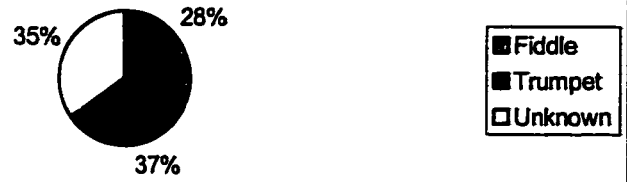


Figure 35
Feeding Budget by Plant Species for Infant Females in Group 1
N=2

Figure 36
Feeding Budgets by Plant Part For Infant Males and Infant Females of Group 1

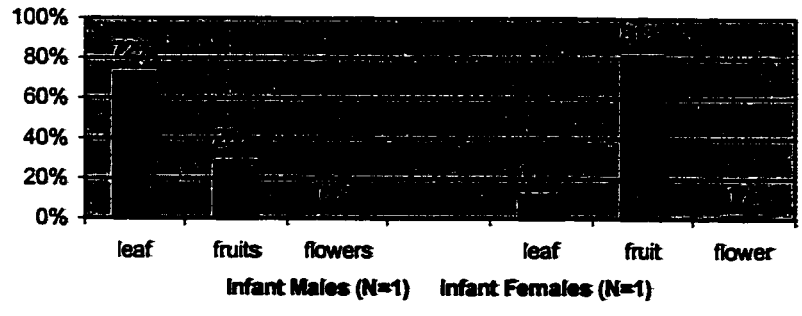


Figure 36 illustrates the feeding budget by plant part of the infant male (N=1) and the infant female (N=1) of Group 1. The largest plant part contributor of the infant male's diet was leaves at 72%, and then fruits at 28%. The feeding budget by plant part for the infant female of group 1 is fruits 81%, leaves 11%, and flowers 1%.

Figure 37 summarizes the overall feeding budget by plant species of all ten members of Group 1. The total time Group 1 was observed feeding was 400 minutes and 35 seconds. Fiddle Wood fruits represented the largest percentage (37%) of all the species the group was observed feeding on. Researchers often looked for monkeys at a large Fiddle Wood tree where they could be easily observed for long periods of time feeding on fruits and resting. Cochito berries were the second largest contributor to the overall feeding budget at 21%. The remainder of the diet is as follows: Common Figs 12%, unknown species 12%, Kaway 5%, Strangler Fig 5%, Sering berries 2%, Trumpet Tree 2%, and Banac, Hog Plum, and Turtlebone each weighing in at 1%.

Figure 38 shows the diet of the three adult males of Group 2. These males were observed a total of 249 minutes and 41 seconds feedings. Cochito berries make up the largest percentage of the adult males' diets at 26%. Group 2 was the only group that was observed eating mangos *(Mangifera indica)*, which made up 17% of their diet. This is followed by unknown species at 14%, Kaway at 11%, Sering at 10%, Black Bay Cedar leaves *(Gauzuma ulmifolia)* at 6%, Banac berries at 4%, Common Figs at 4%, Strangler Figs at 2%, Turtlebone leaves at 2%, Sour Plum leaves (*Ximenia Americana)* at 1% and Yellow Bay Cedar leaves at 1%.

Figure 37
Feeding Budget by Plant Species For All Members of Group 1
N=10

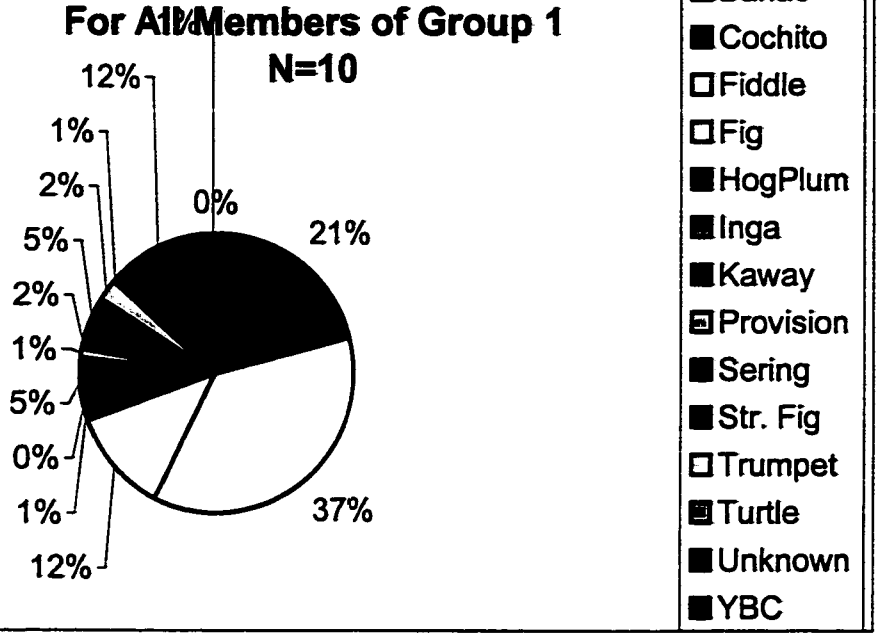


Figure 38
Feeding Budget by Plant Part For All Members of GROUP 1
N=10

Figure 39 depicts the feeding budget by plant species by adult males (N=3) of Group 2. Group 2 males were observed feeding for a total of 249 minutes, 41 seconds. The breakdown of how much time these adult males spent consuming each food is as follows: Cochito berries, 26%; Mango, 17%; unknown species, 14%; Kaway leaves, 11%; Sering berries, 10%; Black Bay Cedar leaves, 6%; Common Figs, 4%; Banac berries, 4%; Wild Yam leaves, 2%; Strangler Figs, 2%; Turtlebone leaves, 2%; and Sour Plums, 1%.

Figure 40 illustrates the feeding budget by plant species for two adult females of Group 2. Group 2 females were observed feeding a total of 104 minutes and 32 seconds. The largest contributors to the feeding budget of these females were Mangos, 39%, followed by Cochito, 23%, Sering, 15%, Hog Plum at 9%, Black Bay Cedar at 8%, and Provision, 4%.

Figure 41 demonstrates the feeding budget by plant part for adult males (N=3) and adult females (N=2) of Group 2. Adult males were observed feeding on fruit for 65% of the time, and leaves 35% of the time. Adult females were observed consuming fruit 79% of the time, while they fed on leaves for 21% of the time. At no time did either sex feed on flowers.

Figure 42 depicts the feeding budget by plant species for the 4 juvenile males of Group 2. These juvenile males were observed feeding for a total of 37 minutes, 18 seconds. They were observed eating Malay Apples (*Eugenia malaccensis)* 34% of the

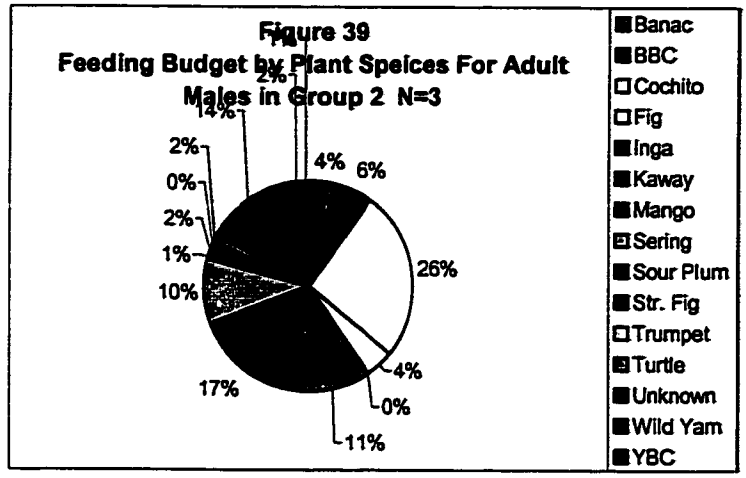


Figure 39
Feeding Budget by Plant Species For Adult Males in Group 2 N=3
2%
14%
2%
0%
2%
1%
10%
4%
6%
26%
4%
0%
11%
17%
Banac
BBC
Cochito
Fig
Inga
Kaway
Mango
Sering
Sour Plum
Str. Fig
Trumpet
Turtle
Unknown
Wild Yam
YBC

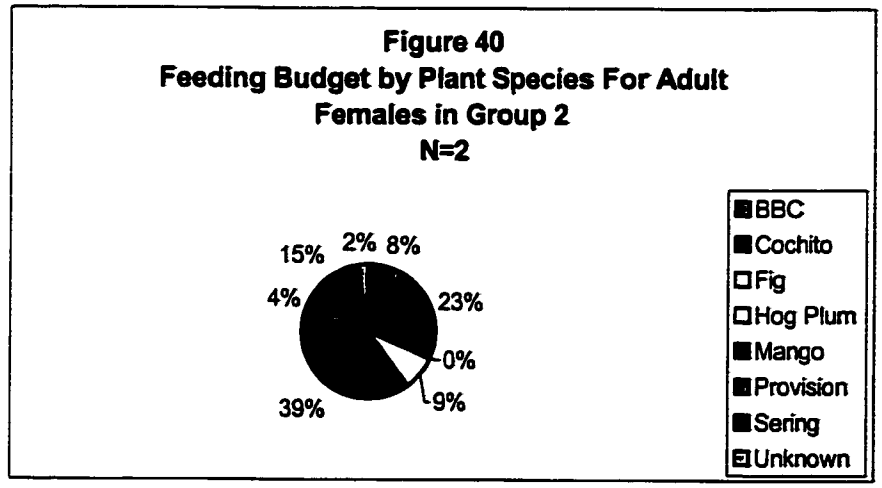


Figure 40
Feeding Budget by Plant Species For Adult Females in Group 2
N=2
15%
2%
8%
4%
23%
0%
39%
9%
BBC
Cochito
Fig
Hog Plum
Mango
Provision
Sering
Unknown

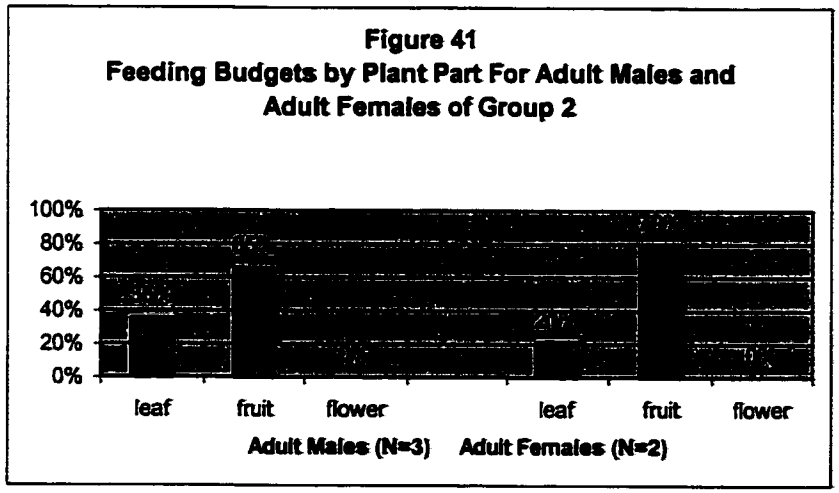


Figure 41
Feeding Budgets by Plant Part For Adult Males and Adult Females of Group 2
100%
80%
60%
40%
20%
0%
leaf
fruit
flower
leaf
fruit
flower
Adult Males (N=3)
Adult Females (N=2)

time, which were virtually ignored by the other age and sex classes, including other groups. Aside from these apples, they ate Mangos for 33% of the time, Wild Yam leaves *(Dioscorea sp.)* were eaten 10% of the time, Black Bay Cedar leaves were consumed 10% of the time, Cochito berries 4% of the time, Kaway 3% of the time, Sering berries 3%, unknown species 2%, and Strangler Figs for 1% of the time.

Figure 43 shows the feeding budget by plant species of the juvenile female of group 2. She was observed feeding for 12 minutes, 19 seconds. She consumed Mangos 52% of the time, and unknown species 48% of the time.

Figure 44 displays the feeding budget by plant part for juvenile males (N=4) and the juvenile female (N=1) of Group 2. The juvenile males consumed fruit 87% of the total observed time, and leaves 13% of the time. The juvenile female fed on fruit 52% of the time, and leaves 48% of the time.

Figure 45 illustrates the feeding budget by plant species of 2 infant males in Group 2. These infant males were observed for a total of 53 minutes, 31 seconds. Sering berries were the largest portion of the diet, at 26%, followed by Cochito berries and Kaway leaves, each at 22%. Strangler Figs were consumed 16% of the time, Common Figs were eaten 6% of the time, Black Bay Cedar leaves 5%, and unknown species 3% of the time.

Figure 42
Feeding Budget by Plant Species for Juvenile Males in Group 2
N=2

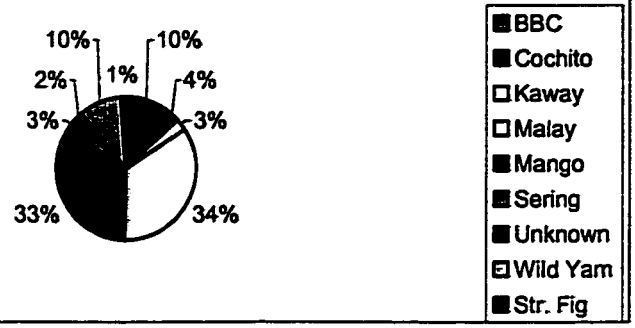


Figure 43
Feeding Budget by Plant Species for Juvenile Females in Group 2
N=1

Figure 44
Feeding Budget by Plant Part For Juvenile Males and Juvenile Females of Group 2

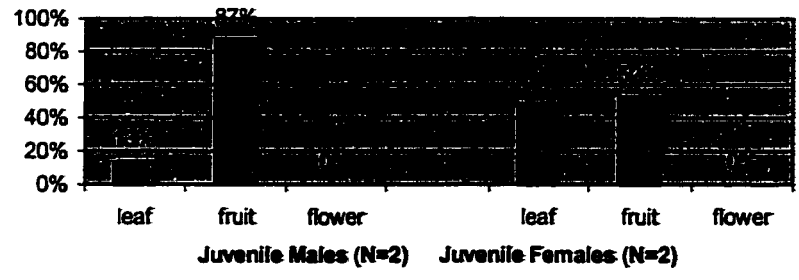


Figure 46 shows the feeding budget by plant part for infant males (N=2) of Group 2. There were no infant females in Group 2. Leaves comprised 67% of the total time observed, and the remaining 33% of the time was spent eating fruit.

Figure 47 demonstrates the overall feeding budget by plant species for Group 2. The 12 individuals of Group 2 were collectively observed feeding for a total of 456 minutes, 43 seconds. The time spent eating each food was as follows: Cochito berries, 23%; Mango, 22%; Sering, 12%; unknown species, 10%; Kaway, 9%; Black Bay Cedar, 6%; Common Figs, 3%; Strangler Figs, 3%; Malay Apples, 3%; Banac, 2%; Wild Yam leaves, 2%; Hog Plum, 2%; Provision Tree leaves, 1%; and Turtlebone leaves, 1%.

Figure 48 summarizes the feeding budget by plant part of Group 2 as a whole. Fruits were consumed in this group for 70% of observed time, while leaves were eaten 30% of the time. At no time were flowers consumed, in contrast to Group 1.

Figure 49 depicts the feeding budget by plant species of the 2 adult males of Group 3. They were observed feeding for a total of 152 minutes, 41 seconds. Cochito berries were observed being eaten 35% of the time, Common Figs 23% of the time, and unknown species 21% of the time. In contrast to the other two groups, adult male members of this group fed on Wild Grapes (*Vitis tiliifolia)*, which made up 9% of the time they were observed feeding. Sering berries made up 7%, Banac comprised 2%, and Fiddle Wood and the Paper Glue tree (*Stemmadenia donnelli-smithii)* were each seen being consumed 1% of the time.

Figure 45
Feeding Budget by Species For Infant Males of Group 2
N=2

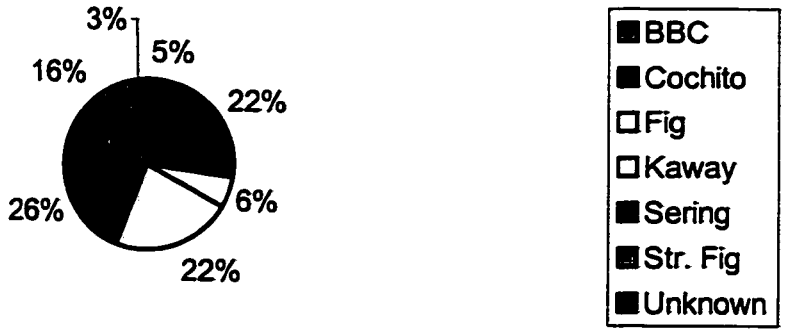
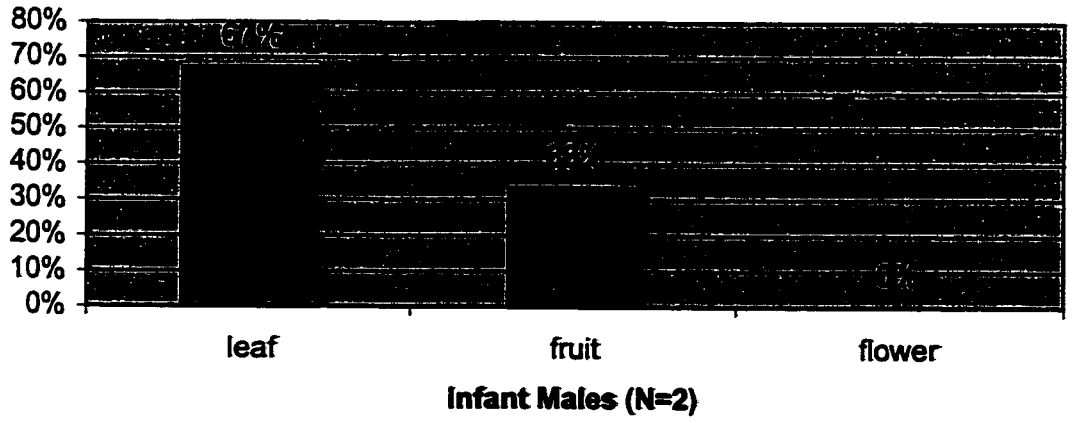


Figure 46
Feeding Budget by Plant Part For Infant Males of Group 2



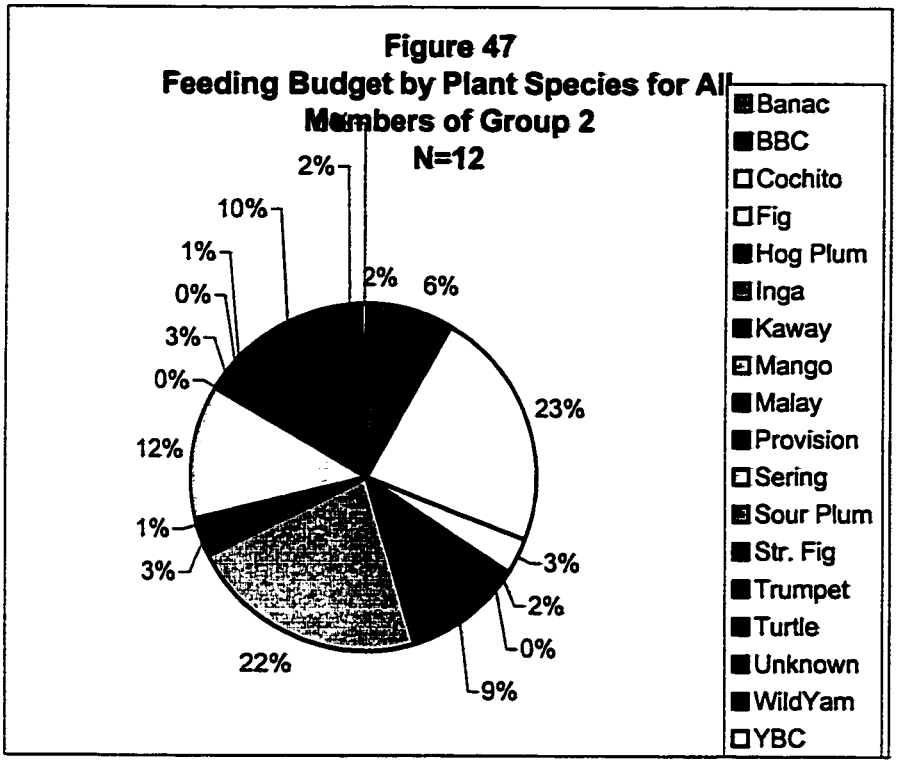


Figure 47
Feeding Budget by Plant Species for All Members of Group 2
N=12
2%
10%
1%
0%
3%
0%
12%
1%
3%
22%
9%
0%
2%
3%
23%
6%
2%
Banac
BBC
Cochito
Fig
Hog Plum
Inga
Kaway
Mango
Malay
Provision
Sering
Sour Plum
Str. Fig
Trumpet
Turtle
Unknown
WildYam
YBC

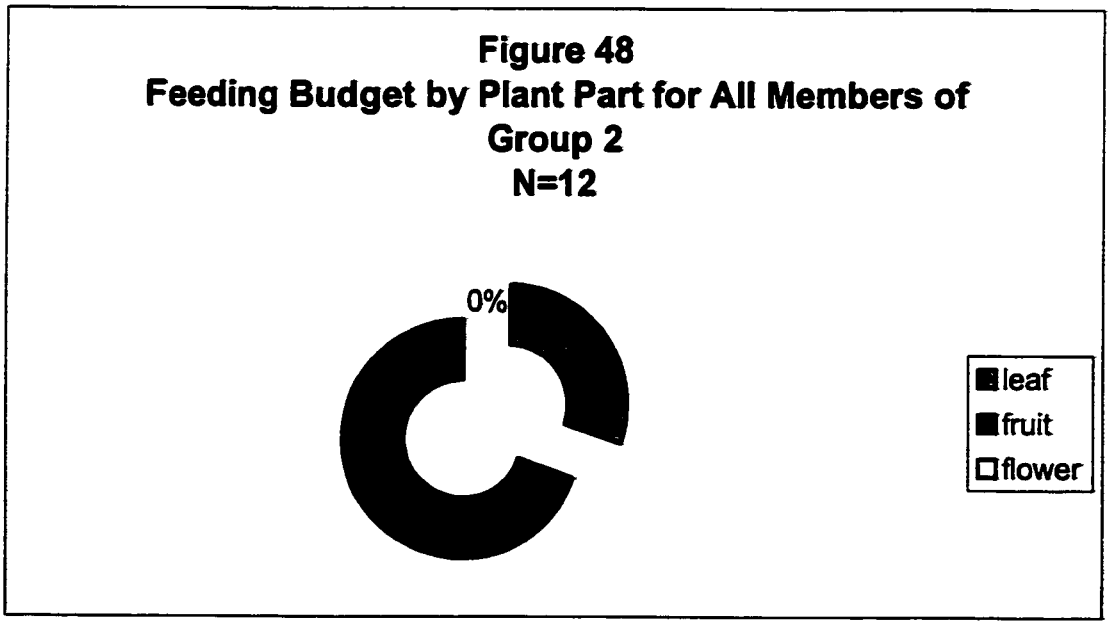


Figure 48
Feeding Budget by Plant Part for All Members of Group 2
N=12
0%
leaf
fruit
flower

Figure 50 demonstrates the feeding budget by plant species of the one adult female in Group 3. She was observed feeding for a total of 138 minutes, 56 seconds. Of this time, she consumed Cochito berries 56% of the time, unknown species, 21% of the time, Sering fruits 9% of the time, Common Figs 6%, Fiddle Wood 4%, Paper Glue leaves 2%, and Inga leaves and Strangler Figs 1% of the total time, each.

Figure 51 displays the feeding budget by plant part for the adult males (N=2) and adult female (N=1) of Group 3. Males spent 69% of their time eating fruits, and 31% of their time eating leaves. The female spent 79% of her time consuming fruit, 18% consuming leaves, and 3% consuming flowers.

Figure 52 shows the feeding budget by plant species of the 3 juvenile males of Group 3. These males were observed feeding for a total of 43 minutes, 37 seconds. Cochito berries comprised 39% of the time observed feeding, followed by unknown species at 30%, Kaway leaves at 15%, Common Figs at 10%, Wild Grapes at 5%, and Sering berries at 1% of the time.

Figure 53 illustrates the feeding budget by plant species of the 2 juvenile females of Group 3. A total of 41 minutes, 46 seconds of observed time was spent feeding by these females. Cochito berries made up 33% of their feeding time, Fiddle Wood 23% of the time, Sering berries 21%, unknown species 17% of the time, and Common Figs 6% of the time.

Figure 49
Feeding Budget by Species for Adult Males in Group 3
N=2

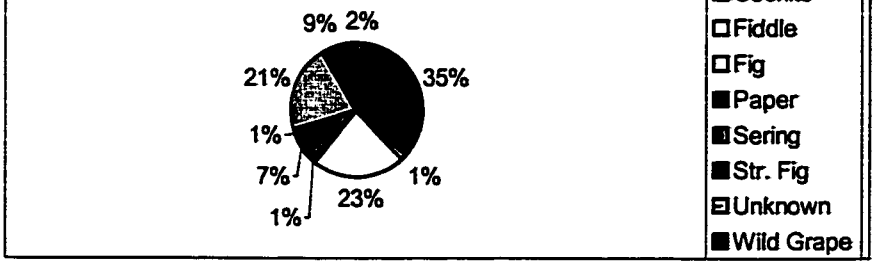


Figure 50
Feeding Budget by Plant Species for Adult Females in Group 3
N=1

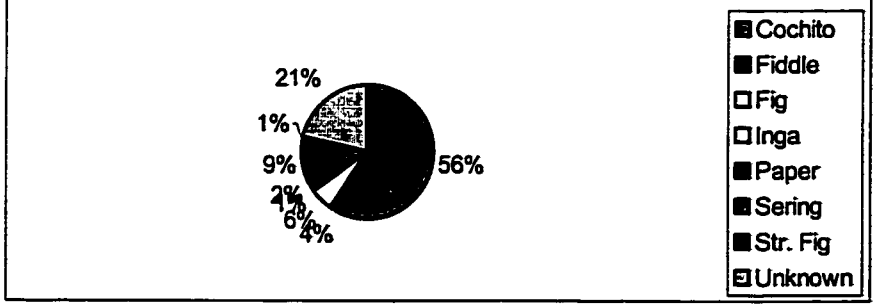


Figure 51
Feeding Budgets by Plant Part For Adult Males and Adult Females of Group 3

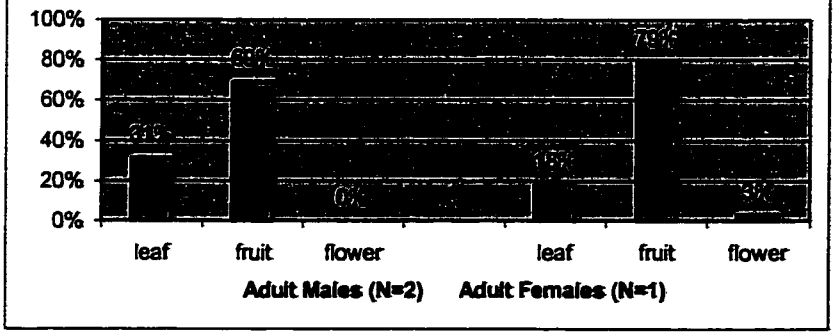


Figure 54 demonstrates the feeding budget by plant part for the juvenile males (N=3) and juvenile females (N=2) of Group 3. The three juvenile males spent 72% of their observed feeding time consuming fruit, 19% of their time consuming leaves and 9% of their time eating flowers. Juvenile females of Group 3 spent 83% of their observed time eating fruits and 17% of their time eating leaves.

Figure 55 illustrates the feeding budget by species for the infant male of Group 3. This infant male was observed eating for a total of 18 minutes, 5 seconds. 52% of this time the infant male consumed Cochito berries, 43% of the time he consumed Sering berries, and the remaining 5% of the time he ate Kaway leaves.

Figure 56 depicts the feeding budget by plant part for the infant male (N=1) of Group 3. 95% of the male's plant part feeding budget consisted of fruits and the remaining 5% consisted of leaves.

Figure 57 is the feeding budget by plant species for all ten members of Group 3. The total amount of time that the group as a whole was observed feeding was 395 minutes and 5 seconds. The feeding budget is as follows: Cochito 44%, unknown species 21%, Common Figs 12%, Sering 10%, Wild Grape 4%, Fiddle Wood 4%, Kaway 2%, and Banac, Paper Glue Trees, and Strangler Figs were observed being consumed 1% of the total time each.

Figure 52
Feeding Budget by Plant Species for Juvenile Males in Group 3
N=3

Figure 53
Feeding Budget by Plant Species for Juvenile Females in Group 3
N=2

Figure 54
Feeding Budgets by Plant Part For Juvenile Males and Juvenile Females of Group 3

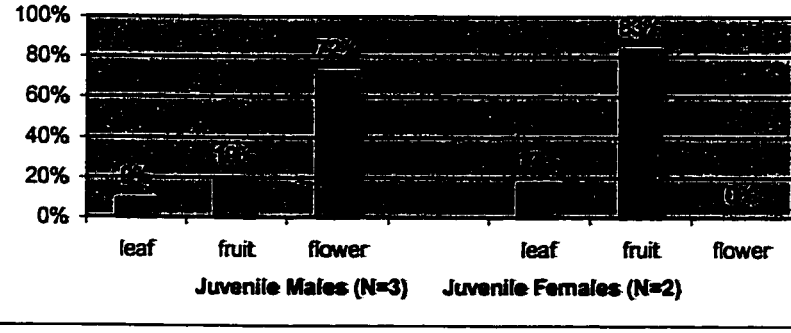


Figure 55
Feeding Budget by Plant Species for Infant Males in Group 3
N=1

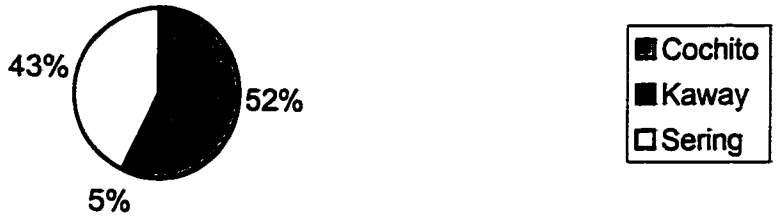


Figure 56
Feeding Budget by Plant Part For Infant Males of Group 3

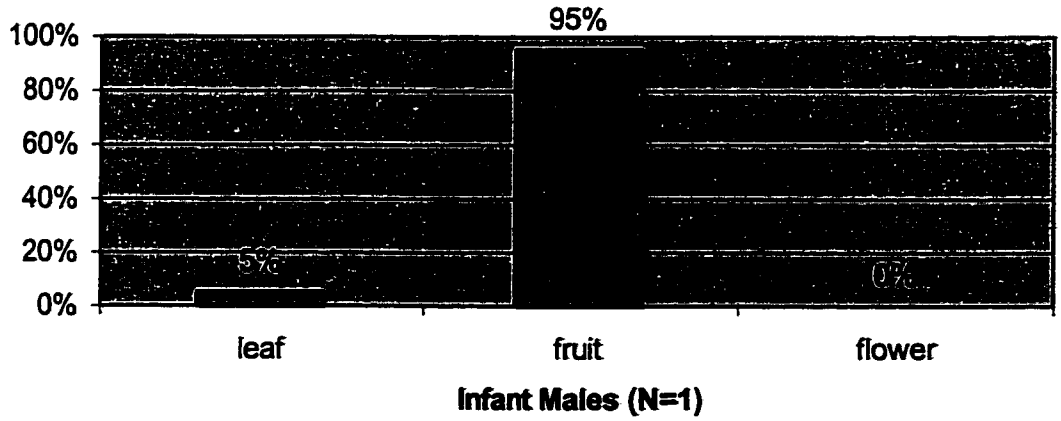


Figure 58 summarizes the feeding budget by plant part for all ten members of Group 3. Overall, Group 3 was observed feeding on fruits 64% of the time, on leaves 34% of the time, and on flowers 2% of the total observation time.

Figure 59 depicts the feeding budget by plant species for all seven adult males of this study population. The overall adult male feeding budget by species is as follows: Cochito 33%, unknown species 16%, Common Fig 8%, Mango 8%, Fiddle Wood 7%, Kaway 6%, Sering 6%, Black Bay Cedar 3%, Banac 2%, Wild Grape 2%, Hog Plum 1%, Turtlebone 1%, and Wild Yam 1%.

Figure 60 illustrates the feeding budget by plant part for all seven of the adult males of this study. Adult males as a whole were observed eating fruit 66% of their time, leaves 32% of their time, and eating flowers 2% of their time.

Figure 61 demonstrates the feeding budget by plant species for all five of the adult females in this study. Adult females spent 39% of their time consuming Cochito berries, 15% of their time consuming Mangos, 16% of their time consuming foods unknown to the researchers, 12% of their time eating Sering berries, 4% of the time consuming Hog Plum leaves, 3% of their time consuming Black Bay Cedar leaves, 3% of their time consuming Common Figs, and 1% of the time consuming each of the following: Inga leaves, Kaway leaves, Paper Glue fruits and leaves, Provision Tree leaves, Yellow Bay Cedar leaves, and Strangler Figs.

Figure 57
Feeding Budget by Plant Species For All Members of Group 3
N=10

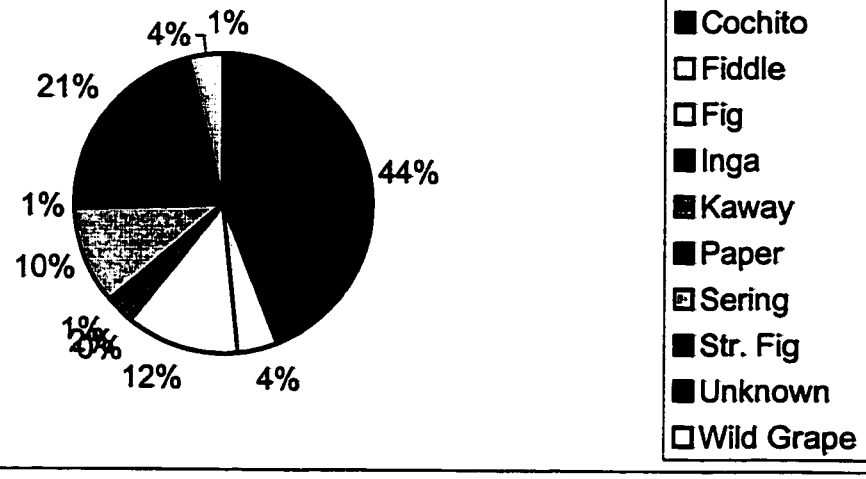


Figure 58
Feeding Budget by Plant Part For All Members of Group 3
N=10

Figure 59
Feeding Budget by Plant Species For All Adult Males
N=7

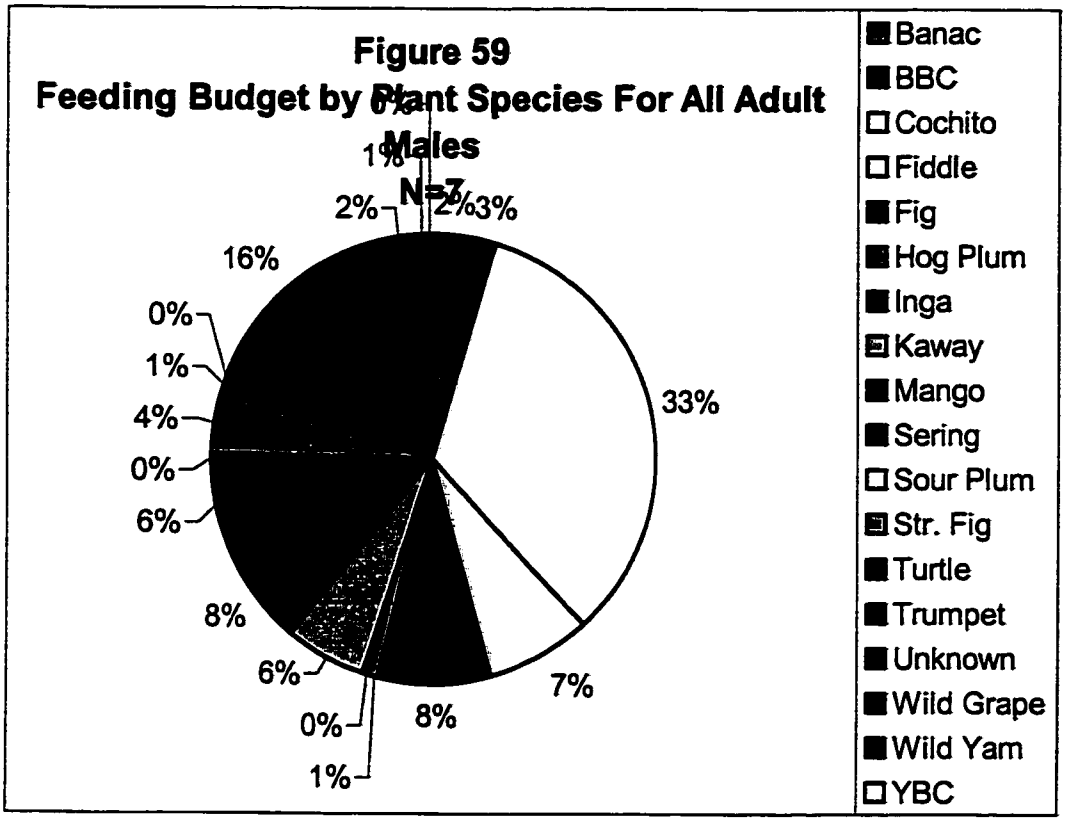


Figure 60
Feeding Budget by Plant Part For All Adult Males
N=7

Figure 62 illustrates the feeding budget by plant part for all five adult females, across all groups. The females spent 75% of the time feeding on fruits, 24% of the time feeding on leaves, and 1% of the time on flowers.

Figure 63 displays the feeding budget by plant species for all 9 juvenile males, across all three groups. The breakdown of time spent eating each plant is as follows: 29% on Common Figs; 13% on Kaway leaves; 12% on Cochito berries; 10% on unknown species; 9% on Fiddle Wood; 9% on Malay Apples; 9% on Mangos; 3% on Black Bay Cedar leaves; 3% on Wild Yam leaves; 2% on Wild Grapes; and 1% on Sering fruits.

Figure 64 shows the feeding budget by plant part for all nine juvenile males. They were observed consuming fruits 81% of the time, consuming leaves 16% of the time, and consuming flowers 3% of the time.

Figure 65 depicts the feeding budget by plant species for all five juvenile females, across all three groups. They spent 31% of observed time eating Fiddle Wood fruits, 20% of the time eating Cochito berries, 16% of the time eating unknown species, 13% of the time eating Common Figs, 11% of the time eating Sering berries, 8% eating Mangos, and 1% of the time eating Banac berries.

Figure 61
Feeding Budget by Plant Species For All Adult Females

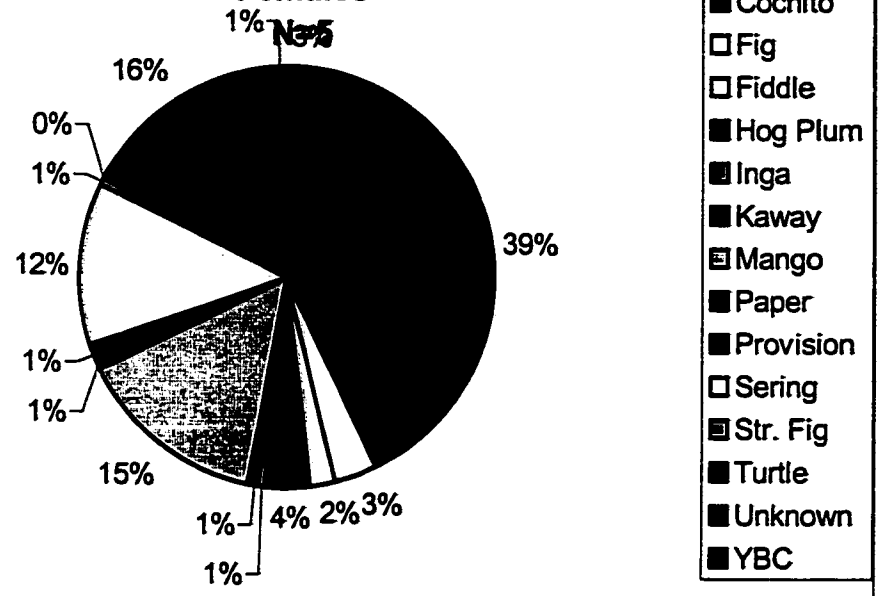


Figure 62
Feeding Budget by Plant Part For All Adult Females
N=5

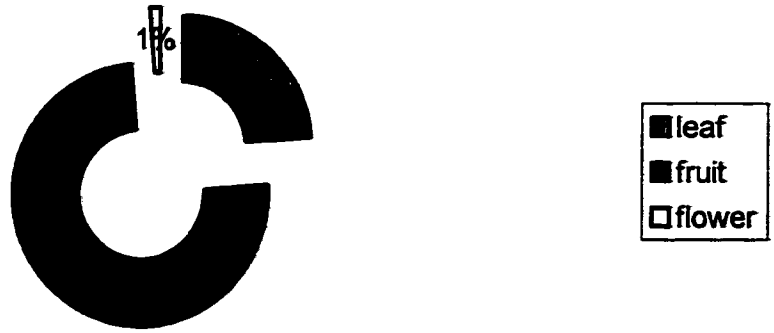


Figure 63
Feeding Budget by Plant Species For All Juvenile Males
N=9

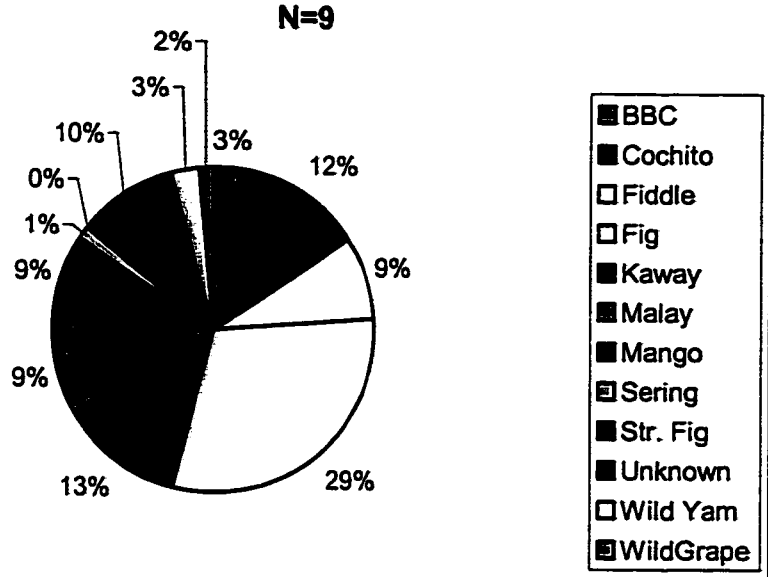


Figure 64
Feeding Budget by Plant Part For All Juvenile Males
N=9

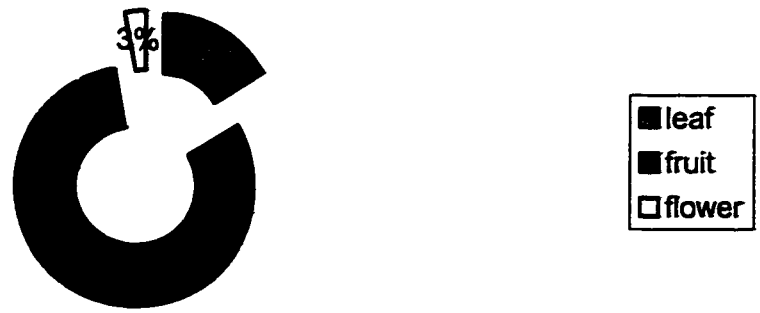


Figure 65
Feeding Budget by Plant Species For All Juvenile Females N=5

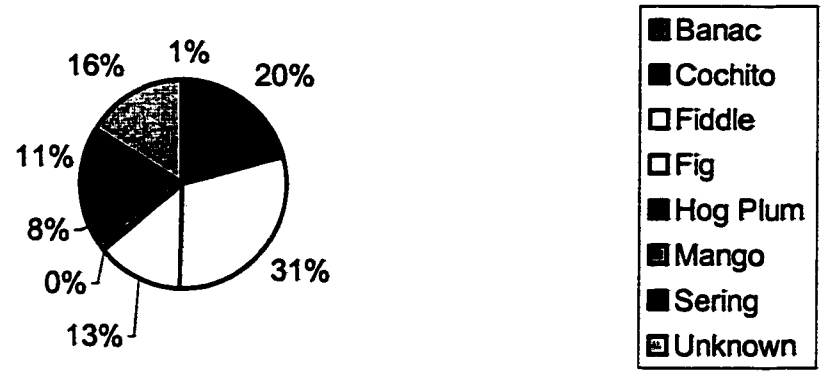


Figure 66
Feeding Budget by Plant Part For All Juvenile Females N=5

Figure 66 illustrates the feeding budget by plant part of the five juvenile females in this study. They spent 55% of the observed feeding time consuming leaves, and 45% of the time eating fruits.

Figure 67 displays the feeding budget by plant species for all 4 infant males, across all groups. These infant males spent 22% of the feeding time eating Cochito berries, 22% eating Sering berries, 13% eating Kaway leaves, 11% eating unknown species, 10% eating Trumpet Tree leaves, 9% Strangler Figs, 7% Fiddle Wood fruits, and 3% each for Black Bay Cedar leaves and Common Figs.

Figure 68 shows the feeding budget by plant part for all four infant males. They spent 55% of the observed feeding time eating leaves, and 45% of the time eating fruits.

Figure 69 demonstrates the feeding budget by plant species for the two infant females across all groups. 86% of the observed feeding time was spent eating Fiddle Wood fruits, 6% on unknown species, 5% on Provision Tree leaves, and 3% Kaway leaves.

Figure 70 depicts the feeding budget by plant part for these infant females. They spent 88% of the observed feeding time eating fruits, 11% of the time eating leaves, and 1% of the time eating flowers.

Figure 67
Feeding Budget by Plant Species For All Infant Males
N=4

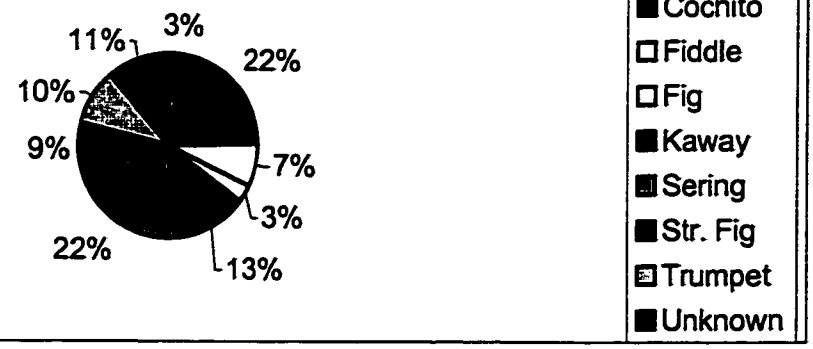


Figure 68
Feeding Budget by Plant Part For All Infant Males
N=4

Figure 67
Feeding Budget by Plant Species For All Infant Males
N=4

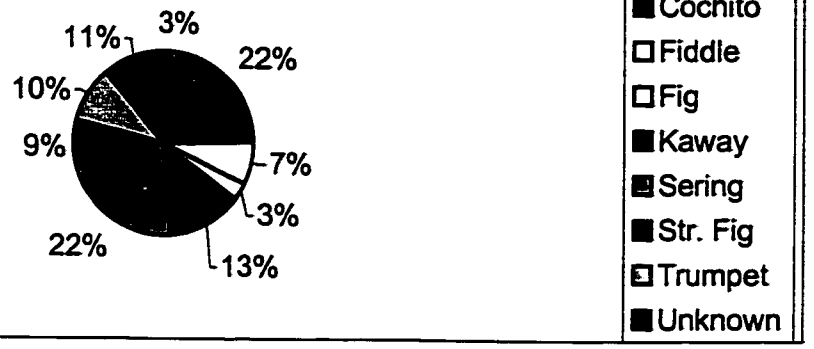


Figure 68
Feeding Budget by Plant Part For All Infant Males
N=4

Figure 71 summarizes the feeding budget by plant species for all 32 individuals sampled, including members of all three groups. Of the observed feeding time, all individuals pooled spent: 28% of the time eating Cochito berries; 14% of the time eating Fiddle Wood fruits; 14% on unknown species; 9% on Common Figs; 8% on Mangos; 8% on Sering berries; 6% on Kaway leaves; 3% on Strangler Figs; 2% on Black Bay Cedar leaves; and 1% on each of the following: Banac berries, Hog Plum leaves or fruits, Malay Apples, Provision Tree leaves, Trumpet Tree leaves, Turtlebone leaves, Wild Grapes, and Wild Yam leaves.

Figure 72 summarizes the feeding budget by plant part of all 32 individuals sampled, in all three groups. They spent 68% of observed feeding time eating fruits, 30% of the time eating leaves, and 2% of the time eating flowers.

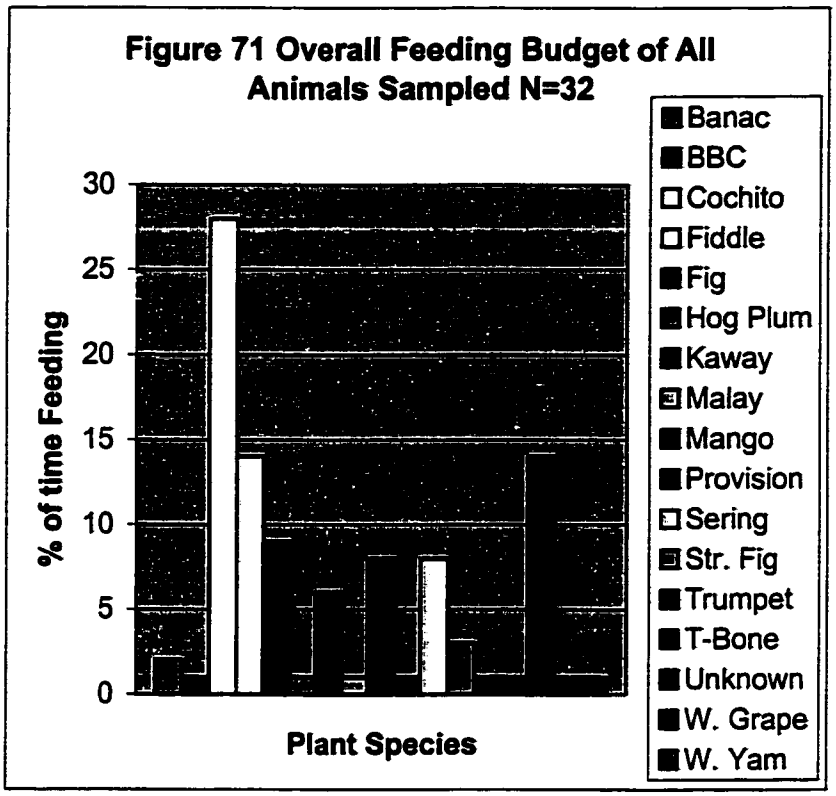


Figure 71 Overall Feeding Budget of All Animals Sampled N=32
% of time Feeding
30
25
20
15
10
5
0
Plant Species
Banac
BBC
Cochito
Fiddle
Fig
Hog Plum
Kaway
Malay
Mango
Provision
Sering
Str. Fig
Trumpet
T-Bone
Unknown
W. Grape
W. Yam

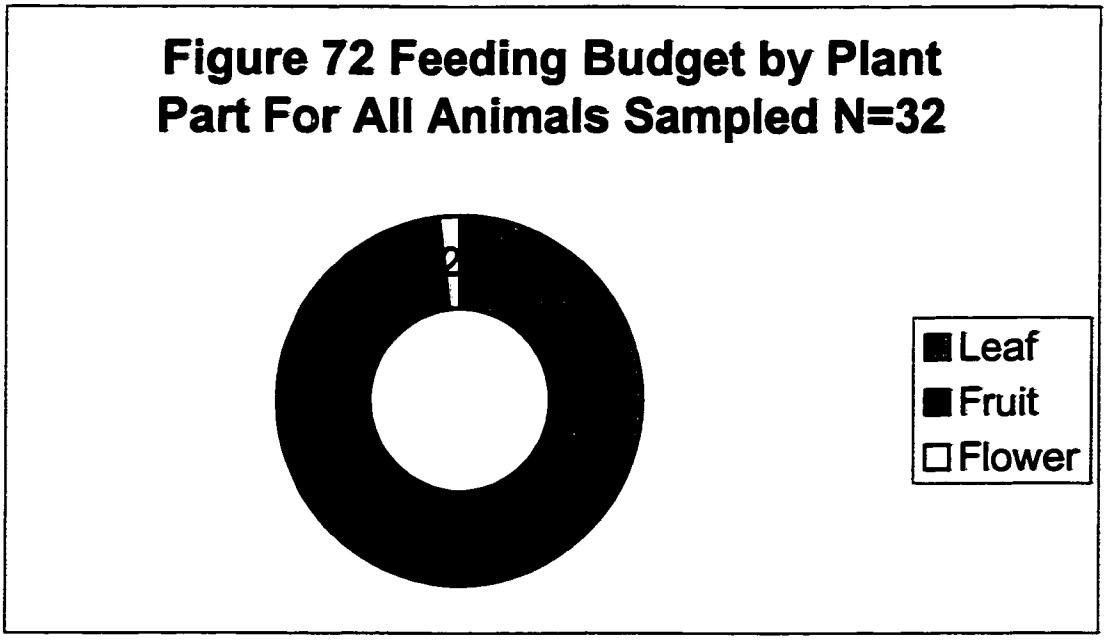


Figure 72 Feeding Budget by Plant Part For All Animals Sampled N=32
Leaf
Fruit
Flower

DISCUSSION

Group Size

The mean group size of each of the three study groups fits within the parameters of published accounts of the genus *Alouatta*. Each group was a mutually exclusive assemblage of animals. Although each group had at least one solitary adult male howler monkey sharing its home range, no attempts were made by solitary animals to immigrate into an existing group. Additionally, no animals emigrated to another group during the study.

The risk of predation existed among each group. The primary predators for the monkeys in this region are jaguars (*Panthera onca*) and ocelots (*Felis pardalis*). Data collectors often observed fresh jaguar tracks in the morning hours but no monkeys disappeared. In the three-month period no births or infanticides were observed. Each troop had at least one animal that was the victim of an unidentified parasite. The infected area festered into a large lesion but did not seem to alter the victim's behavior. During the month of August all lesions were unobservable or had disappeared.

In 1961 the study site was hit by Hurricane Hattie, which ultimately destroyed a large percentage of the forest (pers. comm. Percy Gordon). In the recent years, animals from this study population were removed and translocated. The translocated animals

were moved into a region that formerly had howler monkeys. The population made a full recovery and the each troop displays the typical howler group size.

Group 1

Group 1 is the smallest group, numbering ten animals. Throughout the entire study period no changes were observed in the membership of Group 1. On several occasions a large solitary male was observed sharing the home range of Group 1. This male did not attempt to immigrate into the existing group and avoided the group on all occasions when the researchers focused on Group 1. To the west of Group 1 exists a group of four animals, which didn't belong to the study population, but were noted by the researchers at each of the three sightings. Group 1 and the smaller westward group were not observed engaging in any inter-group behaviors. However, on one occasion a large juvenile male was observed leaving Group 1's home range and moving eastward towards Group 2 and Group 3's side of the field. The juvenile male was alerted to the presence of the researchers and didn't cross the field.

Group 2

Group 2 is the largest group with twelve individuals. During the study there were no changes in the size of Group 2. Group 2 shared their home range with a solitary adult male that made no attempt to join the established group. On two different instances Group 2 was observed across the field in Group 1's home range. On the first crossing both groups engaged in a howling bout that lasted several minutes. Interactions between the two groups led the researchers to conclude the Group 1 and Group 2 were two

separate groups. On the second occasion, Group 2 was observed in Group 1's home range and Group 1 was not found. On both invasions Group 2 pushed Group 1 in a westward direction. Researchers also witnessed a juvenile male from Group 2 that crossed the field into Groups 1's home range. The juvenile fed in Group 1's range then crossed the field again and reunited with Group 2.

Group 3

Group 3 has ten individuals and is the second largest group. Group 3 had an unidentifiable number of solitary individuals sharing its range. On two occasions Group 2 and Group 3 were observed howling toward one another from long distances (200 meters). On occasion Group 3 fragmented into smaller sub-groups. One such fission occurred while foraging. The group was never seen reuniting, and the number of individuals counted in Group 3 was variable from day to day. Smaller group sizes were observed during the months of July and August when fruit availability diminished and more reliance on leaves was observed.

Researchers were alerted to a howling bout and observed two Group 3 sub-groups howling at one another. Each group roared and displayed. Agonistic behaviors included charges, branch throwing, and branch shaking but no physical contact was observed. The interactions lasted approximately 15 minutes with juvenile and adults of both sexes taking an active role in agonistic behaviors. At the conclusion of the interaction, both sub-groups moved in opposite directions, the first northward to the road and the second group southward to the river.

The division of Group 3 may be attributed to the seasonal variation in the troop's diet. However, Group 3 has the largest home range and two fewer animals than Group 2. The size of Group 2 may not have allowed Group 3 to invade their home range. By decreasing group size foraging efficiency increases (Van Schaik & Van Hoof 1983). With smaller groups foraging efficiency increases but without one group ranging in a new area the rate of food depletion remains constant.

Group 3 broke up and reunited on multiple occasions. After the two sub-groups roaring bout the group was never observed in its entirety. That is, after the roaring bout the original ten animals were not seen together as a cohesive unit. The formation of a new group may be rooted by seasonal changes. Howler monkeys do not live in large aggregations that frequently split up and reunite. This fission-fusion social system has been observed in spider monkeys (Chapman 1987). However, if group size is dependent on the carrying capacity of the environment, it maybe adaptive for a group to split and range in another area. If group size is based on food availability it may be necessary to temporal or permanently split. After the split each smaller sub-group was observed using the same home range. Due to the short-term nature of this study, it is impossible to infer that Group 3 split into two distinct groups on a permanent basis.

Group Composition

Each of the three study groups is a multi-male multi-female unit. Although two of the three groups have more adult males than adult females, each group exhibits typical howler monkey social composition, as described by Clarke et al (1986). Species of howler monkeys may have one to four adult males in each group (Crockett & Eisenberg 1987). Adult females usually comprise the larger proportion of adult troop size, however it is not unsual for adult males to outnumber adult females.

Differences in the number of adult males to adult females can be influenced by bisexual emigration. At present there are no published accounts focused on the emigration and immigration patterns of *Alouatta pigra*. Glander (1992) noted interspecific variation between red howler and mantled howler monkey dispersal patterns. Glander (1992) found that female mantled howler monkeys spend up to a year as solitary individuals. Juvenile male mantled howler monkeys may spend more than three years as solitary individuals. Extended periods of solitary existence increases predation risks and lowers the survival rate of juvenile males, which would favor the adult sex ratio of groups to females. Glander (1992) also noted female red howler monkeys do not transfer into existing groups and red howler monkey males may transfer multiple times, a behavioral pattern not observed in mantled howler monkeys of either sex.

Variation in these two different species suggests that *Alouatta pigra* may have bisexual dispersal patterns that differ from other species of the genus *Alouatta*. Perhaps one sex emigrates at a younger age or emigrants transfer directly into an existing group, or the dominant male allows younger animals to remain in their natal group for longer periods of time.

Differences in the number of adult males to adult females may be based on morphological differences as well. Mantled howler monkey males' testes descend at a younger age in comparison with other species of *Alouatta* (Neville et al. 1988). This may lead to differences in the number of adult males to adult females per group. Neville et al. (1988) also claimed that researchers use different criteria to determine adults, sub adults, and immatures.

Other differences in a group's composition include more adults per group than immatures. Immature animals should outnumber adult animals in each group (Crockett & Eisenberg 1987). This result is found in all three study groups. Rudran (1972) noted that natural disasters, disease, deforestation, or hunting could skew the adult to immature ratio. Hunters may selectively target younger animals and disease or natural disasters may wipe all the younger and weaker animals out of group.

Group 1

Group 1 contains two adult males, two adult females, two juvenile males, two juvenile females, one infant male, and one infant female. The adult to immature ratio is 2:1.5 and the male to female ratio is 1:1.

Group 2

Group 2 contains three adult males, two adult females, four juvenile males, one juvenile female, two infant males, and zero infant females. The adult to immature ratio is 1:1.8 and the male to female ratio is 3:1.

Group 3

Group 3 contains two adult males, one adult female, three juvenile males, two juvenile females, one infant male, and one infant female. The adult to immature ratio is 1:3.3 and the male to female ratio is 3:2.

The entire study population consisted of seven adult males, four adult females, nine juvenile males, four juvenile females, four infant males, and two infant females. The adult to immature ratio for the entire study population is 1:1.7. The male to female ratio for the entire population is 1.8:1.

Home range

There are dramatic differences in the home ranges reported for the three study groups when compared to published materials from other study sites. Group 1 has the smallest home range measuring .41 of a hectare. Group 2's home range was calculated at .89 of a hectare, and Group 3 at 1.2 hectares.

One of the largest sources of disparity between this study's home range sizes and published reports could be due to the short study duration. This study lasted a total of 72 days. Had this study been longer, we may have found larger day and home ranges for the three troops. Ostro et al. (1999) studied the ranging behavior of translocated and non-translocated groups of *Alouatta pigra* in two different regions in Belize. Their study lasted over a year and they concluded that a full year of monitoring the animals is not sufficient to determine size and location of home ranges. Ostro et al. (1999) also recommended that monitoring groups should continue through all seasonal phases of food abundance.

During the period of time when the researchers studied the groups for this study, seasonal changes in the vegetation did occur. At the beginning of the study each group fed heavily on Sering and Cochito berries. As the study progressed other fruits ripened and the Sering and Cochito berry season ended. This shift in diet caused a shift in ranging patterns. Sering and Cochito trees are found in clumps throughout each range. Thus, ranging behavior was initially quite small. Towards the end of the study, each troop had

a larger reliance on leaves and figs. Fig trees were randomly distributed throughout each range. This required each group to range farther from one feeding site to the next. As the diets shifted to figs, it became more difficult to collect data on each troop.

The degree of flooding also limited the researchers' ability to successfully follow a focal animal. After rainy periods the river flooded the forest at "ankle to hip" levels. The high depths of water reduced mobility and made accurate follows nearly impossible. On many instances the group was spotted but high levels of water did not permit the researchers to observe the animals at a close enough distance to take accurate notes of their behavior. The researchers had two options if this situation occurred: wait for the monkeys to move into an area in the forest which was not flooded (higher ground) or seek out another troop to follow. Despite all of these data collection problems, the extremely small home ranges found in this study could be quite accurate, due to the natural and human-made geographical constraints, such as rivers, fields, and roads that may not be present at other study sites.

Daily ranging behavior was strongly influenced by feeding. Most movement was from one feeding site to another. Each morning the focal troop roared, then was fairly inactive. Following this period of inactivity, the troop moved to a feeding site. After the first feeding bout, the afternoon hours began. This period of time was best characterized as another period of inactivity. The troop would move again to another feeding site. The group usually moved once more to a sleeping site. None of the three groups was observed returning to the same sleeping site two consecutive days. This behavior of

ranging from feeding site to feeding site agrees with the Million's observations of mantled howler monkeys on Barro Colorado Island (1980).

As mentioned above, the largest constraint on the each group's daily ranging activities and overall home range is the geographic isolates. To the north of the study site lies a road that runs east to west. To the south of the site is a river running east to west. The river doesn't run exactly parallel to the road and at many locations the river penetrates into the forest causing small ponds, and during heavy rains completely floods.

Group 1 Home Range

Group 1's home range was the smallest by comparison to the other groups. Group 1 was the only group geographically isolated on three sides. To the north lies the road, to the south lies the river, and to the east lies the field. The western side of the range drastically tapers into a narrow forest belt. On a few instances the researchers observed a group of 4 animals inhabiting the belt. This group was not studied but was noted when seen.

The road and the field would not permit crossing without coming to the ground. Retreating to the ground increases the risk of predation by terrestrial predators. Although this behavior has been observed at this site and others, it is quite rare (Bicca-Marques 1992, Glander 1992, Gilbert & Stouffer 1989). The fact that howler monkeys rarely come to the ground allows for the possibility that they may cross the road or field more

often in the absence of an observer. Such behavior would increase daily ranges and perhaps overall home ranges.

Group 2 Home Range

Group 2 has the second largest home range, measuring approximately .89 hectares. Group 2 was geographically isolated to the south (river) and to the west by the field. As mentioned above, Group 2 was observed in Group 1's home range across the field on two instances and researchers observed a juvenile male from Group 2 cross into Group 1's home range to feed on mangos and Malay Apple trees. When the researchers first observed Group 2 in Group 1's range, the group was feeding on a Strangler Fig tree that was ripe. On both invasions Group 1 retreated, therefore the researchers determined that Group 2's home range extended into Group 1's home range. It seemed that both groups' home ranges overlapped in the forest on the western side of the field.

Group 3 bordered the northern front of Group 2's home range. Group 2 engaged in only two howling bouts with Group 3. The interactions were brief and it appeared that each group was announcing its location to their neighbors. The researchers became familiar with Group 2's home range, which contained two riverbeds that flooded on the first rain and did not drain. Due to the large portion of flooding in this range the troop could rarely be followed for two consecutive hours. However, the ranging patterns of this troop were well understood. The researchers would often locate the group above the riverbeds and wait for their movement into other feeding areas. As the study progressed the troop ranged farther to feed on mangos, figs, and leaves.

Group 3 Home Range

The home range of Group 3 is bordered to the north by the road and to the south by Group 2's home range. There is no geographic border to the east but the researchers observed a group inhabiting that area. To the west lies the northern portion of Group 2's range. The calculated home range for Group 3 is 1.2 hectares.

The daily ranges of this group were much longer in comparison to the two groups. On few instances the groups broke up into sub-groups and fed in different directions. During the later months of the study the group ranged farther and consumed more figs and immature leaves. Four large fig trees were found within the range and the troop moved from fig tree to fig tree. Ostro et al (1999) found that day ranges increased when food abundance decreased. Their results agree with the observations at this site. When clumped fruit resources (Sering and Cochito trees) were no longer fruiting, common figs were. The results of the Ostro et al. (1999) found that group size had no effect on daily ranging activities or home ranges.

Activity Budgets

Group 1

The activity budgets of each age-sex class differ when compared to other age-sex classes within the group. One would expect that the adult animals would have higher percentages of inactivity and lower percentages of locomoting when compared to

juveniles and infants. Adult males were inacative 52% of their time, which represents the highest percentage of inactivity in comparison to the other age-sex classes. However, adult females were inactive only 39% of their observed time, which is less than the percentage of time juvenile females (42%), infant males (46%), and infant females (41%) engaged in this behavior.

The results showed higher levels of social behavior among adult females and immatures of both sexes. Adult females often carried infants when traveling throughout their home range. Adult females were also observed sitting in spatial proximity or in contact with infants or juveniles. Increased proportions of social behavior in immatures also result from social play. Infants often engaged in play while the adults were resting.

The infant males and infant females of Group 1 devoted larger proportions of their time feeding in comparison to adult animals. Smaller animals require more energy due to their constant moving. However, infant males and females were observed moving only 5% and 7% of their time. Infants were often observed moving much more during the day.

Group 2

There is little variation in the activity budgets of each age-sex class for Group 2. Adult males and juvenile females spent comparable amounts of time inactive, as did adult females and juvenile males. Adult females and infant males had the largest percentages engaged in social behavior. This is due to the fact that each adult female was a mother to

an infant. Both females and males engaged in parental care of infants, such as assisting in bridging, grooming, and providing protection from predators, (hawks,) although females carried the infants more often than males.

Group3

Differences exist between adults and immatures (excluding juvenile males) in the percent of time spent inactive. Adults spent more time inactive than their younger counterparts. The data for infants do not accurately represent their behavioral patterns. For example, the results suggest that infant males of Group 3 spend 26% of the in social activities, 35% of their time "other" behaviors, 15% of their time inactive and only 8% of their time feeding.

Infant females may be misrepresented by the results of the data. The overall low level of data collected on the infant female of group 3 is expressed in her activity budget, suggesting that she spent 100% of her time in social behaviors. Group 3 had two extremely small infants and determining each infant's sex was difficult. A large portion of the infant data could not be used because sex of the focal could not be identified.

Group Budgets

Each group's overall activity budgets are very similar. The largest percentage of disagreement is merely 5% (in social behaviors) with many percentages in complete agreement with another group's results. Similar results occur when each group is compared to the results of the activity budget of all the animals sampled.

Comparisons to Published Accounts

Neves & Rylands (1991) reported three behavioral categories for their activity budget: resting 67%, feeding 11%, and moving 11%. The activity budget for each group and the overall activity budget for all animals sampled suggests that the population at Monkey River, Belize is more active and devotes more time to eating behaviors. Moreover, the results for Group 1, Group 3 and the overall activity budget of all animals sampled, suggest that this population engages in less locomotion behavior. It is difficult to accurately compare the results of this study to Neves and Rylands without their definition of each behavioral category. It is probable that each researcher operationalizes their definition of a specific behavior or what behaviors belong to a behavioral category differently than other researchers, including us. This makes direct comparisons difficult.

Silver et al (1998) reported the activity budgets of six troops of *Alouatta pigra* inhabiting the banks of the Belize River. Each group spent 24.4% feeding, 61.9% resting, 9.8% traveling, 2.3% in social play, and 1.5% vocalizing each month. The Silver et al. study groups engaged in larger proportions of inactive and feeding behaviors. Again, differences in proportions are perhaps due to operationalizing the data categories. The inactive behavior used by the researchers here are probably different than other researchers operationalized definition of "inactive".

The percentage of time feeding and resting reported by Silver et al. (1998) exceeds the results of each of the three groups and the overall activity budget of all

animals sampled. However, the percentage of time spent traveling or locomoting by each of Monkey River troops and the overall activity budget of all animals sampled is similar to Silver et al.'s (1998) study and only deviates by 2.2% at the most (Group 2).

All Age-Sex Class Activity Budgets

The activity budget for each age-sex classed varied, sometimes slightly and sometimes drastically. With the exception of infant females, each age-sex class devoted 15-18% of their time feeding. Infant females engaged in feeding behaviors 31% of the observed time, and this is actually twice as much in comparison to the results of adult males.

Adult males spent a larger portion of time inactive in comparison to the other age-sex classes. Once again, with the exception of infant females, the overall time spent locomoting by each age-sex class is similar. Infant females were observed locomoting only 5% of the time, in comparison to adult males which moved about 10%. The largest divergence between the behaviors is found in the social behavioral category. Infant females engaged in social behaviors 35% of the time. This result may be inflated by the results of the Group 3 female.

Differences between groups in the percentages of time spent in each category could be the result of a variety of influences including ecological factors, group size and group composition. The distribution of feeding sights throughout the groups' home

ranges will determine the amount of time spent moving, feeding, and remaining inactive. The group composition could have skewed the data in favor of a particular age-sex class, as our results have shown.

Bicca-Marques & Calegaro-Marques (1994) constructed activity budgets for a group of black howler monkeys in Brazil based on a year of observations. The authors provided only a bar graph depicting the activity budget of each age-sex class. The range for resting for each age sex class was 55-78%. The range for locomotion was 15-25%, feeding ranged from 15-20%, and social behaviors accounted for approximately 5% of the observations. Without exact percentages and a definition for each behavior or behavioral category, it is difficult to make comparisons to these three study groups. However, each age-sex class studied here spent less time engaged in inactive and locomoting behavior and more time in a social context. The feeding results of each sex class (excluding infant females) falls within the parameters Bicca-Marques & Calgaro-Marques suggest.

Differences in the amount of time an age-sex class engages in a particular behavior can be attributed to diet, rank, and gestation or lactation. Lactating females have higher energy requirements and should devote larger portions of time to feeding. Higher-ranking animals can dominant contested resources such as fruit or engage in higher levels of sexual behaviors.

Age specific behaviors such as "dorsal clinging" are observed more frequently in younger animals. Bicca-Marques & Calegaro-Marques (1994) suggested that differences in body size are responsible for percentages in behavioral categories such as feeding. Smaller animals require larger proportions of food and thus devote a large amount of time eating. In contrast, the increased proportion of an adult animals' inactivity is due to larger intakes of leafy material that requires long periods of digestion (Bicca-Marques & Calegaro-Marques 1994).

Diet

Howler monkeys were observed eating 21 species of plants from 12 different families. The species diversity of plants that were consumed is small in comparison to other studies (Silver et al. 1999, Chiarello 1994 and Julliot & Sabatier 1993). This low level of species diversity is probably due to the short study period. A long-term study is required to assemble an accurate list of all food items used by the monkeys. In the short period of this study, feeding patterns switched from a large reliance of Sering (*Miconia argentea*) and Cochito berries to immature leaves, Fiddle Wood (*Vitex gaumeri*) fruits, and common figs (*Ficus sp.*).

The researchers observed changes in diet when the principle food sources no longer were fruiting. Judging from these criteria, diets changed due to semi-seasonal variation and not from feeding preferences. These observations suggest that leaves are eaten only when fruits are not available. Silver et al. (1998) suggest that howler monkeys

maybe "facultative folivores" whose diet is as frugivorous as possible given the limitations of fruit abundance and may eat leaves in order to obtain protein requirements.

Feeding Budgets

Group 1

The majority of foods eaten by adult males of Group 1 are fruits. Fruits comprised 65% of the food resources while leaves comprised 28% and flowers 7% respectively. Cochito berries dominate the species-feeding budget for adult males from Group 1. As noted above, Cochito berries were consumed heavily at the start of the study. The bias in the feeding budget by plant species is due to seasonal variations and field conditions. Due to flooding, more hours of data were collected in the earlier weeks of the study when Cochito berries were consumed at high quantities. Fiddle Wood fruits contributed 24% of the diet and were heavily consumed in the latter weeks of the study. Fiddlewood trees produce a green fruit, which are comparable in size to a common fig. Figs were consumed during the last weeks of the study. Most Common Figs trees were distributed deep within the forest and out of sight from the trails.

Leaves comprised 28% of the feeding budget by plant part. The majority of leaves consumed by adult males were Kaway (*Pterocarpus belizensis*) leaves. Males were observed eating Kaway leaves when Cochito and Sering trees no longer fruited. The majority of Kaway leaves consumed were immature, judging by size, color, and texture.

Flowers made up the smallest percentage of foods consumed. Researchers were not able to identify the species of plant that produced the flowers.

The feeding budget by plant part for adult females of Group 1 differs in comparison to the feeding budget of adult males. Adult females consumed a larger portion of leaves (52%) and a smaller proportion of fruits (42%). However, the most dominant food species consumed by adult females was Cochito Berries. The two species that represented the largest proportion of leaves were from Kaway, Yellow Bay Cedar trees, and various unknown species

Group 1's overall feeding budget, by plant species, is represented by 14 different plant species. At 37%, Fiddle Wood fruits were consumed more than any other food source. Two Fiddle Wood trees existed in Group 1' s home range. A very large Fiddle Wood tree grew next to a major trail in a small semi-clearing. The second largest contributor to Group 1's feeding budget was Cochito fruits (21%), which were near a major trail, followed by Common Figs at 12% of the total time. Two Common Fig trees existed in Group 1's home range, one of which was not discovered until the last week of the study, but the other stood on the periphery of the field, which allowed the researchers an excellent view of the troop.

Fruits accounted for 70% of the total feeding budget, leaves represented 27% and flowers contribute 3%. On one specific occasion the researchers observed the

members of Group 1 feeding approximately 2 hours on yellow flowers from an unknown tree species.

Group 2

Group 2 adult males consumed 15 species. Cochito berries (26%) contributed the largest portion of the feeding budget. Mangos (*Mangifrea indica*) at (17%), Kaway leaves (14%), and Sering berries (10%) followed. As noted before, Cochito and Sering berries were consumed mainly during the early weeks of the study. Mangos were consumed midway through the study. Two mango trees stood at the edge of the field. This allowed the observers to note feeding behavior at a close range, unobstructed by heavy foliage. Group 2 fed heavily on the mangos for approximately three weeks. On several instances the troop fed on mangos in the afternoon and the researchers waited at the mango trees if no other troops could be found.

The adult females of Group 2 fed primarily on fruits (79%) and supplemented their diets with leaves (21%). Mangos were consumed more than all other species, followed by Cochito and Sering berries. Provision and Hog Plum trees were the primary sources of leaves.

Juvenile males consumed the highest percentage of Malay Apples (*Eugenia malaccensis*). Two Malay Apple trees stood on the edge of the field across from the mango trees. In order to feed on the apple trees a juvenile male had to cross the field.

Both researchers witnessed the crossing and recorded detailed descriptions of his behavior. This one juvenile male was the only individual who fed on Malay Apples. 87% of the juvenile male diet is fruits, and leaves represent 13%. In addition to Malay Apples, Mangos and Cochito and Sering berries were consumed. Wild Yam (*Dioscorea sp.*) contributed 10% and accounted for the all leaves eaten.

Group 2's feeding budget by plant part is comprised of only leaves and fruits. Fruits accounted for 70% of the diet and leaves accounted for 30%. A total of 18 species contributed to the diet of Group 2. Cochito fruits were the largest portion of Group 2's diet, at 23%, and Mangos contributed 22%. Contrary to Group 1, Fiddle Wood fruits were not consumed by any animals of Group 2. Differences in diet between the two groups are probably attributed to differences in available foods in each group's home range. For example, Group 1 did not have access to Mangos, Malay Apples, or Wild Yam trees.

Group 3

Fruits represented 69% of the diet of adult males of Group 3. Seven species of fruits were consumed: Banac (*Virolia kosechnye*), Cochito, Fiddle Wood, Common Fig, Sering, Strangler Figs (*Ficus crassiuscula*), and Wild Grapes (*Vitus tiliifolia*). Cochito berries were the overall dominant species consumed. Leaves accounted for 31% of the diet and were represented by Paper Glue (*Stemmadenia donnelli-smithii*) trees and several unknown species. Adult males of Group 3 had the largest home range, yet were observed consuming the fewest number of species.

The feeding budget by plant part of adult females of Group 3 consists of fruits (79%), flowers (3%), and leaves (16%). Adult females were observed feeding on seven species. 56% of the budget was Cochito, 21% was an unknown species, and 9% of the budget was comprised of Sering berries.

The overall feeding budget of Group 3 was comprised of fruits (64%), leaves (34%), and flowers (2%). Eleven species were represented of which Cochito was the dominant species at 44%. Unknown species contributed 22% of the budget followed by Common Figs at 12% and Sering berries at 10%. Group 3 was the only Group that was observed eating Wild Yam Leaves and Wild Grapes.

Feeding Budget For All Adult Males

The feeding budget by plant species of adult males contains 18 different species and all three parts of food. Fruits accounted for 66% of the feeding budget, leaves comprised 32% and flowers accounted for 2% of the feeding budget. The dominant species was Cochito at 33% followed by unknown species at 16%.

The feeding budget of adult males is composed of more plant species, in comparison to other age-sex classes. The high number of species that represents the feeding budget for adult males may be due to the overall higher number of hours collected on adult males.

Adult Female Feeding Budget

Each of the three food categories is included in the adult female feeding budget: fruits comprised 75% of the budget, 24% of the budget is represented by leaves, and flowers accounted for 1% of the budget. The budget consists of 15 species. Cochito represented 39% of the budget, unknown food accounted for 16% of budget, followed by Mangos at 15%.

Juvenile Male Feeding Budget

81% of the juvenile feeding budget is fruit, 16% of the budget consists of leaves and the remaining 3% is flowers. Twelve species were included in the feeding budget. Common Figs were the dominant species (29%) followed by Kaway leaves at 13%, and Cochito berries at 12%.

Juvenile Female Feeding Budget

The juvenile female feeding budget is comprised leaves (55%) and fruits (45%). Eight species are included in the budget: Banac, Cochito, Fiddlewood, Common Fig, Hog Plum, Mango, Sering, and unknown species. The dominant species was Fiddlewood at 31% followed by Cochito at 20%.

Infant Feeding Budgets

Fifty-five percent of the foods eaten were fruits the remaining foods were leaves. Nine species were represented in the feeding budget. The dominant species were Sering

(22%) and Cochito (22%). Infant females consumed each of the three food types. Fruits accounted for 88%, leaves consisted of 11%, and flowers were 1% of the feeding budget.

The greater breadth of plant species in adult diets could be due to two things. First, more data was collected on adult individuals, and therefore their feeding budgets should be more complete. Secondly, however, Bicca-Marques & Calegaro-Marques (1994) suggested that adults could displace younger individuals, which may lead to differences in diet. The dietary differences in this group were not extreme, though. Few (<5) displacements were observed throughout the entire study. The researchers did not observe adults actively displacing juveniles and infants and intragroup agonism was extremely low. During feeding bouts the group moved as a cohesive unit and usually fed on the same food patch. This behavior was consistent with the two sub-groups of Group 3.

Differences in food consumed between groups can be attributed to those foods that are available within the range. The overall feeding budget of Group 2 does not contain flowers, which were not sighted in the home range. Flowers represent 3% of Group 1's overall feeding budget and 2% of Group 3's budget. This can also be illustrated at the species level. Group 2 consumed each of the following species: Wild Yams, Mangos, Malay Apples, and Black Bay Cedar Leaves. Group 3 was the only group that consumed Paper Glue Leaves, and Wild Grape both of which were found in high numbers throughout the range.

Comparisons to Published Accounts

Silver et al (1998) reported *Alouatta pigra* plant part feeding diets as follows: leaves 45.1%, fruits 40.8%, flowers 10.6%, and other food items at 3.4% of the feeding budget. Each of Silver et al.'s study groups consumed higher levels of leaves and flowers and a lower level of fruit consumption when compared directly to Group 1, Group 2, Group3, and the feeding budget by plant parts of all animals sampled.

In contrast, Julliot (1996) studied fruit choice in *Alouatta seniculus* at French Guiana and constructed a feeding budget for her study group. The results of her feeding budget by plant part were: leaves 57%, fruit 25.5%, and flowers 12.6%. Each Monkey River group consumed larger proportions of fruits and lesser proportions of leaves and flowers when compared to the result of Julliot's study.

Chiarello (1994) observed the diet of red howler monkeys and constructed the following dietary budget: Leaves comprised of 73%, fruits made up 5%, flowers were 12%, petioles and twigs were 3%, and unidentified foods were 8%. Each Monkey River study group consumed far less leafy materials and flowers, and more fruits. The large degree of variation in diet is due to the poor marginal environment that Chiarello's study group inhabited. It should be noted that no Monkey River animal was observed feeding on any plant part but fruits, flowers, or leaves.

The feeding budget constructed by Neves and Rylands (1991) for red howlers is as follows: leaves 57%, 13.5% fruits, 4% flowers, and 27% seeds. The percentage of feeding on leaves in Neves and Rylands' group exceeds the percentage of folivory in all three Monkey River groups and all three study groups exceed Neves and Rylands' group in frugivory. However, each group and the plant part feeding budget of all animals sampled have similar values for the percentage flowers that were consumed.

Chapman (1987) studied mantled howlers for a total of 394 hours and constructed the following feeding budget: fruits 28.5%, flowers 22.5%, and leaves 49%. The results of the current study do not agree fully with Chapman's feeding budget. Each study group and the Monkey River population as a whole exceed the total percentage of fruit consumption and were observed consuming smaller percentages of flowers and leaves.

Estrada and Estrada-Coates (1986) constructed the following feeding budget by plant part for mantled howler monkeys at Los Tuxtlas, Mexico: 46% leaves, 53% fruits, and 1% on other food resources. Estrada & Estrada-Coates (1986) report higher percentages of leave consumption and smaller percentages of fruit consumption in comparison to Group 1, Group 2, Group 3, and the overall feeding budget by plant part for all animals sampled at Monkey River.

Milton (1979) studied mantled howler monkeys on BCI and constructed the following feeding budget: 48.2% leaves, 42.1% on fruit, 9.6% and on flowers. Group 1, Group 2, and Group 3, and the Monkey River population as a whole consumed a higher

proportion of fruits and a lower proportion of leaves and flowers compared to results of Milton's study.

Limitations of this Study

The focus of this study is to compare the results of size and composition, home range, and activity and feeding budgets to other published accounts to the genus *Alouatta*. The study was limited by many extraneous variables. The largest of theses variables was the restraint on time. After a review of the results it becomes clear that an entire year is required to make any accurate assumptions regarding this population.

With the exception of Group 3, group size and compositions remained the same. However, a longer period is required to describe the split in Group 3. A longer period of time would allow the researchers to determine if the group split permanently or formed sub-groups on the basis of feeding sites.

Home ranges were much smaller than other published results. Small ranges appeared to be the result of geographic isolation but may be due to the researchers lack of understanding each range. Group 2 was observed crossing the field on two occasions and it is highly probable they cross the field more often. This behavior suggests that a group will come to the ground to obtain other feeding sites. Perhaps Group 1 or Group 3 cross the road and range on the continuos forest.

Additionally, the researchers had limited knowledge of each groups' range. It is necessary to identify as many feeding sites as possible to locate the group and track it to other sites.

The activity and feeding do not fully represent the behavior of the monkeys. Juveniles and infants engaged in social behaviors and locomoted much more than adults although this is not accurately displayed by the results. The feeding budgets also suggest that the population consumed large amounts of fruits, lower levels of leaves, and very small amount of any other plant part. This populations should be monitored for a minimum of a year to determine percentages of all plant species that are consumed and each plant part.

If researchers continue to study the Monkey River population and build a larger data set accurate comparisons can be made to other species of *Alouatta* and other populations of *Alouatta pigra*.

Conclusion

The study groups of this study fit easily into the parameters of published accounts of *Alouatta*. Group sizes did not deviate from other reports but the number of adult males in each group is interesting. In order to explain the large number of adult males, a long-term study is required. Adult male membership may be due to chance alone, and

may not represent a real difference in dispersal patterns or the length of adult animal tenure.

The home ranges of each group appear extremely small compared to the published materials. Reduced ranges may be due to the methods applied. The focus of the study was activity and dietary budget, while home range and ranging behaviors was received less emphasis. In order to obtain accurate ranging patterns and home range use, a study of longer duration is required based specifically on this topic.

It appears that each study group is folivorous and frugivorous. A higher portion of fruits was consumed in these groups than in the published accounts, but a shift in diet was observed in the final weeks the study. This shift appeared to be a reaction to seasonal variations at the study site. The large portion of fruits in this study may be inflated; leaves may be consumed in greater portion in the following months. A long-term study would better illustrate the percentage of fruits, leaves, and flowers. The monkeys at this site consumed only 29 species. This is a relative low number of species in comparison to work done at other sites.

The activity budget results were similar to other published activity budgets. It is possible that differences in activity budgets are due to operationalized definitions of a behavior or behavioral category. The majority of data collected on this population was on adults, so these results should be used with caution to describe the activity patterns of immature howler monkeys.

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APPENDIX

Inter-Observer reliability

Inter-observer reliability was performed on six occasions to determine if the researchers were identifying behaviors on a reliable basis. Each reliability scan was chosen on a random day and on a random focal animal. Reliability was determined for each scan on two levels: the behavior itself and occurrence of the behavior. For example, if the researchers observed a focal inactive for five minutes, then locomotes for the remainder of the sample, the sample would require each observer to agree that the focal was inactive and then moved (Level 1) and agree on the time at which the behavioral change occurred. Any behavioral scan that did not agree 100% on the observed behaviors was considered unreliable and any scan that did not agree on the occurrence of a behavioral change within 95% (30 seconds) was also deemed unreliable. Researchers agreed on every scan on both the behavior observed and when the behavior changed.