Feeding Ecology of the Black Howler Monkey (*Alouatta pigra*) in Northern Belize

S.C. SILVER,[1,2]* L.E.T. OSTRO,[1,2] C.P. YEAGER,[3] AND R. HORWICH[4]
[1]*Wildlife Conservation Society, Bronx, New York*
[2]*Biological Sciences Department, Fordham University, Bronx, New York*
[3]*World Wildlife Fund, Indonesia Program*
[4]*Community Conservation Consultants, Gays Mills, Wisconsin*

We studied the feeding ecology of the black howler monkey (*Alouatta pigra*) from March 1994 to April 1995 in the Community Baboon Sanctuary in northern Belize, Central America. Activity and diet composition were recorded using continuous focal animal sampling. Diet composition was compared with the relative abundance of plant parts eaten by the howlers within the study site. The study animals spent an average of 24.4% of their time feeding, 61.9% resting, and approximately 9.8% traveling. In contrast to previously published reports on *A. pigra,* we found the diet composition to be similar to that of other *Alouatta* species (conforming to the folivore/frugivore profile), with 41% of feeding time spent eating fruit, 45% foliage, and 11% flowers. This contrast may indicate a wide degree of dietary flexibility that allows *A. pigra* to inhabit a variety of habitat types. We suggest that a high level of resource abundance throughout the year makes the Community Baboon Sanctuary excellent habitat for *Alouatta pigra*. Am. J. Primatol. 45:263–279, 1998. © 1998 Wiley-Liss, Inc.

Key words: *Alouatta pigra*; diet; activity; feeding ecology

INTRODUCTION

The six species commonly recognized as comprising the genus *Alouatta* extend from Mexico to Argentina, making them the most widespread genus of neotropical primate [Crockett & Eisenberg, 1987]. *Alouatta* is found in many habitat types [Glander, 1975; Gaulin & Gaulin, 1982; Julliot & Sabatier, 1993] with varying levels of disturbance [Neves & Rylands, 1991; Julliot & Sabatier, 1993; Bicca-Marques & Calligaro-Marques, 1994]. The genus also exhibits great variability in group size and the ratio of adult males to adult females [Crockett & Eisenberg, 1987]. However, studies of diet have found all *Alouatta* species to be more or less folivorous, with variable levels of frugivory [Neville et al., 1988]. The contrast between the variability of habitat and social structure and the uniformity in dietary regime within the genus may present some intriguing questions concerning the relationship between social structure and foraging behavior.

Since abundance and distribution of food resources have often been cited as important factors in determining primate social structure [Clutton-Brock, 1974; Chapman, 1990; Isbell, 1991], documenting the feeding ecology of socially variable taxa may have important consequences for questions regarding the evolution of social organization.

Alouatta pigra was first suggested as a separate species by Smith [1970]. It was previously considered a subspecies of A. palliata [Hill, 1962]. Horwich [1983] described behavioral and ontogenic differences with A. palliata, and Whitehead [1995] differentiated between the two species on the basis of vocal patterns. Among the behavioral differences outlined were consistently smaller group sizes in A. pigra than in A. palliata [Horwich, 1983; Horwich & Johnson, 1986]. Early studies of A. pigra found average group sizes ranging from 4.2–6.2 animals per troop [Coelho, 1976a; Bolin, 1981; Horwich, 1983] and an adult sex ratio approaching 1:1 [Bolin, 1981]. Alouatta palliata typically lives in multimale, multifemale groups containing more than ten members and may contain from 25–40 individuals [Carpenter, 1934; Crockett & Eisenberg, 1987; Chapman, 1988].

Smith [p. 365, 1970] suggested that A. pigra prefers "extensive, undisturbed and mesic tropical forest," but subsequent studies found A. pigra to inhabit highly disturbed semideciduous forests as well [Bolin, 1984; Horwich, 1983; Horwich & Johnson, 1986]. In a survey of the distribution of A. pigra, Horwich and Johnson [1986] suggested riverine and seasonally flooded areas are particularly attractive to this species.

To our knowledge, only two studies of the feeding ecology of A. pigra have been published to date [Coelho et al., 1976a,b; Schlichte, 1978], both in the quasi–rain forest of Tikal, Guatemala, and of 66 and 7 days duration, respectively. Both these studies found A. pigra to rely heavily on the fruit and leaves of a single species (Brosimum alicastrum). Schlichte [1978] found the howlers spent 87.5% of their feeding time on Brosimum alicastrum and 70% of their feeding time on fruit of that species. Not surprisingly, Schlichte [p. 555, 1978] concluded the A. pigra observed "were extreme food specialists." As a result, the only dietary information published on the species to date suggests little dietary diversity and levels of frugivory approaching that of Ateles [Neville et al., 1988]. Documenting high levels of dietary specialization and frugivory in A. pigra would challenge the perception of Alouatta as being restricted in resource-exploitation tactics by the behavioral, morphological, and physiological traits characterizing the genus [Milton, 1981; Gaulin & Gaulin, 1982]. Alternatively, if the degree of frugivory of A. pigra in Belize is found to be closer to that previously reported for other Alouatta species, it would indicate a high degree of dietary flexibility and perhaps a broad tolerance of habitats. Thus, it is important to determine if the dietary profile previously reported in this species can be demonstrated in other studies encompassing an annual cycle.

As part of a larger study of the ecology of translocated howler monkeys [Horwich et al., 1993; Koontz et al., 1994], we examine the feeding ecology of the Central American black howler monkey (Alouatta pigra) at the site that served as the source population for the translocation. This study is the first to describe the feeding ecology of A. pigra through a complete annual cycle and the first to describe its diet outside Guatemala. We seek to determine if the diet of A. pigra is indeed more specialized and frugivorous than that reported for other Alouatta species or if they exhibit a dietary flexibility that enables them to adjust their degree of frugivory to the resources available. This study should also enable us to assess the quality of a seasonally flooded, highly fragmented and disturbed habitat for A. pigra.

STUDY SITE AND METHODS
Study Site

The study took place in the village of St. Paul's Bank (17° 33' N, 88° 35' W), located along the banks of the Belize river, in the Belize District of northern Belize. The village is one of eight comprising the Community Baboon Sanctuary (CBS). The area is a subsistence agricultural community with a patchwork of pastures, gallery forest, and fragments of semideciduous broadleaf forest of variable size and stage of succession. The area experiences a distinct dry season, usually lasting from January through May, when many tree species lose their leaves. The area also experiences seasonal flooding. During this study, most forest patches were inundated with water for 4 months at the end of the rainy season. Calculated densities of *A. pigra* within forest patches throughout CBS range from 47–250 howlers per square kilometer [Ostro et al., submitted]. Within CBS, human hunting pressure is high for most animals except the howler monkeys, and grazing pressure from livestock (horses and cattle) is also high.

Rainfall and Climate

During the study, rainfall was measured daily, and an annual total of 1,955 mm of rain fell (Fig. 1). Months with the least amount of rainfall were January through April, when <100 mm of rain fell each month. Rainfall during the remainder of the year was >100 mm per month. Temperature data were taken from
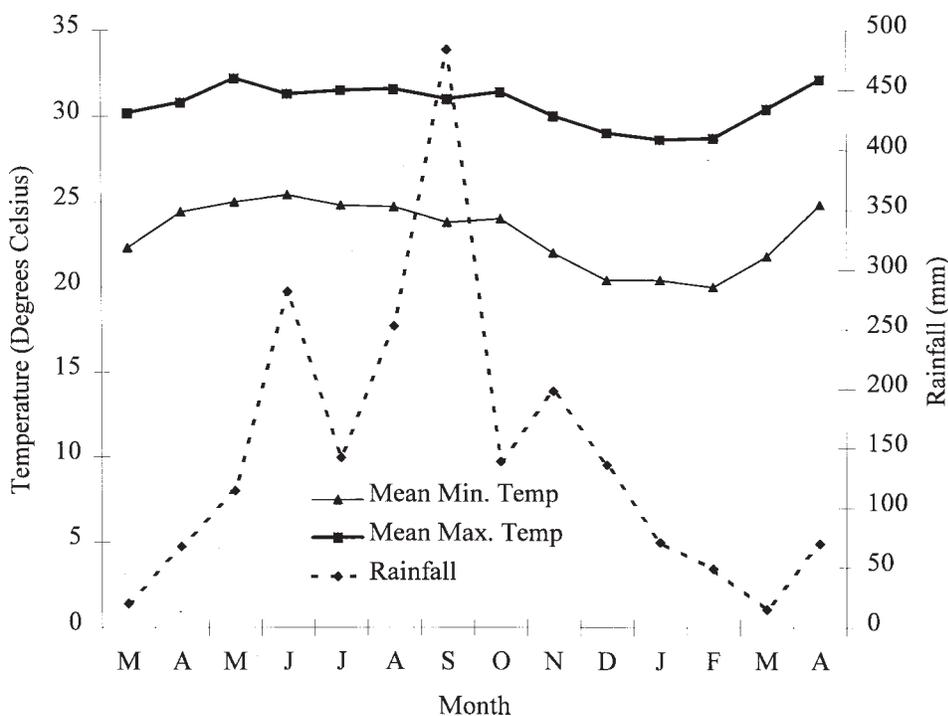

Fig. 1. Temperature and rainfall during the study period (March 1994 to April 1995). Rainfall measured on a daily basis in St. Paul's Bank. Temperature is the mean monthly minimum and maximum as measured at Philip Goldson International Airport.

the Belize Weather Bureau station at Philip Goldson International Airport (approximately 30 km east of St. Paul's Bank) and ranged from a mean monthly minimum of 20°C in January 1995 to a mean monthly maximum of 32°C in May 1994 (Fig. 1).

Vegetation Transects

Belt transects were established within the home ranges of the study animals until a species–area curve approached an asymptote. The ten transects were randomly placed with regard to location, direction, and drainage. The transects were each 10 m wide and had a combined total of 1,000 m length. All stems ≥30 cm in circumference at breast height were tagged and identified. Tree species were identified in the field with the help of local assistants. Voucher specimens were collected of all tree species encountered on the transects and later identified at the New York Botanical Garden (Bronx, NY).

Circumference at breast height (CBH) was recorded for each tagged tree. Trees with more than a single trunk were measured directly at the base. Circumference was converted to diameter at breast height (DBH) and used to calculate the basal area. DBH has previously been shown to be an accurate estimator of fruit abundance [Chapman et al., 1992] and foliage biomass [Kool, 1992]. Relative density was calculated for each species found in the transects using formulae from Brower et al. [1990]:

Relative density = number of stems of species i/total number of stems in all transects;
Coverage (C_i) = Σ basal areas for species$_i$;
Relative coverage (RC_i) = (C_i)/sum of coverage for all species.

Relative coverage was used as a measure of dominance, reflecting the relative size and abundance of each species within the vegetation transects.

Food Abundance

The relative abundance of different plant parts known to be potential food items was assessed on a monthly basis by visual inspection of 214 trees belonging to 33 species found within the study area. We identified potential foods based upon 1) personal observation, 2) primate literature, or 3) information received from field assistants. Together, individuals of these 33 species represented 0.63 of the relative density of trees in the study area as determined by the transects. Due to the difficulty of quantifying the relative dominance of vine species, we confined the food abundance study to trees.

Once a month following data collection, each tree in the food abundance study was inspected for the presence of mature leaves, young leaves, fruits, and flowers. An abundance value was assessed for each tree part ranging from 0–3. A value of 0 corresponded to a complete absence of that plant part, a value of 1 was recorded when that part encompassed <25% of the crown, a value of 2 when it encompassed 25–50% of the crown, and a value of 3 when it encompassed >50%.

We calculated monthly food abundance indices for plant parts eaten by the monkeys. We multiplied the average monthly abundance value of each plant part by the relative dominance of that species. We then summed all these species scores to yield a monthly abundance index for each plant part. As we were interested only in assessing the relationship between the monkey's foraging behavior and the relative abundance of food items, plant parts not eaten were not included in calculating the food abundance scores.

Study Troops

Data were collected from six troops of howler monkeys from March 1994 until May 1994. All groups occupied home ranges in forest patches of variable successional stage between 0.25 km^2 and 0.5 km^2 in size [Ostro et al., in press]. Mean group size was 5.9, with a range of three to nine animals per group. All groups contained at least one adult male, two or three adult females, and their offspring.

In mid-May, four of the troops were translocated to the Cockscomb Basin Wildlife Sanctuary (CBWS). The remaining two troops were studied in CBS until April 1995. Data collected from the four troops moved in mid-May were used only in formulating descriptive statistics and in constructing the howler monkey's diet list. All inferential statistical analysis carried out (see below) was confined to data collected on the two groups studied throughout the 14 month study period. These troops occupied a separate patch of secondary forest approximately 0.5 km^2 in size and were not directly affected by the artificial reduction in population density caused by the translocation.

Behavioral Data Collection

Data collection teams consisted of at least two people observing the monkeys from dawn until dusk. Data were collected on six troops for three full-day activity cycles per troop each month for the first 3 months. From June 1994 until April 1995, data were collected for four consecutive days per month on the remaining two troops. We collected a total of 1,160 h of behavioral data.

Data were collected using continuous focal animal sampling [Altmann, 1974] supplemented with opportunistic data to record rare events such as breeding or intergroup encounters. Focal animal sessions lasted 25 min, with 10 min rest intervals between sessions. Focal animals were recorded as performing one of the following mutual exclusive behaviors: resting, traveling, feeding, social affiliative, social agonistic, vocalizing, other, or unknown. During focal animal sessions, the time of any change in behavior lasting more than 5 s was recorded, allowing us to calculate the duration of time engaged in particular activities. Focal animals were selected on a rotating basis, according to age/sex class. These classes consisted of adult male, adult female, lactating female, and immature. Whenever individuals within a class could be identified, all individuals within that class were sampled equally. Infant behavior was not recorded during focal animal sessions. An animal was considered an infant if it was observed to nurse within 1 month of the data collection session. Monthly activity budgets and dietary profiles were constructed using the mean time engaged in each behavior per month.

When the monkeys were observed feeding, plant part and species eaten were recorded. Unknown species were marked and identified later. Dietary diversity was assessed on a monthly basis for each troop using the Shannon-Weiner diversity index ((H´) [Pielou, 1966]).

Analyses

We compared the percentage of time each troop engaged in major activities (feeding, resting, and traveling) each month and the percentage of time feeding on specific plant parts using Wilcoxon's matched pairs test. Spearman's rank correlation tests were performed to assess the relationship between 1) the relative abundance of food items each month and mean time spent feeding on that part for both troops and 2) dietary diversity and diet composition.

RESULTS

Relative Abundance of Food Items

Fruits eaten by the monkeys were available throughout the year, although the relative abundance was lowest in May and June and highest from July through December (Fig. 2). Flower production was highest from April–June. While the relative abundance of young leaves peaked in June, they lacked the pattern of seasonal abundance observed in fruits and flowers (Fig. 2). The mature leaves eaten by the monkeys were available throughout the year, although their relative abundance was reduced during the dry season.

Forest Composition and Diet

We identified 551 trees or woody stems ≥30 cm CBH within the 1 hectare of vegetation transects. We identified 60 tree species within these transects. The Appendix lists these tree species within the transects, their families, and their relative density and dominance.

The study animals fed upon a total of 74 plant species. Fifty-three were tree species, and the remainder were epiphytes or lianas. Nontree species made up approximately 9% of all feeding records. The 24 most commonly used food species (>1% of the total time spent feeding each) are listed in Table I. All but three of these were found on the transects. Approximately 85% of the relative dominance of the forest was composed of tree species used as food. Of the ten most dominant species in the forest, eight were food items which comprise >1% of the overall time spent feeding, and only one species (*Orbigyna cohune*) was not eaten at all.

We identified nine different *Ficus* species. Together they constituted 2.5% of the relative density of trees on the transects, yet the howlers spent approxi-
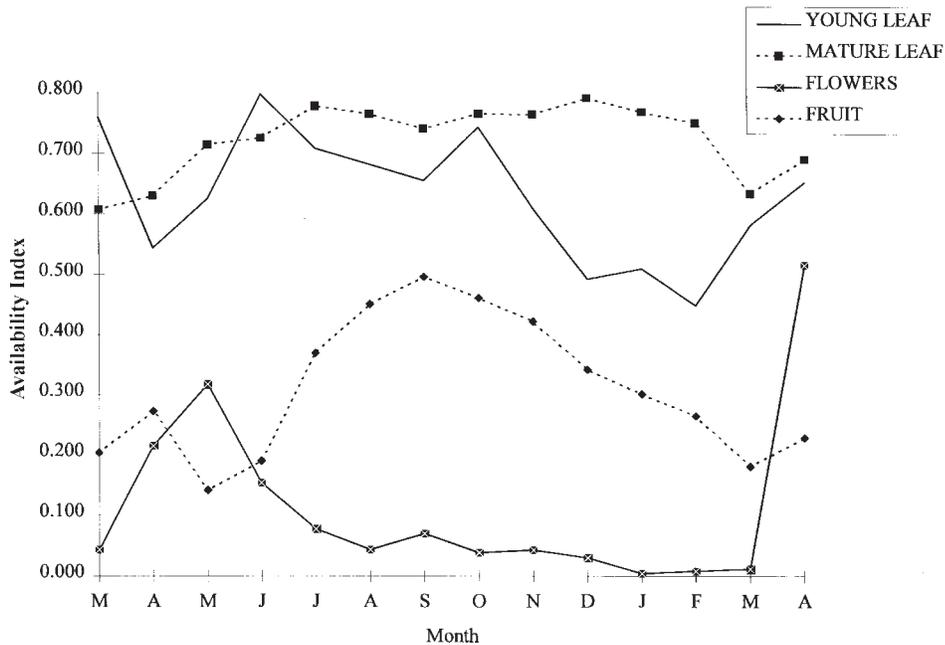

Fig. 2. Abundance of fruits, flowers, and young and mature foliage from March 1994 to April 1995. Monthly variation in the abundance of items eaten by the study animals.

TABLE I. Species, Family, and Parts Eaten of Species Eaten for >1% of Feeding Time*

Species	Family	Common name	Part eaten	Frequency (%)
Ficus americana	Moraceae	Fine fig	YL, FR	12.5
Inga vera	Mimosaceae	Bribri	FR, FL, YL	11.3
Pithecellobium lanceolatum	Mimosaceae	Redfowl	YL	7.2
Ficus maxima	Moraceae	Hicatee fig	YL, ML, FR	6.4
Guazuma ulmifolia	Sterculiaceae	Baycedar	FR	5.4
Ficus aurea/cotinifolia	Moraceae	Ficus sp. 1/2	YL, FR	5.3
Eugenia sp. 1	Myrtaceae	Blackberry	FR	5.0
Andira inermis	Fabaceae	Ball seed	YL, FR, FL	3.7
Miconia argentea	Melastomataceae	White Maya	FR	3.3
Samanea saman	Leguminoseae	Beeftree	ML, YL, FL, FR	3.0
Coccoloba hondurensis	Polygonaceae	Black Grape	YL, FR	2.8
Ficus insipida[b]	Moraceae	Cowfig	ML, YL, FR	2.5
Combretum fruticosum[a]	Combretaceae	Bottlebrush	UKLF, FR, FL	2.3
Sapindus sapinaria	Sapindaceae	Soapseed	ML, YL	2.1
Cecropia spp.	Moraceae	Cecropia	ML, YL, FR	2.1
Paullinia clavigera[a]	Sapindaceae	Inga vine	YL, ST	1.9
Lonchocarpus sp. 1	Fabaceae	Dogwood	YL, FL	1.7
Ficus yoponensis	Moraceae	Quam fig	YL, FR	1.6
Syngonium spp.[a]	Araceae	Jimmy Palm taitai	YL, ST, FR	1.5
Lonchocarpus spp. 2	Fabaceae	Swamp Dogwood	FL	1.4
Ficus obtusfolia[b]	Moraceae	Brown Bat Fig	YL, FR	1.4
Fiscus pertusa	Moraceae	Quash fig	YL, FR	1.3
Coccoloba belizensis	Polygonaceae	White Grape	FR	1.2
Fabaceae sp. 1[b]	Fabaceae	Kaway	YL	1.1

*Presented in order of dietary frequency. FL, flowers; FR, fruit; ML, mature leaves; ST, stems; UKLF, unknown leaves; YL, young leaves. Values for *Ficus aurea* and *F. cotinifolia* are combined.
[a]Vine species.
[b]Tree species not found on transects.

mately 32% of their overall feeding time eating *Ficus* (monthly range 6–65%). The monkeys primarily fed upon fruits (usually ripe) or young leaves, but mature leaves were also eaten from some *Ficus* species (Table I).

The howler diet consisted primarily of young foliage and fruit (Fig. 3). Fruit was consumed by the study animals for an average of 40.8% of the monthly feeding time (range 10.5–64.5%; s.d. = 17.4%). Ripe fruit was eaten 91% of the time fruit maturity could be determined. The howlers were observed to ingest entire fruits from some species (e.g., *Eugenia spp.*), passing the seeds intact, while in other species they ingested only the fruit flesh while discarding the seeds (e.g., *Spondias* spp.). The monkeys were never observed to chew seeds, nor were damaged seeds observed in examination of fecal material.

Young leaf consumption averaged 37.2% of monthly feeding time (range 18.1–64.6%; s.d. = 13.7%). The monkeys ate mature leaves primarily from four species (*Ficus maxima, F. insipida, Sapindus sapinaria,* and *Cecropia sp.*). Mature leaves accounted for an average of 7.9% of the monthly feeding time but ranged from 0.2–31.4% (s.d. = 8.4%). Monthly flower consumption averaged 10.2% (s.d. = 12.4%) over the course of the study, reaching a peak (36.8%) at the beginning of the dry season. Flowers were either a minor component of the diet, or not eaten at all, from July through January (Fig. 4).

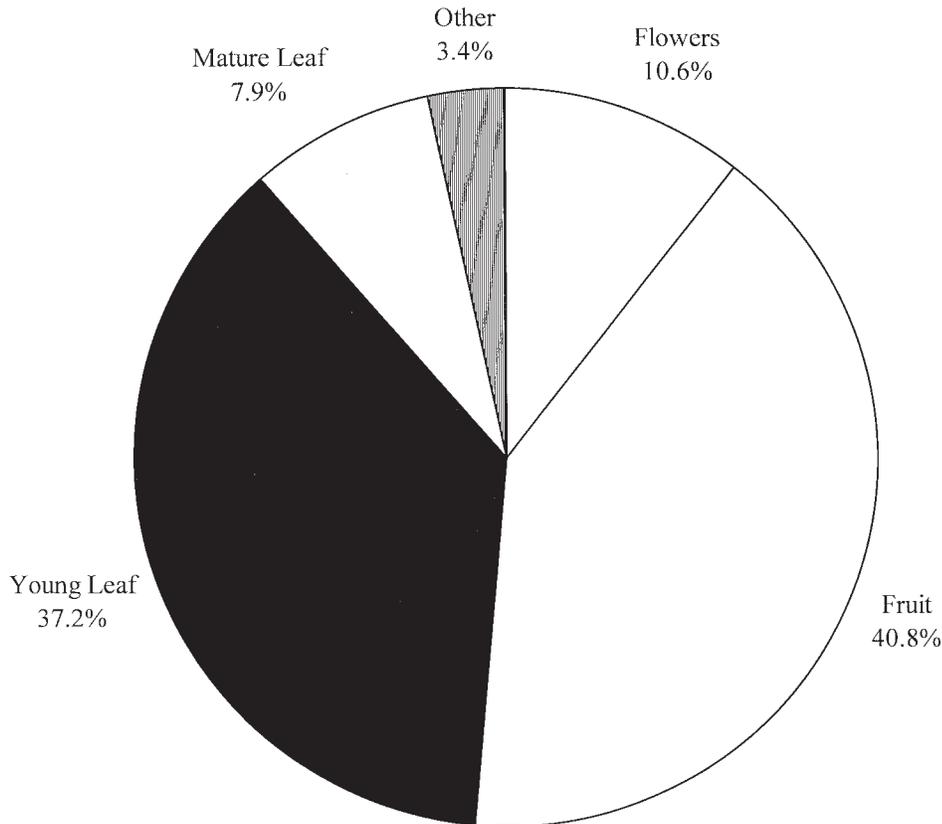We did not observe the monkeys to engage in geophagy or intentionally feed

Fig. 3. Overall diet composition (March 1994 to April 1995). Mean diet composition of identified plant parts averaged across all months. *Other* includes stems, petioles, and vine tendrils.
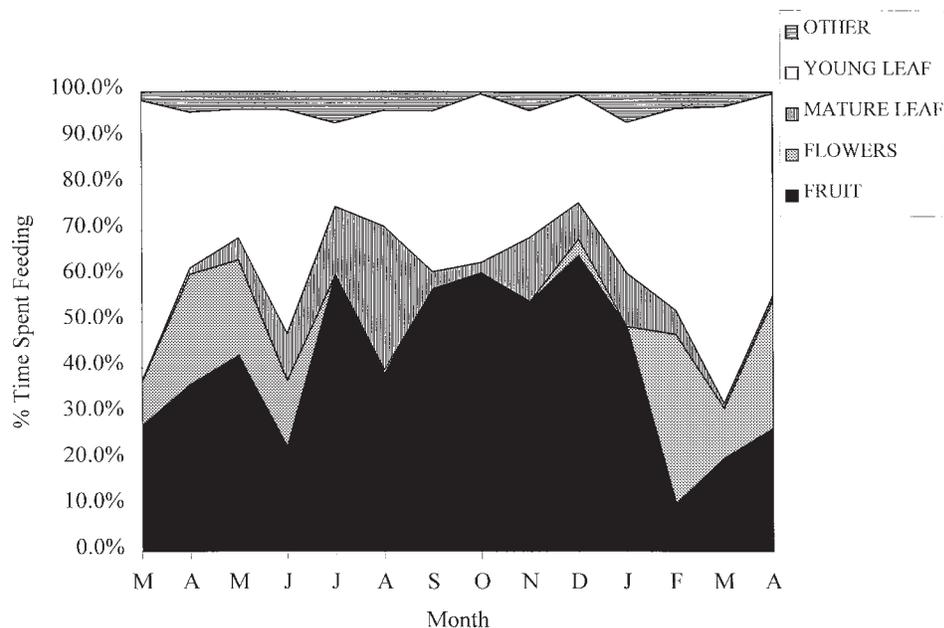
Fig. 4. Monthly diet composition (March 1994 to April 1995). Mean monthly diet composition of identified plant parts. *Other* includes stems, petioles, and vine tendrils. Values are derived from mean monthly values for all available troops.

upon any animal protein. We did observe the presence of insects within some of the fruits (e.g., *Ficus*) collected from trees fed upon by the monkeys, and it is likely that some insects were consumed with fruits. The study animals were observed to drink water out of arboreal cisterns, sometimes scooping out water with their hands and at other times lowering themselves into the boles of large trees. They were never observed to drink water from any ground-level sources.

Food Abundance and Diet

Comparisons between the two troops from which data were collected throughout the entire study period did not reveal statistically significant differences in monthly portions of time spent feeding on fruits ($Z = 0.659$, n = 14, $P = 0.51$), flowers ($Z = 1.245$, n = 14, $P = 0.21$), young leaves ($Z = 1.475$, n = 14, $P = 0.14$), or mature leaves ($Z = 1.851$, n = 14, $P = 0.06$). The relative abundance of fruits and mature leaves known to be eaten by the monkeys was significantly related to the time spent feeding upon them ($r_s = 0.710$, $P = 0.004$ and $r_s = 0.763$, $P = 0.002$, respectively). No significant relationship was found between the relative abundance of young leaves or flowers and the average proportion of time spent feeding upon them ($r_s = 0.204$, $P = 0.48$ and $r_s = 0.307$, $P = 0.29$, respectively).

Activity Budgets

Feeding, resting, and traveling comprised the vast majority of behaviors observed (Fig. 5). Study troops spent an average of 24.4% (range 19.1–31.2%, s.d. = 1.0%) of each month feeding, 61.9% (range 50.0–67.7%, s.d. = 1.2%) resting, and
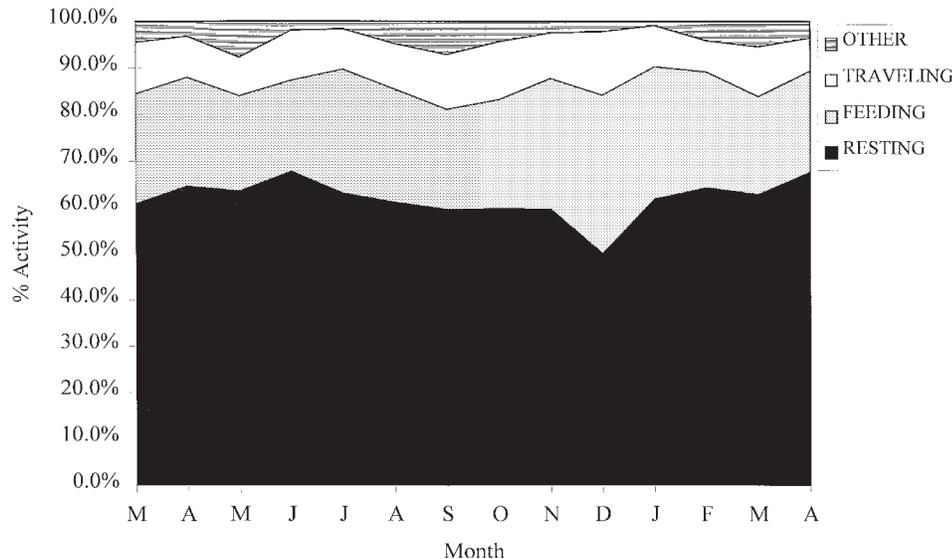
Fig. 5. Monthly activity levels for resting, feeding, traveling, and other (March 1994 to April 1995). Values are derived from mean monthly values for all available troops. *Other* principally includes vocalizing, grooming, and play behavior.

approximately 9.8% (range 6.6–13.5%, s.d. = 0.5%) traveling. In addition, 2.3% of their time was spent engaged in social affiliative behaviors (playing and grooming) and 1.5% of their time vocalizing.

Diet Composition, Diversity, and Time Spent Feeding

There were no significant differences in the time engaged in feeding between either of the two troops studied for the full 14 months (Z = 0.722, n = 14, P = 0.47). Correlation analysis of dietary diversity and diet composition was therefore carried out on the mean monthly values of these two troops throughout the study period.

Dietary diversity was highest in the early rainy season (June 1994) and lowest during the latter part of the rainy season (October 1994). Dietary diversity was significantly and positively correlated with the percentage of time spent feeding upon mature leaves (r_s = 0.340, P = 0.03) but not significantly correlated with time spent feeding on young leaves, fruits, or flowers. There were no statistically significant correlations between the relative abundance of any plant part (as measured by the food abundance) and dietary diversity.

DISCUSSION

Diet Composition and Food Abundance

The diet of *A. pigra* reported here is more similar to that reported for other members of the genus than the diet reported by Coelho et al. [1976a,b] and Schlichte [1978]. The howler monkeys in CBS eat greater numbers of species and spend more time engaged in folivory than was reported in Tikal, Guatemala. The primary food of the howlers in Tikal, *Brosimum alicastrum,* has not been found in our study area, although other *Brosimum* species are present and eaten.

The results of this study suggest the causes for the differences in social structure between *A. pigra* and *A. palliata* are not found in their diet composition. Ostro et al. [submitted] have documented shifts in social structure from single male or monogamous groupings to multimale/multifemale groups within populations of *A. pigra*. This contrasts with the polygynous group structure commonly reported for *A. palliata* troops [Milton, 1980; Crockett & Eisenberg, 1987]. Although some authors have attempted to relate social structure to dietary regimes [e.g., Clutton-Brock, 1974; Harvey et al., 1987], Ostro et al. [submitted] feel population density may be a more important factor in determining social structure within *A. pigra* than diet. If this holds true for the genus, there would be no contradiction between the relative uniformity of diet and variability in group structure exhibited by *Alouatta*.

Like Glander's [1981] study of *A. palliata* and Julliot and Sabatier's [1993] study of *A. seniculus,* we found the abundance of fruits dictated the amount of time *A. pigra* spent eating them. The time spent eating young leaves, however, showed no relation to their relative abundance. Milton [1980] argued that dietary shifts from fruit to foliage when the former became scarce enabled howlers to maintain a constant foraging time rather than increase search time at the expense of resting and digestive efficiency. The absence of a demonstrable correlation between the relative abundance of young leaves and their representation in the diet may mean young leaves are eaten as an alternative to preferred fruits when the latter are less abundant or that the abundance of young leaves is consistently higher than that required by the monkeys. Perhaps the diet presented here is that of a facultative folivore, animals whose diet is as frugivorous as possible given the limitations of fruit abundance and, beyond a minimum level required to satisfy protein requirements, as folivorous as necessary. This may also explain the disparity in the findings between this study and those in Tikal, where fruit loads of *Brosimum alicastrum* were estimated at very high levels [Coelho et al., 1976a,b, 1977]. A study of *A. pigra* at a different site in Belize indicates much lower portions of time spent eating fruits than in this study [Silver et al., 1997]. It may be that *A. pigra* is quite flexible in its degree of frugivory, and this flexibility allows it to subsist in a variety of habitats. This same dietary flexibility throughout the genus may help explain the widespread distribution of *Alouatta* spp. throughout the neotropics.

The time spent eating mature leaves (7.9%) is lower than that found for most of the howler studies mentioned above. The preference for younger leaves by *Alouatta* has been well documented [Milton, 1978; Glander, 1981; Gaulin & Gaulin, 1982; Neves & Rylands, 1991; Stoner, 1996] and coincides with higher protein and lower fiber content of young leaves and/or increased digestibility [Milton, 1979]. However, Glander [1978] found little nutritional difference between mature leaves and immature leaves eaten by *Alouatta palliata*. The portion of time spent eating mature leaves correlates with dietary diversity, and increased dietary diversity has been associated with food scarcity in some primate studies [Terborgh, 1983; Yeager, 1989]. It may be that mature leaves play the role of a secondary or supplemental foliage choice.

Nonetheless, we found the relative abundance of mature leaves eaten by *A. pigra* to correlate with the time spent feeding upon them. Although they may be a secondary foliage choice, the extent to which the monkeys can include mature leaves in the diet is dependent upon the abundance of the mature leaves from a select subset of plant species. The relationship between the relative abundance of mature leaf and its representation in the diet is apparent only because our study of food abundance was limited to mature leaves eaten. The relationship

between relative abundance and feeding time would be obscured by studies of relative abundance that included mature leaves from nonfood species.

Forest Composition and Diet

Stem density at the study site is comparable to other *Alouatta* study sites. While the tree species richness reported here (60 species) is low in comparison to many other *Alouatta* studies (e.g., Glander, 1978; Milton, 1980; Gaulin & Gaulin, 1982; Julliot & Sabatier, 1993), it is comparable to more disturbed howler study areas in Central America [e.g., Glander, 1975]. However, species diversity by itself is insufficient for assessing habitat quality. In a study of habitat selection in *A. palliata*, Stoner [1996] found that species diversity was less important than the density of the most commonly consumed tree species. At our study site, the 12 most commonly eaten tree species (Table I; Appendix) provide 52% of the dominance and account for nearly 69% of the overall feeding time. If the density or relative abundance of the most commonly consumed tree species is an indicator of habitat quality, then habitat quality at this study site is high.

Several studies have identified *Ficus* spp. as being an important component in the diet of *Alouatta* spp. [Milton, 1980; Estrada, 1984]. The importance of *Ficus* for *A. pigra* in St. Paul's Bank is clearly reflected in the monthly pattern of *Ficus* exploitation. *Ficus* species make up >20% of the feeding time for 9 of 14 months of the study despite their 2.5% relative density within the transects. With a density of 551 stems per hectare and a mean home range estimate of 6.4 ha for all study troops [Ostro et al., in press], approximately 88 *Ficus* trees are available within each troop's home range. Given the high fruit load and asynchronous phenological cycles known to occur within the genus [Janzen, 1979], the relative density of *Ficus* at this study site is high enough to allow it to make a major contribution to the diet of *A. pigra*, making this particularly high quality howler habitat.

Despite the high levels of anthropogenic disturbance, the high density of food species (Table I; Appendix) and high relative abundance of fruit throughout much of the year (Fig. 2) combine to make CBS excellent habitat for supporting howler monkey populations. In addition, Lyon and Horwich [1996] suggest a high degree of vegetative reproduction among tree species within CBS results in forest patches containing species from all successional stages. Thus, the howlers may benefit from access to a wide successional range of tree species in a relatively small area.

CONCLUSIONS

1. *Alouatta pigra* exhibits a similar activity and dietary profile in northern Belize as has been reported for other members of the genus elsewhere. Its diet is a mixture of foliage, fruit, and flowers, with at least 74 plant species eaten throughout this study. Both young and mature leaves are eaten throughout the year, and the time spent eating fruit is dictated by its abundance.

2. Tree species belonging to the genus *Ficus* play a major role in the diet of *A. pigra* in the village of St. Paul's Bank in the Community Baboon Sanctuary. *Ficus* trees contribute both young and mature foliage as well as figs to the howler diet, and approximately one-third of all feeding time was spent eating *Ficus*.

3. The study site of St. Paul's Bank in the Community Baboon Sanctuary contains high proportions of tree species used as food by the howler monkeys as well as having fruit available throughout much of the year. This, combined with

the protection from hunting enjoyed by the howlers, allows the Community Baboon Sanctuary to support one of the largest populations of *A. pigra* and makes it one of the most important sites for the conservation of this species.

4. In light of previous studies of *A. pigra*, this study demonstrates the flexible nature of the diet for this species in different habitat types. As has been shown for other members of the genus, this dietary flexibility may allow a broad window of habitat tolerance for this species, which suggests *A. pigra* may be readily able to colonize new habitats, either through natural or human-assisted processes.

ACKNOWLEDGMENTS

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APPENDIX. Frequency, Relative Density, and Dominance of 60 Tree Species Found Within 1 Hectare of Vegetation Transects at the Community Baboon Sanctuary*

Species	Family	Common name	N	Relative Density	Dominance
Coccoloba hondurensis	Polygonaceae	Black grape	56	0.102	0.2052
Inga vera	Mimosaceae	Bri-bri	44	0.08	0.1437
Lonchocarpus spp. 2	Fabaceae	Swamp dogwood	57	0.103	0.0938
Guazuma ulmifolia	Sterculiaceae	Bay cedar	51	0.093	0.0642
Orbigyna cohune	Palmae	Cohune	14	0.025	0.0642
Cassia grandis	Caesalpinaceae	Bucut	30	0.054	0.0524
Lonchocarpus latifolius	Fabaceae	Dogwood	57	0.103	0.0380
Ficus aurea/cotinifolia	Moraceae	Ficus sp. 1/2	2	0.004	0.0355
Samanea saman	Mimosaceae	Beef tree	1	0.002	0.0333
Sapindus sapinaria	Spaindaceae	Soapseed	3	0.005	0.0252
Andira inermis	Fabaceae	Ballseed	9	0.016	0.0240
Tabebuia rosea	Bignoniaceae	Mayflower	10	0.018	0.0238
Faramea occidentalis	Rubiaceae	Waterwood	2	0.004	0.0229
Coccoloba belizensis	Polygonaceae	White grape	13	0.024	0.0191
Parmentiera aculeata	Bignoniaceae	Cow ochre	13	0.024	0.0136
Zuelania guidora	Flacourtiaceae	Wild coffee	11	0.02	0.0115
Ficus yoponensis	Moraceae	Quam fig	1	0.002	0.0094
Morinda panamensis	Rubiaceae	Dogmess	6	0.011	0.0093
Exostema mexicanum	Rubiaceae	Wild lime	19	0.034	0.0091
Spondias radlikoferi (?)	Anacardiaceae	Wild hogplum	9	0.016	0.0085
Randia armata	Rubiaceae	Hawk nail	2	0.004	0.0073
Spondias mombin (?)	Anacardiaceae	Hogplum	4	0.007	0.0071
Pithecellobium lanceolatum	Mimosaceae	Redfowl	11	0.02	0.0065
Cordia sp. 1	Boraginaceae	Jackwood	11	0.02	0.0064
Trichillia hirta	Meliaceae	Pigeon plum	10	0.018	0.0061
Cupania spectabilis	Sapindaceae	Grande Betty	19	0.034	0.0059
Mangifera indica	Anacardiaceae	Mango	1	0.002	0.0054
Cedrela mexicana	Meliaceae	Cedar	4	0.007	0.0049
Zanthoxyllum spp. 2	Rutaceae	Prickly yellow	2	0.004	0.0045

Species	Family	Common name			
Trichilia martiana	Meliaceae	Mama cerilla	9	0.016	0.0029
Ficus pertusa	Moraceae	Matapalo (quash fig)	3	0.005	0.0028
Sapium lateriflorum	Euphorbiaceae	Bastard fig count	2	0.004	0.0028
Luehea seemanni	Tiliaceae	Mampola	4	0.007	0.0027
Miconia argentea	Melastomataceae	White Maya	5	0.009	0.0026
Schizolobium parahybum	Caesalpinaceae	Quamwood	1	0.002	0.0025
Ficus maxima	Moraceae	Hicatee fig	7	0.013	0.0025
Ceasaria arborea	Flacourtiaceae	White poisonwood	6	0.011	0.0021
Eugenia sp. 1	Myrtaceae	Blackberry	2	0.004	0.0021
Eugenia sp. 2	Myrtaceae	Blossomberry	7	0.013	0.0018
Simauruba glauca	Simaurubaceae	Negrito	1	0.002	0.0017
Zuelania guidora	Flacourticaceae	Drunken baymen stick	4	0.007	0.0015
Ficus americana	Moraceae	Fine fig	1	0.002	0.0014
Cecropia spp.	Moraceae	Cecropia	6	0.011	0.0014
Citrus sp. 1	Rutaceae	Tame lime	1	0.002	0.0013
Ceiba pentandra	Bombaceae	Cotton	1	0.002	0.0012
Brosimum guianensis	Moraceae	Red ramon	1	0.002	0.0008
Annona muricata	Annonaceae	Soursop	1	0.002	0.0007
Citharaxyllum fruiticosum	Verbenaceae	Rice seed	2	0.004	0.0006
Bucidea bucerus	Combretaceae	Bullet tree	1	0.002	0.0006
Metopium browneii	Anacardiaceae	Black poisonwood	2	0.004	0.0006
Moraceae sp. 1	Moraceae	Masicho bravo	2	0.004	0.0004
Cochlospermum vitifolium	Cochlospermaceae	Wild cotton	1	0.002	0.0004
Inga sp. 2	Mimosaceae	Tama-tama	1	0.002	0.0004
Allophylus cuminia	Sapindaceae	?	2	0.004	0.0004
Melastomataceae sp. 1	Melastomataceae	Black Maya	2	0.004	0.0003
Enterolobium cyclocarpum	Mimosaceae	Tubroos	1	0.002	0.0003
Genipa caruto	Rubicaceae	Wild mammae	1	0.002	0.0002
Erythrina spp.	Fabaceae	Copna	1	0.002	0.0002
Vismia spp.	Guttiferae	Ringworm wood	1	0.002	0.0001

*Species are presented in order of dominance.