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ECOLOGY OF GUATEMALAN HOWLER MONKEYS

(Aloutta pigra Lawrence)

by

Janene M. Caywood

B.S., Oregon State University, 1976

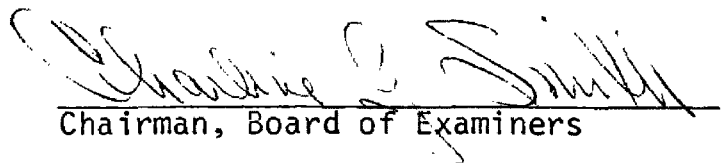
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Caywood, Janene, M., M.A., June 1980 Anthropology

Ecology of Guatemalan Howler Monkeys (Alouatta pigra Lawrence)
(61 pp.)

Director: Dr. Charline G. Smith



The purpose of this study was to identify relationships between several parameters of foraging behavior of Guatemalan howler monkeys (Alouatta pigra Lawrence). Field work was carried out during the summer of 1978 at Tikal National Park, Guatemala, C.A. Data were collected by continuous focal animal sampling of the foraging activities of one adult female howler. Ecological variables were also recorded. Data were coded and the information key-punched so that analyses could be carried out using the University of Montana, DEC-20 computer. Plant part and species utilization data were analyzed 1) as a unit of 56 days, 2) by seven-day subfiles, and 3) by daily increments. Data concerning ranging behavior were plotted and used with the SYMAP and ASPEX programs to determine heavy use areas in the howler home range.

By breaking down dietary data into small segments, patterns of resource exploitation emerged that have not been discussed by previous researchers. Like howler species in other areas, howlers at Tikal exhibit a generalist herbivore behavioral adaptation that enables them to successfully utilize a diet low in overall energy availability.

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CHAPTER I

INTRODUCTION

Researchers in the field of behavioral ecology have felt for some time that there must be an identifiable relationship between the way an animal behaves and the kind and distribution of available food in its environment. The operational problem has been to identify these relationships. Foraging strategies, those actions associated with searching out, processing, and consuming food, represent the optimization of individual fitness through energy utilization (Pyke, et. al. 1978). By clearly delineating the foraging strategy of a certain group of animals, the relationship between its behavior and environmental resources may be more fully understood.

It has been accepted by most researchers that the food available to an animal may not be continuously distributed, spatially or temporally in its environment. Rather, one food patch may be separated from others by areas of forest that do not contain food (Cant 1977). In other words, resources are patchily distributed. This is overtly obvious to one when considering primate species with diets high in fruit, or other heavily clumped foods. The lack of continuously distributed food sources is not so obvious, however, when considering primates that rely primarily upon leaves, the folivorous primates. From recent ecological studies (Glander 1978, Milton 1978), it seems

that especially for folivores, all that is green is not gastronomically acceptable. There are many factors other than mere presence or absence of a food type that determine its availability.

Since the early 1970s, many of the studies in primate ecology have centered on dietary concerns and foraging behavior. Researchers are interested in identifying precisely the kind of food available to an animal, the restraints limiting food availability, and the ways animals best utilize food resources. In conducting this research, I was concerned with several aspects of the foraging behavior of Guatemalan howler monkeys, Alouatta pigra. As such this thesis may be termed an ecological study, the primary objective of which is to identify relationships among several parameters of foraging behavior. The research was carried out during the summer of 1978, at Tikal National Park, in Guatemala, Central America.

Suitability of the Study Animal and Site

Howler monkeys at Tikal National Park are excellent subjects for a study of foraging behavior for several reasons. The howler population in and around the central ruins area has been estimated to be about twenty-five animals. Previous researchers at Tikal have consistently reported low population densities for howlers from this area (Coelho 1973, Schlichte 1974, Cant 1977). Alouatta pigra, the species of howler found at Tikal, have generally been observed in lower densities than the paliatta and villosa species found in other areas. The low population density at Tikal reduces the chances of inter-group contacts, and thus reduces the frequency of displacements that might

affect foraging activities without being directly related to energy utilization.

Another beneficial feature of Tikal as a study site is that there are only two species of primates in the area, howler monkeys and spider monkeys (Ateles geoffroyi). The occurrence of only two primate species is typical of Central American forests north of Honduras. Interspecific contact was not frequent, thus few instances of displacement occurred. Although spider monkeys do occasionally chase howlers from feeding trees, in general it seems that howlers are seldom actively disturbed by other mammalian species at Tikal. Once again, like intergroup contacts, the low frequency of interspecific contact means that the foraging behavior that was observed during my study at Tikal was a response to food parameters, and not clouded by behavioral interactions. (The above statement does not mean that displacement due to interspecific competition for resources is totally absent. Once during this study, coatis (Nasua nasua) were observed feeding in the same tree, on the same food, as our howler group.)

A third advantageous trait of Tikal's howler population for a study of this nature, is its low dietary diversity. A large proportion of the howler diet in this area consists of the fruit, seeds, and leaves of one tree species, Brosimum alicastrum, commonly known as ramon. This condition led to the simplification of species identification within a particular foraging area.

Finally, in terms of data retrieval, the small cohesive group structure of howlers in this area facilitated the collection of data in the field. (Our howler group consisted of five animals.) Further-

more, howlers at Tikal have been habituated to the presence of humans by the many tourists viewing the ruins, but are neither fed nor otherwise disturbed in a way that would bias foraging data.

CHAPTER II

BACKGROUND DATA

Description of the Study Site

Tikal is a major tourist attraction in Guatemala. It is located in the Northern half of El Peten, the department comprising the northern portion of Guatemala (Fig. 1). The national park itself consists of a 24X24 km square, centered on a major Maya ceremonial center. Part of the ruins were excavated and restored by the University of Pennsylvania during the 1950s and 1960s. Access to the park via roads is difficult, especially during the rainy season. Tourists are flown into the ruins daily from Guatemala City.

The terrain of the park is varied. The major temples are located on the highest ridge systems in the area (elevation about 250 m). These limestone ridges are fairly well-drained and are interconnected by low-lying flat areas termed bajos (Cant 1977). Because of the structure of the limestone formation in this area, there are no streams or natural lakes at Tikal.

Vegetation

Researchers working in the Tikal area have classified it as falling within the life zone of Tropical Dry Forest (Holdridge 1967). Within this zone at Tikal, there are three distinct plant communities. This study was conducted in and around the central ruins complex



**Fig.1 Map of Guatemala indicating location of Tikal
(after Cant 1977)**

(Fig. 2), where the vegetation type is Upland Forest; this is distinct from the other two plant associations at Tikal, escobal and tintal. Upland Forest communities exist on well-drained ridges. Escobal and tintal though distinct from each other in major species composition, are both found in less well-drained areas (bajos). Both escobal and tintal derive their names from characteristic species found in the area; escobal refers to a small armed palm Cryosophila argentea, and tintal to a hardwood tree, Haematoxylum campechianum (Cant 1977).

Upland Forest is the predominant vegetation type at Tikal, comprising 55% of land area. Escobal and tintal represent 29% and 16% respectively (Cant 1977). During this study, howlers were seen to utilize only Upland Forest in their foraging activity. They were observed to travel through what could probably be termed "marginal" or "transitional" escobal, but were not seen to utilize any resources from this area.

In his survey of Upland Forest at Tikal, Cant (1977) identified 62 tree species. Field specimens were identified by using Pennington and Sarukhan's plant key, Arboles Tropicales de Mexico (1968). Two species predominate in basal area; Brosimum alicastrum, locally known as ramon, comprises 20.8% of the total basal area, and Spondias mombin 8.5%. Basal area, at least for this kind of research, provides a "useful and practical approximation of how important trees are" (Cant 1977:39). Brosimum also predominates numerically.

Climate

The lowlands of Guatemala have distinct annual wet and dry seasons. At Tikal the majority of precipitation falls during the

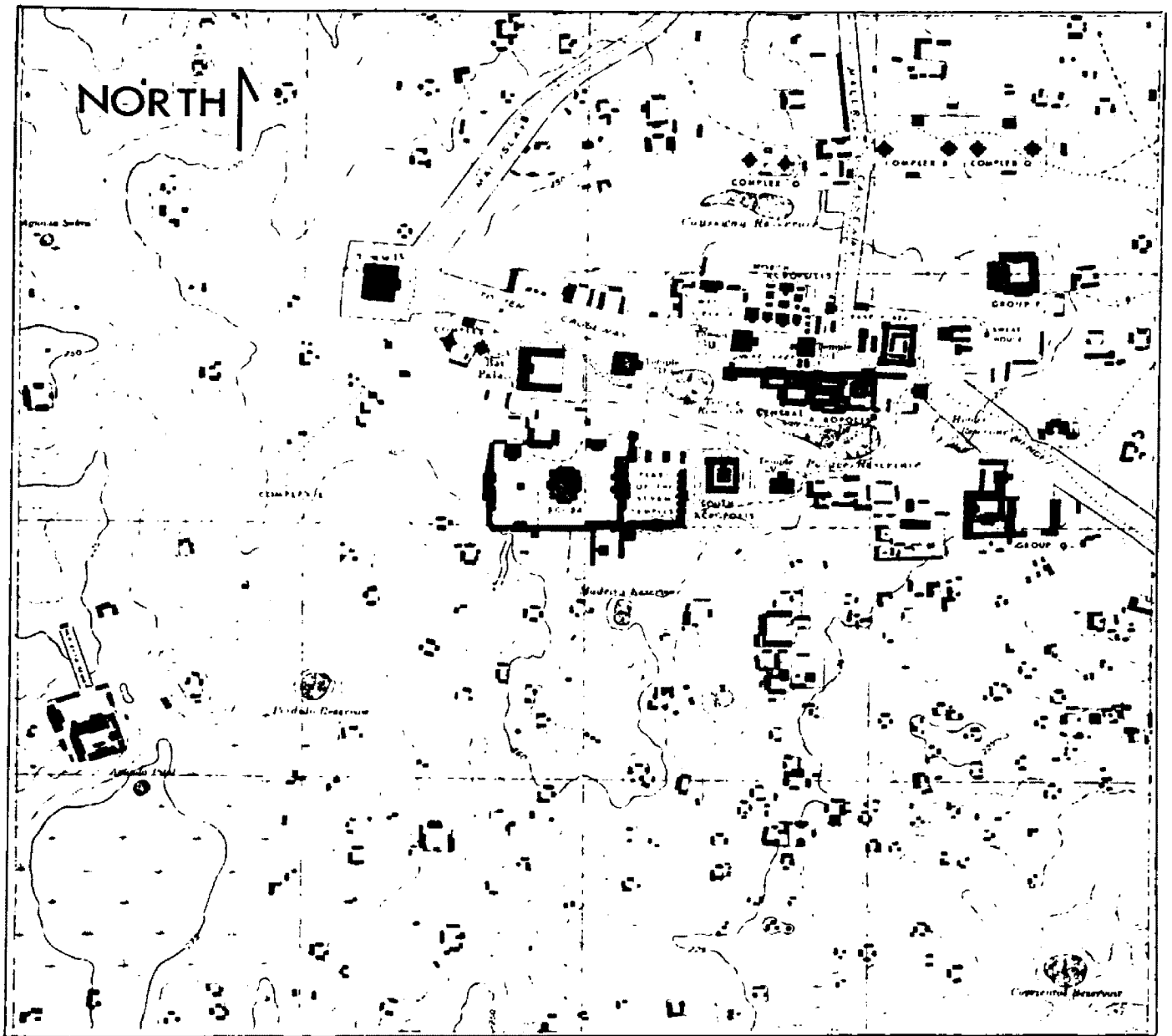


Fig.2 Map of Central Ruins area, squares are 500 m/side

months of May through November. The mean annual rainfall, figured from six years of complete precipitation data (1960-1962 and 1966-1968), is 1376 mm (Cant 1977:28). During these six years, the percentage of annual precipitation that fell during the wet season varied from 78% to 83%.

Temperatures are highest during the wet season, and showers may be expected each afternoon. The quantity of foliage is greatest during the middle of the wet season, after many trees have flowered and have mature leaves.

The dry season continues from December through April. Temperatures are generally milder during this period, and of course the humidity is much lower than during the wet season. Toward the end of the dry season, many species begin to flower and to produce fruit and new leaves.

Mammalian Species

Beside the two species of primates, there is a variety of small and large mammals at Tikal. Faunal species composition is typical of the Peten region (Murie 1935). Several of the felids found at Tikal may be predators of howler monkeys; these include: jaguar (Felis onca), puma (F. concolor), yaguaroundi (F. yaguaroundi), ocelot (F. pardalis), and the margay cat (F. wiedii). The tayra (Eira barbara), a large weasel-like animal may also molest primates at Tikal (Defler 1979). Howlers in other areas have been observed to respond defensively to visual stimuli from the air, i.e., passing shadows, etc. It may be that some of the larger raptors also represent a predatory threat to immature animals.

Howler Background--Classification and Distribution

Howlers belong to the family Cebidae, the largest family of South and Central American monkeys, which excludes only the marmosets and tamarins (Napier 1967). Male howlers weigh between sixteen and twenty pounds, females between twelve and eighteen pounds. Howlers are considered to be quadrupeds, but they use their prehensile tails for extra stabilization when traveling between trees. Howlers also suspend themselves by their tails to reach elusive food sources.

It is easy to identify the sex of adult howlers. Males have a very large, yellowish-white scrotum that contrasts greatly with their dark fur. Female genitals, although similar to the males in color, are easy to distinguish.

Alouatta species (howlers) are widely distributed throughout Central and South America, in coastal and inland tropical forest areas. Alouatta pigra Lawrence, formerly considered a subspecies of Alouatta palliata has been designated a distinct species by Smith (1970). Smith makes this distinction based upon inter-group differences in cranial measurements, molar size, body weight, pelage, and habitat preference. Alouatta pigra inhabits the tropical forests of Northern Guatemala, Belize and Southern Mexico. "Whereas pigra seems to prefer extensive undisturbed and mesic forest, palliata apparently thrives in less extensive, subclimax or secondary forest, which also may be somewhat xeric in nature" (Smith, 1970:365). A. pigra and a subspecies of A. palliata (A. p. mexicana) occur sympatrically in Tabasco, Mexico.

Anatomy/Physiology

Howlers have traditionally been classified as leaf-eating specialists, the New World "analogues" of Old World specialized folivores, the colobines and indriids. It does not appear that howlers possess the typical anatomical and physiological characteristics of the Old World folivores: i.e. sacculated stomachs; enlarged caecums and colons; and specialized, abundant bacteria that aid in the breakdown of fibrous plant materials. According to Milton, ". . . thus far there is little morphological evidence to support the view that it (howlers) can be considered a folivore in the same sense as colobines and indriids" (1978:537). Milton suggests that howlers are "behavioral folivores," meaning that they possess certain behavioral adaptations that enable them to successfully utilize large quantities of otherwise low-quality foods.

Social Organization

Estimates of group size in howlers vary from different areas. Chivers (1969) gives the following list of average group sizes from several different studies conducted on Barro Colorado Island (B.C.I.), Panama Canal Zone.

1951 (Collias and Southwick)	Average group size = 10.25
1959 (Carpenter 1962)	Average group size = 20.00
1967 (Chivers)	Average group size = 12.80

Milton's (1978) two study groups from B.C.I. each consisted of seventeen animals. It is clear from these figures that, even in a rather confined area, howler group size varies considerably. From his Costa Rican study site, Glander (1975) reported two groups, one

consisting of thirteen animals, the other of thirty-six animals. The animals on B.C.I. as well as those at Glander's site, belong to the species paliatta. Alouatta seniculus has been observed in small groups in Venezuela (Neville 1976). Of nineteen troops censused in 1970, the average group size was 7.7; in 1972 the average group size calculated from nineteen groups was 8.6.

Researchers at Tikal have consistently reported small group sizes for howlers, and low overall population densities. Coelho et. al. (1976) reported four groups of howlers in and around the central ruins complex: two multi-male groups and two one-male groups. Total howler population at Tikal during the time of Coelho's study was estimated at twenty-five animals. There were no more than seven and no fewer than six animals in each group. In 1974, Schlichte (1978) observed only two groups in the same area: one multi-male group with seven animals, and one single-male group consisting of four animals.

During our study at Tikal, we determined the composition of only two howler groups, both of which could be termed "monogamous" as they contained only one adult male and one adult female. Solitary male howlers were observed by Schlichte in 1974, and also during the summer of 1978. These may have been young adult males dispersing from their natal groups.

On the whole, howler social groups are fairly cohesive. The animals travel together throughout their home range, foraging in close proximity to one another. More often than not, all five animals of our group were observed feeding in the same tree. Glander reported that

his study group of thirty-five animals sometimes broke up into subgroups of twenty-seven and eight animals to forage.

Activity Budgets

Howlers are rather lethargic animals. During 65% of our observation time, the group was inactive (Cunningham in preparation). This is consistent with reports from other sites: 66% time spent in inactivity at Tikal during Schlichte's 1974 study, 64% in Costa Rica (Glander 1975), and 59% on B.C.I. (Chivers 1969). It has been suggested by Milton (1978) that the low activity level of howlers is a behavioral adaptation to a low quality diet, i.e. one low in available energy.

Table 1 is from Cunningham's analysis of activity budgets for our group of howlers. Nineteen percent of the adult female's time was spent in feeding activity whereas the total feeding time of the adult male was only fifteen percent. The adult female fed for more time than the adult male on twenty-nine of thirty-three days. "Utilizing the t-test, this day-to-day difference was significant at the .001 level" (Cunningham in preparation). The same sex-difference in the percent of a day spent feeding has been reported by C.C. Smith (1977) from his study of howlers on B.C.I. This appears to be a common pattern among many primate species:

Males might be expected to feed for less time per unit of body weight than females because (a) they do not incur the costs of pregnancy and lactation. This is supported by differences in feeding time between females with dependent offspring and those without (e.g. Smith, Ch. 4); (b) in most species males are dominant to females and maintain priority of access to the areas of maximal food availability; (c) they tend to feed faster than females . . . (Clutton-Brock 1977:545).

TABLE 1
ACTIVITY BUDGETS--PERCENT TIME SPENT IN MAJOR ACTIVITIES DURING DAYLIGHT HOURS

Activity	% Activity by Time				
	Adult Male	Adult Female	Juvenile Female	Juvenile Male	Infant
Feed	15	19	17	16	11
Inactive	66	63	59	58	67
Travel	11	12	11	12	12
Move	3	4	6	7	9
Social Play	<1	1	7	7	2
Vocalization	3	1	<1		
Misc	1	<1	<1	<1	

Cunningham, in preparation

Not all investigators have looked for this kind of difference in their analyses of howler activity budgets. In some studies the selection of sampling procedure has been based upon the assumption that howlers "perform most activities as a unit" (Milton 1978:539).

Home Range

A major problem in determining home range estimates is that there are several different methods, and the method of calculation is often not specified by the researcher. This makes comparison of results from different studies difficult. One method of calculating home range is to form a boundary line by connecting several peripheral points, and then estimate the area inside the boundary. A problem with this method is that inclusion of all outlying areas may greatly increase the total estimate of home range.

Home range estimates for this study were arrived at by counting the number of one-hectare squares the howler group passed through during the fifty-six days of the study. This method results in an estimate that is greater than the actual area utilized by the howlers for forage, since it includes some area used only for traveling. However, this method would seem to produce less error in the estimate than the first technique discussed.

It should be noted that an animal's home range is likely to change with the season. It also may "expand and contract over a period of years in response to changes in population density, amount and type of food available, and the like . . ." (Harding 1973:967). Therefore comparisons of the estimates made here should be limited to those made with wet season home range estimates from other study sites.

During the fifty-three days of study at Tikal, the home range of our study group was approximately forty-seven hectares. Schlichte reported a home range of close to one hundred hectares during his four-month study at Tikal. Both these estimates are much greater than the home ranges reported for howlers in other areas. For example at Glander's study site in Costa Rica, the total home range was only 9.9 ha over the period of a year.

Inter-Group Spacing

One of the distinctive features of howler "society" is the roaring or vocalizations that occur when two groups of howlers are in close proximity to one another. It is fairly likely that the home ranges of any two howler groups within a given area will overlap on the periphery. It has been suggested that when the adult animals of two different groups roar at each other, in effect they are notifying each other of their locations. Roaring can be said to serve as an inexpensive spacing mechanism, since little energy is needed to vocalize and make one's presence known (Carpenter 1934, Chivers 1969).

CHAPTER III

SELECTED REVIEW OF THE LITERATURE CONCERNING HOWLER ECOLOGY

In a general sense, this thesis falls in the category of optimal foraging research (Pyke et al. 1977). In all such studies researchers attempt to identify the methods by which animals balance the energy cost of obtaining food with the energy they receive from food resources. Many optimal foraging studies are formulated as mathematical models, this research does not fit such a description. An attempt has been made to describe the foraging strategy employed by one group of howlers in terms of several aspects of their diet and behavior.

It seems impossible to take into consideration all environmental requirements, limitations, etc., imposed upon an animal that would dictate energy availability. Nonetheless it is possible to elucidate the ecological parameters operating on a particular species, by breaking research into small manageable pieces. In a review of optimal foraging studies, Pyke et al. (1978) identified four topic areas:

1. Choice by an animal of which food types to eat.
2. Choice of which food patch type in which to feed.
3. Optimal allocation of time to different patches.
4. Optimal patterns and speed of movement.

The present research is a study of choice of food types, and to some extent, optimal patterns and speed of movement.

The following is a review of the major ecological studies conducted on howler monkeys, and pertinent studies of general ecological theory. Each in its own way contributes information about the foraging strategies of howlers specifically and, ultimately, of primates in general.

One way of elucidating the foraging strategy of a particular species is to consider the kinds of foods that they consume. By looking at the dietary proportions of howlers from different study sites, it is obvious that there is a wide range of exploitation within and between Alouatta species. One general statement that can be made concerning howlers is that they utilize large quantities of "low-quality" foods. Low-quality foods are those that have little nutritional value, or those that contain substances that either interfere with assimilation of nutrients or are toxic to the animal consumer.

In the past, researchers have compiled percentages of the kinds of plant part utilized (Smith 1977, Glander 1975), as well as percentages of the species utilized. It is important to know what species of plant are being utilized by a consumer, since different patterns reflect different foraging strategies. Generalist herbivores, those animals that use many different species of plants in their diets, are utilizing a very different strategy than specialists, animals that use one or a restricted number of species in their diet.

Howlers are considered to be generalist herbivores, but the results from dietary analyses are mixed. Two other studies of an ecological nature have been carried out at Tikal previous to my 1978 study. Coelho (1976) recorded the amount of time spent feeding on different species by spider and howler monkeys at Tikal. Unfortunately, Coelho did not separate the diet of howlers from the diet of spider monkeys, so that his data cannot be directly compared with the results from this study. One thing that can be inferred from the results of Coelho's study is that there is a high single-species dependency at Tikal. Eighty-six percent of the food consumed consisted of some part of ramon, Brosimum alicastrum. Schlichte dealt only with howler monkeys during his four-month study. During this time, 87.5% of the howler diet consisted of ramon, including fruits, leaves and buds (Schlichte 1978). During my study, 67% of the howler diet consisted of different parts of ramon (fruit, seeds, and leaves).

From information of this kind (dietary proportions), one can interpret in a general sense the kind or quality of nutrients (energy) available to howlers, and make a statement concerning strategies of optimization.

Besides considering dietary proportions, researchers have been investigating certain aspects of herbivorous diets that limit the assimilation of energy from foods. For example, Janzen (1978) has documented the existence of chemical components in the leaves of some plant species that act to discourage leaf predation. Because the survival of an individual plant depends upon its ability to trap energy through photosynthesis, the loss of large quantities of leaves

(the medium of photosynthesis) would be deleterious. Glander (1975) points out that, for herbivorous primates, there are many toxic compounds that limit access to energy:

The secondary substances which the plants have evolved as defences against herbivores may be of critical importance both to the individual animals and to group social behavior. The action of these plant toxins may be direct as illustrated by the rat poison made from the bark and leaves of Gliricidea sepium. Or, it may be indirect in the manner of tannins, as found in mature oak leaves, which bind proteins into indigestible complexes . . . (Glander 1975:54).

The presence of toxins in food necessitates an energy-costly process of detoxification. Thus in addition to the costs of finding food (i.e. traveling to a food patch, etc.), once an animal actually ingests the food, it must pay an additional energy cost in processing out nutrients and dealing with the toxins in its system. Ultimately, what the conclusions of Glander and other researchers lead to is the realization that the vast sea of greenery in a herbivore's environment is not all edible.

This kind of interpretation is very different from that of earlier researchers. For example, Coelho et al. (1973) maintain that the environment of Tikal has the potential to support 8,500 monkeys per km², based upon the calculated caloric value of available food. The actual population of monkeys (spiders and howlers) during their study was estimated at fifty monkeys per km². Thus, when looking only at the amount of available "green" volume, and translating this into available calories, Coelho et al. would say that food availability does not limit population. (An adequate explanation for the low population density of howler monkeys at Tikal has not yet been offered.)

According to Janzen (1978b), whether or not an animal can ingest plant parts of a given species:

depends on the condition of the animal, the dose, the past experience of its inducible enzyme systems with the compound or related compounds, the past experience of its gut microflora with that compound, the simultaneous ingestion of synergists or antagonists of the secondary compound, the tasks to be asked of the animal's detoxification system and of the animal in the immediate future, the expectations of the animal for the later use of the habitat, the use of the secondary compound as a medicine and the use of the secondary compound as a scent marker or pheromone (Janzen 1978b:80-81).

Milton (1978) has described howlers as being "behavioral" folivores, that is they have no specialized anatomical features that enable them to process large quantities of foods high in fiber and relatively low in nutrients. Rather they possess certain behavioral adaptations that allow them to successfully utilize low-quality diets. For example:

(1) a persistent, regular pattern of daily inactivity, (2) use of high energy foods when available, (3) an extremely efficient system of food location, (4) body postures to conserve or dissipate heat, and (5) a "division of labor" between adult male and female howlers which could reduce energy demands on females and enable them to invest more energy in reproduction (Milton et al. 1979:374).

Glander also describes a kind of behavior that may benefit howlers in dealing with certain aspects of their diet, namely plant toxins. During the wet season, there is a large amount of food available to howlers in the form of mature leaves. ". . . though the wet season appears to be a time of food abundance, it may actually be a time of stress since most of what is available are mature leaves, a tree part with large amounts of toxins" (Glander 1978:572).

Howlers may be coping with this stress by drinking from arboreal water sources during the wet season, a behavior not observed during the dry season when young leaves are more prevalent. Glander suggests that the wet season diet of mature leaves necessitates large amounts of water to flush toxins from the system. During the dry season, when many new leaves are available, the toxin load is decreased, and enough water may be obtained directly from the food source to handle the toxic stress.

From her long-term study of howler monkeys on B.C.I., Milton (1979) has tested several elements that might influence leaf choice among howlers. It is often the case that herbivores, when given the choice between mature and immature leaves, will eat the young leaves. Howlers on B.C.I. follow this general pattern. The following is a list of the hypotheses that might account for the selection of immature leaves:

1. Young leaves contain more protein than mature leaves, or contain more available protein (after the effects of digestibility-reducing secondary compounds).
2. Young leaves contain less fiber than mature leaves, which would make them more digestible and would also imply that howlers could eat more of them within a given period of time (i.e., the limit on the intake of young leaves would be higher).
3. Young leaves contain less toxins than mature leaves. (As defined by Rhoades and Cotes 1976, toxins are substances which act in metabolic processes that are topologically internal to the herbivore whereas digestibility-reducing substances act within the gut of the herbivore to reduce the availability of plant nutrients).
4. Young leaves contain more non-structural carbohydrates than mature leaves, particularly simple sugars that are rapidly digested.

5. More than one of the above factors determine the preference of howlers for young leaves (Milton 1979:365).

It appears that since howlers are relatively small herbivores, with no specialized digestive features, they cannot process sufficient quantities of foods high in fiber to meet their nutritional needs. Instead of relying on mature leaves, they must be more selective in their food search patterns and seek out young leaves.

Given their small size (for a mammalian herbivore), their lack of extensive areas for fermentation in the foregut or hindgut, and the relatively low protein content of most of the leaves analyzed, howlers apparently must be very selective in their leaf-eating in order to maintain nitrogen balance. But this selectivity must require howlers to spend more energy in food search than otherwise (Milton 1979:374).

Milton suggests that howlers need a diet that provides adequate protein while being relatively low in fiber. Also needed are fruits or other foods high in soluble carbohydrates, or ready energy. By using fruit to "subsidize" the search for young leaves (relatively low in fiber/high in protein), howlers offset the energy requirements of the food search.

If the distribution of "fruit" resources is such that a great deal of time and energy are required to find the food, then the energy ultimately derived from the resource is negated by search costs. In such cases, howlers may eat large amounts of mature leaves. Even though this kind of diet provides less available energy, a balance is again achieved because less energy is expended in searching for food. Mature leaves are easy to find.

The data from my field study will be presented and discussed in Chapter V, within the theoretical context presented in this review of the literature.

CHAPTER IV

FIELD METHODS

The collection of data in the field was in part a compromise between environmental restrictions and the need for quantitatively accurate measuring techniques. The environment of Tikal, especially during the wet season, posed some very real limitations on the kind of data that could be collected. Consequently, this research has gone through several stages of evolution, from the ideal to the real and back to a point in between.

Two primary field workers were involved in collecting data, Teri Cunningham, a fellow M.A. degree candidate, and I. Dr. John Cant and Earthwatch volunteers from his project were extremely helpful in keeping track of our study group when either Teri or I were unable to follow the monkeys.

During the initial weeks of the study, two groups of howlers were identified in the central ruins area; these were designated as the "North" and "South" groups. Both were monogamous and each consisted of five animals. Since Ms. Cunningham's primary interest lay with social behavior, we decided to use the "South" group in our study because of its diversity in terms of age and sex classes. The South group consisted of an adult male, an adult female, a juvenile male and female, and an infant. The North group consisted of one adult male, one adult female, and three juvenile males.

Due to the different character of our research projects, the sampling methods employed by each were also different. Ms. Cunningham and I were collecting data for each other, thus two types of variables, behavioral and ecological, were being sampled at one time.

The field day was divided into morning and afternoon shifts. One of us began observations at approximately 0600, followed howlers until 1200, at which time she was relieved by the second field worker. The person on the afternoon shift stayed with the animals until they bedded down for the evening, sometime between 1630 and 1800. The individual who observed the animals in the evening resumed the observation the following morning; thus we seldom had trouble locating the group in the morning. Most of the time the monkeys were found in the same tree, on the same branch as the previous evening. If the animals had to be left in an unusually remote area in the evening, the path out to the central ruins was flagged for easy return the following morning. By almost continuous daytime observation of the study group, we accumulated approximately five hundred hours of observation.

Due to the limited visibility, and the fact that howlers tend to occupy the upper portion of the forest canopy, observations had to be carried out with binoculars (7X35 Bushnells).

Three major sampling methods were used: scan, focal-animal, and ad-lib sampling (Altmann 1974). Scan sampling refers to instantaneous sampling conducted on groups of animals. Altmann defines instantaneous sampling as a "technique in which the observer records an individual's current activity at preselected moments in time (e.g. every minute on the minute throughout the day). It is a sample of states, not events"

(Altmann 1978:258). Scan samples were taken every five minutes to record the major activity of each of the five members of the study group. For purposes of this study, major activities were defined as follows:

Feeding--An animal engaged in within-tree foraging. Upon entering a tree, an animal was considered to be feeding if its hand or mouth was in contact with a food item. Active searching was also considered to be part of feeding time. One feeding bout continued as long as there was no pause greater than three minutes, or until the animal moved to a different tree.

Traveling--Directional movement with at least two tree-to-tree transitions with no pause greater than three minutes.

Inactive--Refers to such activities as auto-grooming, auto-play, and postural shifts. Does not include time spent in three-minute pauses during traveling or feeding.

Move--Movement between two points or loci in a single tree, or movement between two trees. This does not include shifts made during feeding bouts.

Allo-grooming--Grooming between two or more animals.

Elimination--Urinating or defecating.

Roaring--Vocalizations made by the adult male, adult female, or juvenile female, directed at another group of howlers.

Sexual Activity--Active solicitation and copulation.

Each activity was assigned a code number. The information gathered by the use of scan-sampling is being used primarily by Ms. Cunningham in her analysis of activity budgets.

The data for my part of the study were collected by recording the foraging activities of one focal animal. Focal animal sampling is defined by Altmann as:

. . . any sampling method in which (i) all occurrences of specified (inter)actions of an individual, or specified group of individuals, are recorded during each sample period and (ii) a record is made of the length of each sample period and, for each focal individual, the amount of time during the sample that it is actually in view. Once chosen, a focal individual is followed to whatever extent possible during each of his sample periods (Altmann 1978:242).

The ideal collection of data would include both the adult female and the adult male as focal subjects, with a continuous record of all their activities. Since this proved to be impractical, the adult female was selected as the focal animal. This decision was based on the fact that the reproductive role of the female requires greater energy input than that of the adult male. Also, it would be in the male's best evolutionary interest not to impede the energy-gathering process of the female since by doing so he would be restricting the flow of energy to his own offspring. Simply stated, if any individual animal would influence the foraging activities of a group, it would most likely be the adult female.

For each feeding bout of the focal animal, the following variables were recorded:

1. Bout Start Time--Bouts began when the hand or mouth of the adult female came into contact with a food item, or when she was actively searching for food. The bout continued as long as there was no pause longer than three minutes, or until the animal moved from the tree.

2. Bout Stop Time--The time when the focal animal ceased feeding in a tree. Also, if the adult female moved from one tree to another while feeding, a stop time would be recorded for the bout in the first tree, and a new start time recorded for the beginning bout in the second tree.
3. Species of plant being utilized.
4. Plant part utilized (i.e. fruit, leaves, etc.).
5. Maturity of plant part utilized (mature or immature).

The trees in which the adult female fed were numbered sequentially from the beginning of the study, their species identified, and their diameter at breast height (DBH) measured. This information was recorded in the field and formed part of the data for each feeding bout of the focal animal. When possible, the distance between feeding trees was recorded by pacing. If the animals were moving very quickly, distances were estimated, either in the field, or later after the numbered trees had been plotted on a map. This information was necessary for calculating, daily, weekly, and seasonal ranging patterns. A typical entry in the field notebooks for focal animal sampling would appear as follows:

08:31 A♀ B1 R#33, 2, 1

Decoded, this means that at 08:31, the adult female began feeding in ramon tree number 33, on immature fruit. During fifty-six days of observation, 398 feeding bouts were recorded: however, not all of these are complete bouts. For instance, in some cases, either the start or stop times were missed. If possible, these times were estimated by looking at the activity recorded for the focal animal during the scan

sample immediately preceding or following the feeding bout. This information was noted in the field and later added to the total information relevant to each feeding bout.

Howlers seem to do quite a bit of "snacking" or perhaps testing of their food (Glander 1978). For instance, during a progression, they may take one bite from a leaf or fruit, and almost immediately spit out the part. This kind of activity should be considered part of foraging behavior, but it proved to be impractical to record fully during our study. In order to delineate clearly between snacking activities and actual feeding bouts, an arbitrary limit had to be set on the minimal length of a feeding bout. The shortest bout as defined in this study cannot be less than two minutes.

Ad-lib sampling (Altmann 1978) was used to record the occurrence of infrequent activities, i.e. drinking from arboreal water sources, roaring, and sexual behavior. Altmann (1978) defines data derived from this kind of sampling as:

the result of unconscious sampling decisions, often with the observer recording "as much as he can" or whatever is most readily observed of the social behavior of a group in which behaviors, individuals and often the times for behavior sessions are chosen on an ad libitum basis (Altman 1978:235).

The data for each feeding bout (N=398) were coded and keypunched. This resulted in one data card, or case, for each feeding bout of the adult female. Much of the data manipulation was carried out with the use of the DEC System-20 computer at the University of Montana. Programs from the Statistical Package for the Social Sciences (SPSS) were used, as well as the program SYMAP.

CHAPTER V

DATA AND ANALYSIS

Dietary Percentages: Plant-Part Utilization

As stated before, all Alouatta species are considered to exhibit a generalist herbivore adaptation, that is they are supposed to utilize large quantities of leaves in their diet. Figure 3 represents the percentages of different plant parts utilized throughout the entire fifty-six days of study. Seventy-two percent of the howler diet during this period consisted of fruit. Leaves and seeds represented 8% and 16% respectively. The category of "other," including items such as flowers, new fruit and leaves, etc., comprised 4%. Table 2 compares the dietary percentages from Tikal with wet season diets from two other study sites, B.C.I. (Smith, C.C. 1969) and Hacienda La Pacifica, Guanacaste Province, Costa Rica (Glander 1975).

TABLE 2
COMPARISONS OF PLANT PART PERCENTAGES FROM THREE STUDY AREAS

<u>Food Part</u>	<u>Percent Feeding Time</u>		
	<u>Tikal 1978</u>	<u>B.C.I.</u>	<u>Costa Rica</u>
Fruit	72%	32%	16%
Leaves	8	66	57
Seeds	16	--	--
Flowers	--	3	20
Other	4	--	6

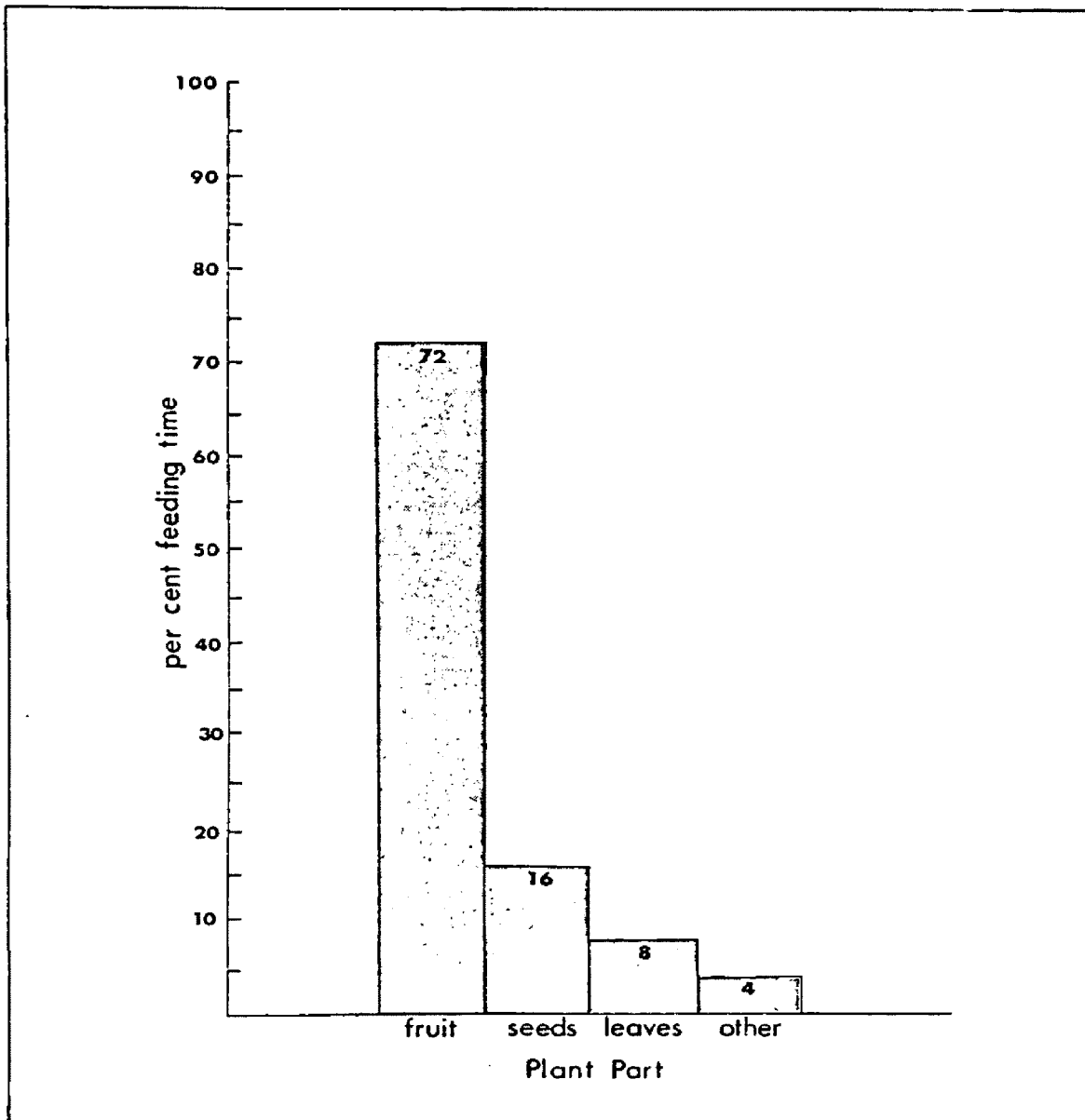


Fig.3 Per cent plant-part used during 56 days

By breaking down the diet only into major food part components, it appears that howlers at Tikal must be utilizing a very different feeding strategy than howlers in other areas. That is, one would not expect to find a generalist herbivore that has a diet composed of 72% fruit. This is a reversal of the results from other areas.

If the major plant parts are broken down by maturity, a rather different picture emerges. Figure 4 is a breakdown of fruit and leaves by maturity. Of all fruit consumed, 47% (1472 minutes) was immature, green fruit. Only a little over half, 52% (1617 minutes), of the total time spent feeding on fruit was spent consuming mature fruit.

At this point it is necessary to discuss the relative nutritional qualities of some major food types:

1. Ideally, the best kind of food for a consumer is animal matter, because it is usually high in protein and/or fat. In terms of caloric value, fat is capable of generating 9.5 kcal/g, and protein 5.7 kcal/g. Glucose and starch are capable of producing 3.7 and 4.2 kcals respectively, for every gram consumed. Animal foods satisfy caloric need since they are high in the top two ranking components of energy value. They also satisfy protein requirements better than any other type of food (Kleiber 1961).
2. Second on the list in terms of food value (and preference on the part of the consumer) should be ripe fruit. Mature fruit generally contains a large percentage of readily available energy in the form of non-structural carbohydrates. Mature fruit satisfies energy requirements, but it is usually low in protein value.

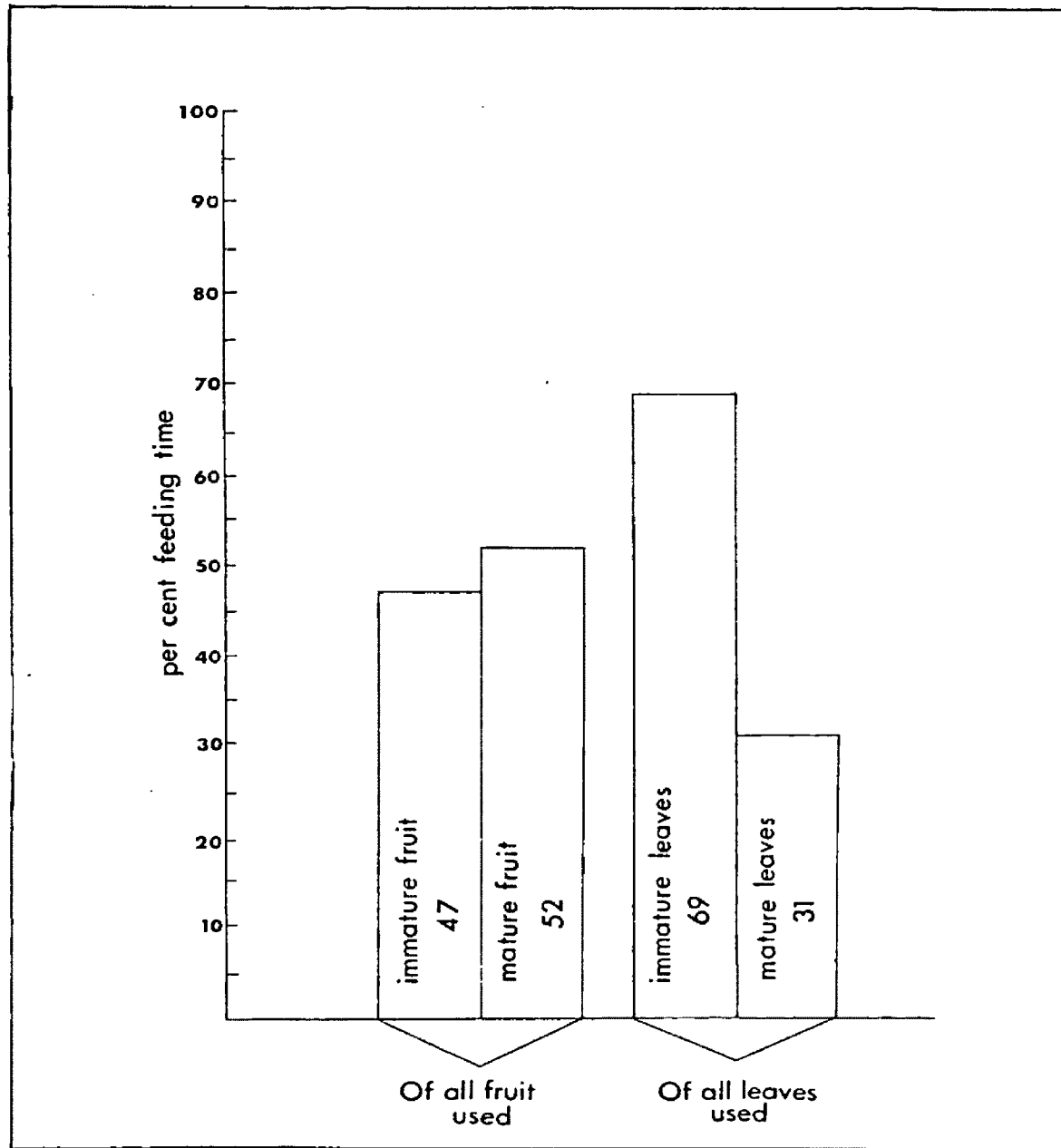


Fig.4 Breakdown of fruit and leaves by maturity

3. Unripe fruit, unlike its mature counterpart, does not usually contain a large amount of sugar. Hladik et al. (1971) have reported that within one species of fig, sugar content for immature and mature fruit was 11% and 42% respectively. This kind of analysis has not been conducted on many species utilized by primates. It is generally accepted, however, that immature fruit is lower in sugar content than mature fruit of the same species.

The benefit of immature fruit is that it may contain more protein than ripe fruit, although one expects a great deal of variation between species. Also, this type of food is generally low in fiber so that a small amount of energy is required on the part of the consumer to assimilate the available nutrients.

One problem with immature fruit is that, depending upon the species, it may contain a large amount of toxins or secondary compounds. Secondary compounds are those elements produced by a plant for interaction with individuals of other species (Janzen, D.H. 1978:165). As previously discussed, the reason for the existence of secondary compounds in various plant parts is to discourage predation. It would be in the best evolutionary "interest" of a plant to lose as few developing fruits to predators as possible. Any loss reduces the number of plant offspring that could possibly reach adulthood.

4. Young leaves should be next on the list in terms of desirability, because they are low in fiber and high in protein relative to mature leaves. Even though immature leaves do not contain a great deal of ready energy, the obstructions to assimilation of available protein may not be great.

5. Finally, mature leaves are considered to be the lowest quality food in this rank ordering of food types. Even though mature leaves are abundant in tropical ecosystems, they are generally low in protein value, low in ready energy, and high in fiber and secondary compounds.

This rank ordering of food type preference has been demonstrated in a troop of chacma baboons (Papio ursinus) by Hamilton et al. (1978). The baboons appear to utilize animal resources whenever available; next they prefer fruits, seeds, bulbs, etc., and if nothing else is available, they will use leafy vegetation.

Considering the preceding information about relative values of food types, it can be seen that the difference between the wet season diet at Tikal and other areas is not as great as it appears. Almost one-half the fruit consumed was immature, and therefore nutritionally similar to immature leaves, the latter representing the "staple" of howlers in areas other than Tikal (Milton 1978). Howlers at Tikal may be said to exhibit a dietary adaptation similar to Alouatta species in different areas. It should be noted however that the distribution of immature fruit, an important part of the howler diet at Tikal, is probably different spatially and temporally, from the distribution of immature leaves. Because the distribution of foods affects the search patterns of consumers, one might expect howlers at Tikal to exhibit search patterns different from howlers in other regions.

Plant Part Utilization on a Daily Basis

When looking at the dietary data on a day-to-day basis, an interesting pattern of short-term resource exploitation emerged. One

problem that a generalist herbivore must overcome is how to ingest enough energy to find foods of a sufficient quality to provide for body maintenance (Milton 1978).

It can be argued that the consumption of large amounts of foliage will provide the consumer with as much protein as is required. However, the problem as stated before is that the most abundant foliage type is mature leaves, a food high in fiber (cellulose and hemicelluloses) as well as secondary compounds. It would be better to concentrate on eating young leaves. The problem with young leaves is that they are not as abundant as mature leaves, thus more search time and energy are required to find the primary food source (Milton 1979, Struhsaker 1974).

Milton suggests that howlers utilize mature fruit to subsidize their search for young leaves, a food relatively low in fiber and high in protein content. The fiber/protein ratio may be the most important factor in determining howler leaf choice (Milton 1979).

By looking at the daily feeding pattern exhibited by the adult female, it would appear that, at least for short periods, howlers may be more interested in exploiting sources of ready energy than in balancing their protein input-requirement needs. Figure 5 represents the percent of total daily feeding time spent in fruit consumption for the last thirteen days of this study. From August 27 to September 1 there is a good deal of fluctuation in the amount of fruit consumed, from 56 to 91%. From September 2 to September 9, there was a gradual increase from 61% to 85%. The important thing to note is that, on any one of the thirteen days, the percentage of foods that are high in

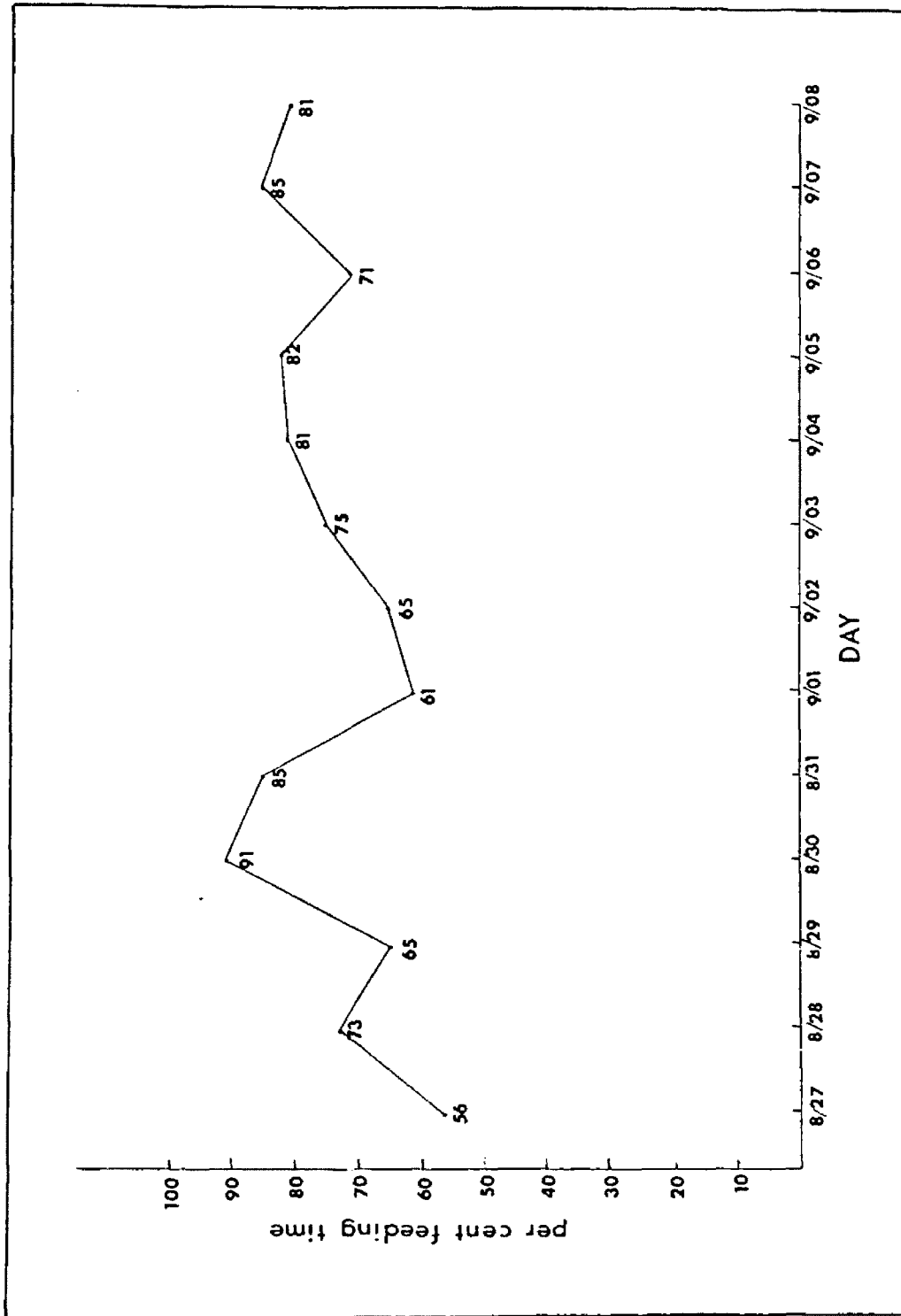


Fig. 5 Per cent feeding time on fruit for 13 days

energy but low in protein never falls below 50%. Furthermore, when an animal spends as much as 91% of its feeding time consuming mature fruit, it is virtually certain to be utilizing far more than is necessary to subsidize the quest for immature leaves.

The above statement is especially important when one considers the fact that mammals do not have a mechanism by which they can store protein. Within four to six hours after being ingested, protein is either combined into components needed by the consumer, or discarded. If more protein is not obtained after this six-hour period, the body begins to break down:

1. White blood cells, making the body more susceptible to infection.
2. Liver tissue.
3. Muscle protein (personal communication Nancy Munro, Crampton 1959).

It would appear that, at least in the short run, howlers may be choosing to exploit foods that provide them with nutrients (fats, carbohydrates) that are easily stored. With sufficient energy reserved in the form of fat, howlers may essentially be hedging their bets against periods of food shortage. It is true that during periods of high fruit consumption, howlers may suffer a mild form of protein stress. However, the body may be able to deal with small protein shortages over short periods of time, if no serious long-term damage or weakening of the individual results.

Milton's hypothesis, that animals are essentially "choosing" foods on the basis of protein and fiber content, is not incompatible with the

statement made above concerning "energy hoarding." It is logical to assume that the analysis of daily patterns of consumption may expose patterns of behavior which do not, or cannot, appear in the analysis of dietary data that are lumped into seasonal categories. Researchers working with howler ecology have not analyzed their data in daily or weekly increments. Such analyses should prove to be beneficial to the study of optimal plant part utilization.

Energy hoarding may be another example of the behavioral adaptations that, as Milton (1979) suggests, allow howlers to cope with diets that are low in overall energy availability.

Percent Feeding Time on Fruit

Given that food types vary a great deal in terms of the benefits the consumer may derive from them, it is logical to assume that the amount of feeding time per day will vary in accordance with concurrent dietary proportions. However, it is difficult to predict the character of this variation. One might suppose that when ripe fruit is readily available, an animal would feed for a longer total period of time in order to take full advantage of this resource. Since ripe fruit is generally low in fiber, bulk would not pose a great problem to the consumer. On the other hand, one could argue that if animals have fixed energy requirements, they need to feed on fruit for shorter periods of time because it is high in available energy.

In a test of linear regression, no relationship was found between the percent of time spent feeding each day and the percent of time spent feeding on fruit. One could interpret this to mean that, when fruit is available, the adult female is not necessarily feeding for a

longer total time to take advantage of this resource. There was however a notable exclusion of other items from the diet during periods when ripe fruit was readily available.

The larger question of the kind of feeding strategy associated with specific food types cannot be resolved because no positive or negative relationship was demonstrated.

Plant Part Change Through Time

Figure 6 is a graph of the percent consumption of different plant parts during seven-day increments. Each of the eight seven-day increments represents one data subfile, labeled A through H. (See Appendix I for the days included in each subfile.) For instance, in subfile A, mature fruit made up 73% of the diet, immature fruit 24%, and leaves 3%. As can be seen from Figure 6, there was a great deal of fluctuation, week to week, in terms of the major plant part being eaten.

The very high percentage of fruit during subfile A was due to the utilization of copal (Protium copal). After copal ceased to bear ripe fruit, there were essentially no trees in the forest with ripe fruit. After the reduction in ripe fruit availability, immature fruit (mostly ramon), seeds, and leaves increased in importance in the diet. During the third week, subfile C, the proportion of seeds in the diet increased rapidly from 24% to 57%, while leaves decreased by one-half, from 35% to 18%. After this period, immature fruit became the dominant food type eaten. From the fourth week until the end of the study, the amount of immature fruit varied inversely with the proportion of ripe fruit in the diet. Subjectively, it appears that howlers are

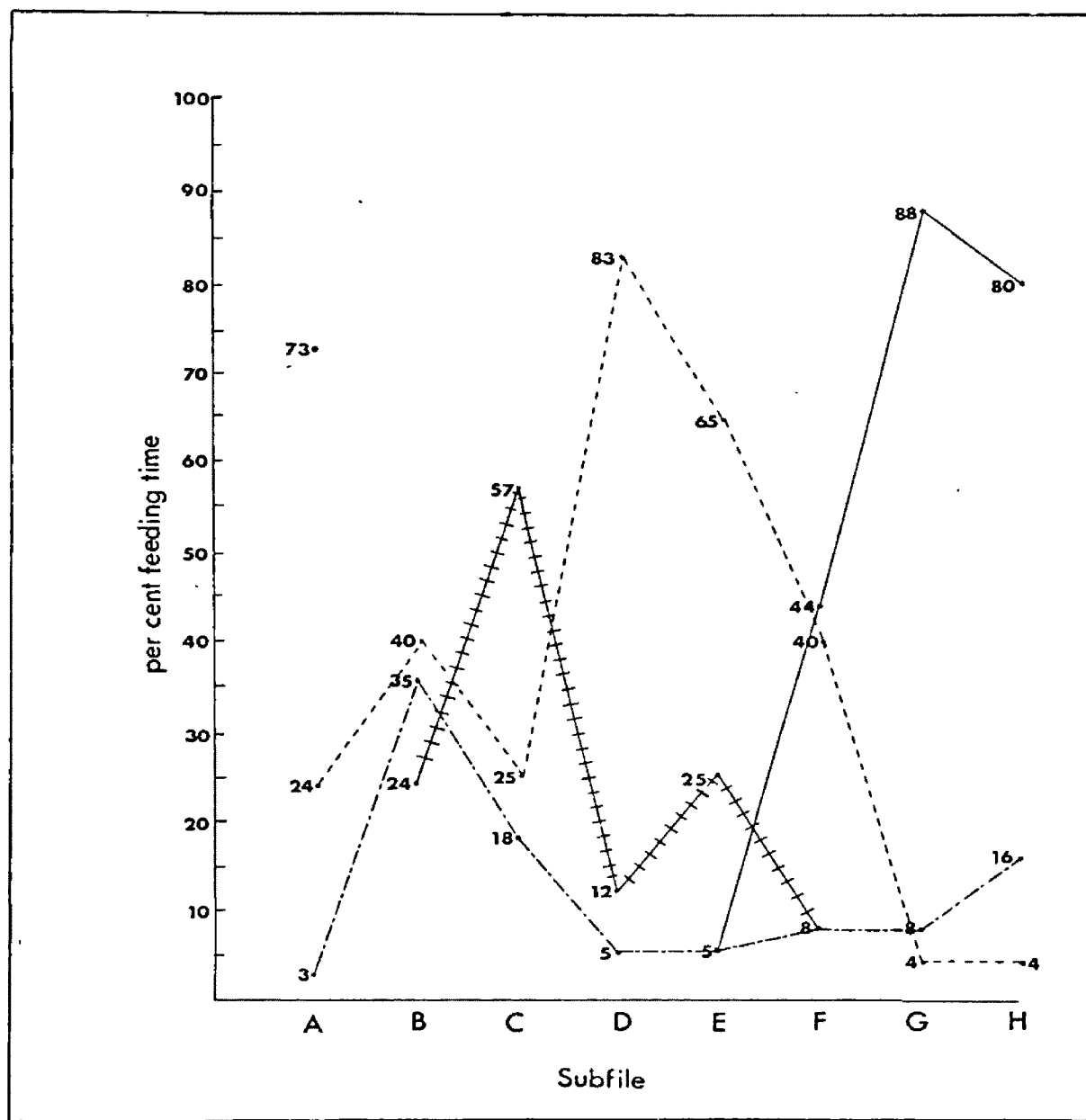


Fig. 6 Plant part change through time

————— mature fruit
 - - - - - immature fruit
 + + + + + seeds
 - - - - - leaves

consistently utilizing the food source with the highest energy yield. The only time that leaf intake increased greatly was when foods of higher quality were not available.

Changes in Plant Part Utilization through the Day

The final analysis concerning plant part deals with the time of day at which different food types are eaten. Two patterns emerged after looking at the type of food consumed during the first and last feeding bouts of the day.

1. The first feeding bout of the day consisted of leaves on only two of the fifty-six days of the study. Of the remaining days, mature fruit was the first food eaten on twenty days; immature fruit eighteen days; and seeds six days. (On nine days of observation, the first feeding bout was not observed.)

In the morning, an animal has not taken in any energy since the final feeding bout of the previous evening, creating a fasting period of between eight and twelve hours. For this reason it makes good sense to utilize the best quality food available in the morning in order to obtain enough energy to begin another day's activities (Raemakers 1978).

That howlers do not always begin their day with a feeding bout of mature fruit may be attributed to the fact that howlers do not spend a great deal of time and energy searching for quality foods. In this regard, howlers are energy conservers. A reduction in energy that has to be expended on food search activities leads to a reduction in the total amount of energy required. In other words, if a "quality" food is easily obtained in the morning, then

howlers will take advantage of it, if not they will use what is close at hand. At some point, search costs outweigh the benefits of high quality food.

2. A second rather indistinct but nonetheless discernible pattern is that, like other species of primates, howlers tend to ingest leaves late in the day (Raemakers 1978). The relative quality of leaves as a food source has already been discussed. Due to the high fiber content of most leaves, a good deal of energy is required to assimilate the available nutrients (protein). If leaves are ingested late in the day, they can be processed during the evening, when the animal is at rest and energy is not required for other activities.

Because howlers at Tikal were using so few leaves in their diet, this pattern was not as "subjectively" apparent as the results from other studies, but there is a statistically significant association of food type with time of day, at least for first and last bouts ($\chi^2=8.92$, $p<0.01$, 1 degree of freedom). Howlers appear to be conserving energy by eating quality foods early in the day, and waiting until periods of relative inactivity to use hard to digest food types.

Species Utilization

The typical pattern for resource utilization among generalist herbivores is to use a wide range of plant species in their diet. Figure 7 represents the total species composition of the diet during fifty-six days of observation. Two species make up 89% of the diet; ramon (Brosimum alicastrum), and capulin (taxonomic designation

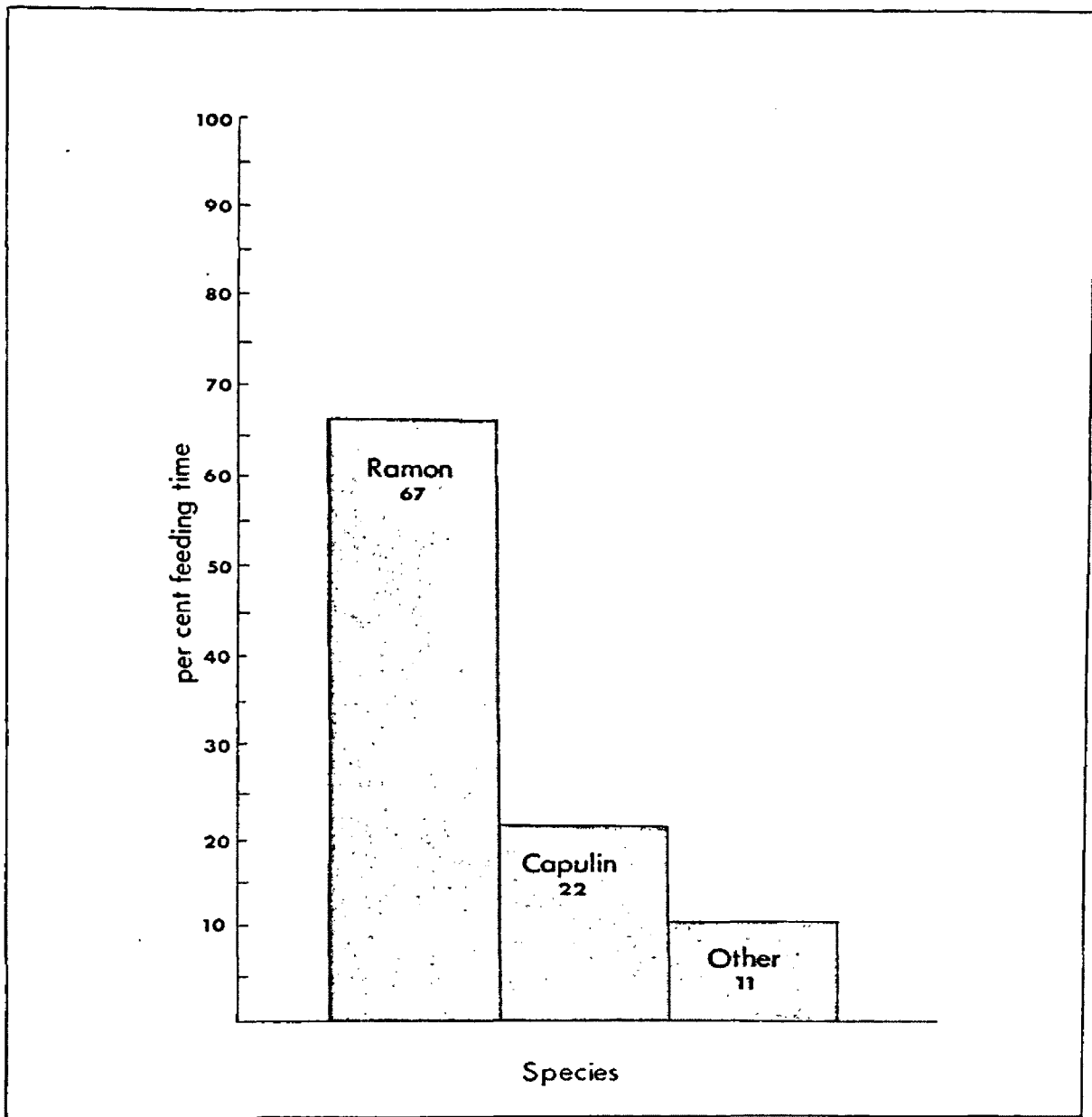


Fig. 7 Per cent species used during 56 days

unknown), represented 76% and 22% respectively. The remaining 11% of the diet consisted of thirteen other species, none of which made up more than 3% of the total. (See Appendix II for a list of the species and plant part utilized during this study.)

The heavy reliance upon two tree species would seem to be unusual behavior for a generalist herbivore. Dietary data from other studies, however, have usually been lumped into seasonal categories. If such data are broken down into smaller increments, one may find that for any given period of time a single species or a few species predominate in the diet. For example, among red colobus monkeys (Colobus badius tephrosceles), during each of several months, two food species made up a little over half of the total diet (Struhsaker 1974); 59% was the largest value reported.

Figure 8 is a breakdown of species used during each seven-day subfile (A-H). During any subfile, two tree species make up at least 84% of the total diet. There is, however, a good deal of variation from subfile to subfile in the amount of utilization of any single species. Ramon varies from 39% to 94%, capulin varies from 6% to 45%. It is probably the case that any species that has quality food parts for the taking will be heavily utilized. Mature capulin fruit represents 83% of the total capulin feeding time, and 79% of the total time spent feeding on mature fruit. This heavy reliance upon capulin is interesting in view of the fact that the density of capulin at Tikal has been estimated to be only .5 trees per hectare (Cant 1977). Thus the second most prominent food species used at Tikal was a fairly rare tree. Milton (1979) suggests that one of the

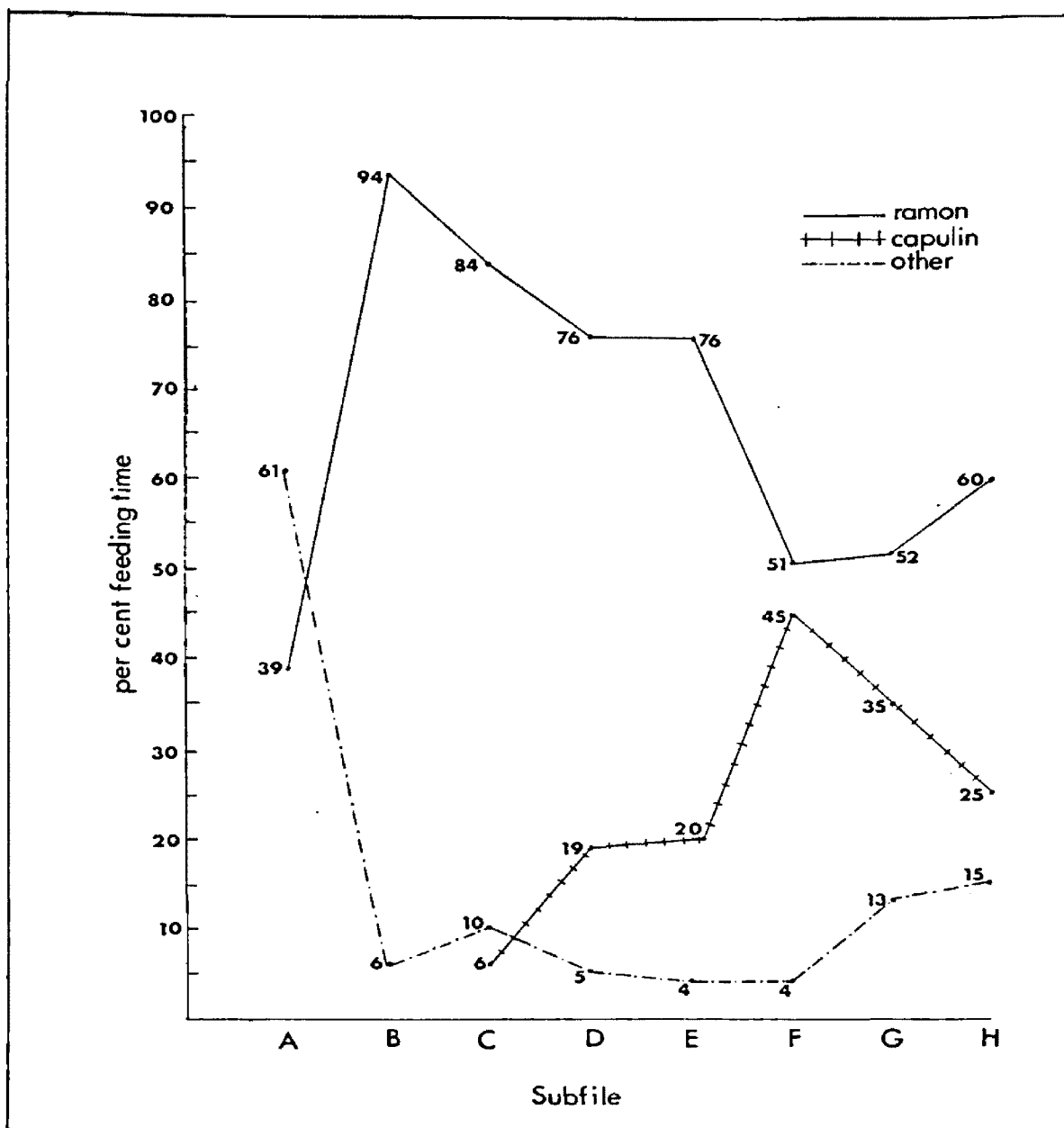


Fig.8 Per cent species used / 7-day subfile

behavioral strategies employed by howlers in order to deal with their low quality diet is to use well developed travel routes to areas of "known" resource availability. The efficient use of low-density species would tend to support this assumption.

The high reliance upon ramon in the diet is easier to explain since it is the highest density tree species at Tikal, forty per ha² (Cant 1977). It is the fruit from this tree species that makes up the majority of immature fruit consumed at Tikal. Ramon seems to be an unusually "edible" tree species. The immature fruit and seeds especially seem to be consumed in large quantities by several species of mammals at Tikal. The seeds are consumed by humans after being ground into a meal, and the foliage of ramon is cut for livestock when other food is not available. Unfortunately, no analysis of the contents of ramon has been made (i.e. protein, secondary compounds). It is logical to assume from the high rate of ramon consumption that the immature fruit and seeds are fairly low in secondary compounds. Ramon seeds may even resemble ripe fruit in terms of non-toxicity and edibility.

Finally, in terms of species utilization I would like to discuss the use of the thirteen other species in the diet. If Glander is correct in suggesting that plant secondary compounds figure prominently in the selection of dietary items, the continuous inclusion of species other than the main food source may be explained within this context.

Essentially two strategies are available to herbivores that have to deal with secondary compounds:

1. Be a specialist and reduce the number of different secondary compounds with which your system has to deal.

2. Be a generalist, and avoid ingesting too much of any single secondary compound (Glander 1978).

If an animal is a generalist herbivore, it is necessary to maintain the ability to detoxify compounds from many different species. Essentially, an animal using a wide resource base needs to keep its system desensitized to the presence of many toxic substances. Figure 8 shows that even during periods when one species represented 94% of the diet, subfile B, a few other species were being utilized. As stated previously, the ability of an animal to deal with secondary compounds depends in part upon its past experience with the substance (Janzen 1978). The limited use of several different species in addition to the predominant food species may be explained as a behavior that aids in the build-up and continuation of resistance to secondary compounds.

Ranging Behavior

Previous researchers working with howlers have noticed a pattern described by Carpenter (1935) as several days of limited travel, followed by unusually long and fairly continuous marches. Milton describes a similar pattern, namely the use of core areas. A howler group may have a small area through which they forage for several days. After a period of time, the group moves--Carpenter's "long march"--and settles once again to begin foraging in a new core area.

The pattern of core area utilization was observed during the summer of 1978 at Tikal. The total home range for howlers during the fifty-six days of the study was forty-seven hectares. Daily distances varied from between approximately one hundred meters to more than five hundred meters. Within the boundaries of the central ruins area

there appeared to be several areas of high feeding density that formed a rough triangle. Between the points of the triangle formed by these core areas, there appeared to be well-developed travel paths along which the animals foraged.

In order to represent this kind of behavior graphically, the position of feeding trees in the howler home range and the total feeding time for each tree, were used with the computer graphics program, ASPEX, to produce a map of high density feeding areas. (Every plotted tree was given X and Y coordinates. The value given to each point was the total time spent feeding in the tree represented by the point.) The end result of this program appears in Figure 9.

Figure 9 represents the howler home range as viewed from its northwest corner. (The area included in this topographic map corresponds to the area of the central ruins in Figure 2.) This perspective (170 degrees) was used in the mapping program because it resulted in the best unobstructed view of the total area. There are three distinct peaks in Figure 9 that have been labeled A, B, and C. These peaks represent areas that had a high value in terms of feeding time. The flat areas on this map represent parts of the forest in which howlers did not feed. The area within the triangle formed by peaks A, B, and C contains a number of small "hills" that represent areas that were used as the animals traveled from one core area to another.

The area of high relief labeled A is interesting because it indicates an extensive use area. That is, many trees spread out over a fairly large area were intensively used. On the other hand, area B was not as extensive in overall surface area, but contained a few trees that were fed in for long periods of time. Both A and B may be

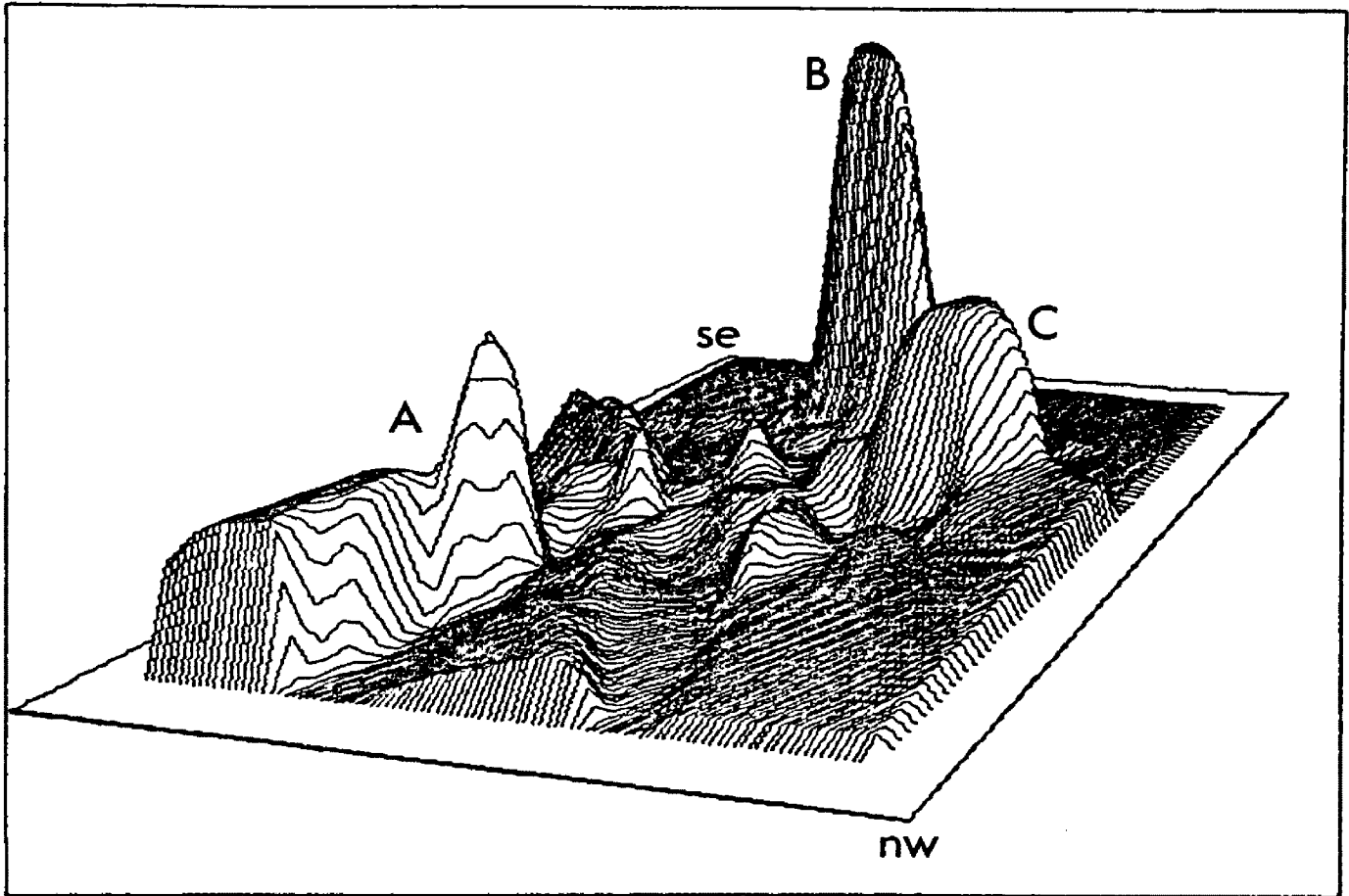


Fig.9 Map of howler home range indicating use areas

considered core areas, in spite of the dimensional differences between the two. Area C, also a core area, is not as extensive in surface area as A, nor does it contain individual feeding values as great as in area B. The existence of core areas to which howlers repeatedly return, in addition to well-defined travel routes, indicates that howlers are adept at locating "quality" foods when available.

The same kind of dimensional differences found in core areas will make the determination of patch size difficult. Theoretically, one could find two trees of different species, different sizes, different shapes and different food types that represent equivalent feeding patches in terms of the energy available to the consumer. Determining an adequate measure of patch size is going to require species-specific data for both the animal predator and the plant species being consumed.

CHAPTER VI

SUMMARY AND CONCLUSION

By analyzing the different type of plant parts consumed over a fifty-six-day period, by seven-day increments, and individual days, it was found that howler monkeys at Tikal, like howlers in other areas, exhibit a generalist herbivore adaptation. That is, their diet includes large quantities of foods that are low in quality. At Tikal this food type is immature fruit, whereas young leaves form the staple of the howler diet in other areas (Milton 1978, Glander 1978). A possible difference between the foraging strategy of howlers at Tikal and howlers in other areas may result from differences in the temporal and spatial distribution of immature fruit as opposed to immature leaves.

When the dietary data were broken down into daily and weekly increments for analysis, howlers exhibit short-term patterns of exploitation that have not been discussed by previous researchers. The almost exclusive use of foods high in ready energy during periods of peak availability suggests that howlers are optimizing their caloric intake at the expense of other bodily requirements (namely protein). The results from this study do not indicate whether this is the major criterion for the selection of dietary items. However, as a short-term strategy, energy hoarding seems to be one of the behavioral strategies used by howlers to prepare for periods when only energy-poor foods are available.

In addition to eating high quality foods whenever possible, howlers conserve energy by utilizing hard to digest foods late in the day. At this time activity is reduced and energy is available for the assimilation of nutrients from fibrous materials. Foods higher in ready energy are more often included in the first feeding bout of the day presumably to begin the day's activities with a "dose" of energy and avoid depleting energy reserves.

Howlers at Tikal depend heavily upon the fruit, seeds, and leaves of one tree species, ramon (Brosimum alicastrum). Another tree figuring prominently in the diet is capulin. The pattern of limited dependence upon one or a few tree species for short periods is not necessarily strange for generalist herbivores. It is often the case that all individuals of a tree species will produce new leaves or bear fruit during the same period of time. (This is true of ramon and capulin.) If an animal is taking maximum advantage of high quality foods, then dependence upon the species of tree producing such food can be expected.

The fact that howlers do not entirely exclude other species from their diet may indicate that, at times, instead of relying predominantly on ramon and capulin, they must depend upon a variety of foods. The ability to assimilate nutrients from various food species depends in part upon maintaining a resistance to secondary compounds contained in the food. Thus continual sampling of a variety of food types may enable howlers to utilize these species when high quality foods are not available.

From the analysis of the data on ranging, it appears that within the howler home range there are several core areas of resource use to

which the study group repeatedly returned. Well-developed travel paths connect these core areas. It is likely that core areas change according to the season and food availability. "Familiarity" with an area may be another behavioral strategy that howlers use to save energy in terms of search costs.

In general, it can be said that howlers are utilizing a foraging strategy that minimizes energy expenditure and maximizes energy intake.

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APPENDIX I

Subfile A includes the days of 6/25 to 7/02

Subfile B includes the days of 7/21 to 7/27

Subfile C includes the days of 7/28 to 8/03

Subfile D includes the days of 8/04 to 8/11

Subfile E includes the days of 8/12 to 8/18

Subfile F includes the days of 8/19 to 8/25

Subfile G includes the days of 8/26 to 9/01

Subfile H includes the days of 9/02 to 9/08

APPENDIX II

SPECIES AND PLANT PART UTILIZED

<u>Common Name</u>	<u>Taxonomic Designation</u>	<u>Part Utilized</u>
<u>Ramon</u>	<u>Brosimum alicastrum</u>	Immature, mature fruit seeds, immature and mature leaves
<u>Capulin</u>	unknown	Immature and mature fruit, immature leaves
Copo fig	<u>Ficus</u> species	Mature fruit, immature mature leaves
Philodendron	unknown	Mature leaves
<u>Chakah</u>	<u>Bursera simarouba</u>	Immature fruit, mature and immature leaves
<u>Chico Zapote</u>	<u>Archas zapota</u>	Immature and mature fruit, immature and mature leaves
Rough-leaf strangler	unknown	Mature leaves
<u>Tzol</u>	<u>Cupania prisca</u>	Mature fruit
<u>Copal</u>	<u>Protium copal</u>	Mature fruit
<u>Yaxnic</u>	<u>Vitex guameri</u>	Immature leaves
<u>Malario blanco</u>	<u>Aspidosperma megalocarpon</u>	Immature leaves
<u>Zapatillo hembra</u>	unknown	Mature leaves
Unidentified species	unknown	Immature leaves
Unidentified species	unknown	Mature leaves