University of Montana

ScholarWorks at University of Montana

Graduate Student Theses, Dissertations, & Professional Papers

Graduate School

1982

Activity budgets of Guatemalan howler monkeys (Alouatta pigra Lawrence)

Teri L. Cunningham
The University of Montana

Recommended Citation

Cunningham, Teri L., "Activity budgets of Guatemalan howler monkeys (Alouatta pigra Lawrence)" (1982). *Graduate Student Theses, Dissertations, & Professional Papers*. 7255.
https://scholarworks.umt.edu/etd/7255

ACTIVITY BUDGETS OF GUATEMALAN HOWLER MONKEYS

(<u>Alouatta</u> <u>pigra</u> Lawrence)

by

Teri L. Cunningham

B.A., Colorado State University, 1975

Presented in partial fulfillment of the requirements

for the degree of

Master of Arts

UNIVERSITY OF MONTANA

1982

Approved by:

Chairman, Board of Examiners

Dean, Graduate School

_12-13-82_
Date

UMI Number: EP38056

UMI

Dissertation Publishing

ProQuest

Cunningham, Teri L., M.A., December 1982   Anthropology

Activity Budgets of Guatemalan Howler Monkeys (Alouatta pigra
Lawrence) (77 pp.)

Director: Dr. Charline G. Smith

   The primary objective of this study was to identify differences
in adaptive strategies between males and females as they were re-
flected in activity budgets. Fifty-six days of research were con-
ducted on a small group of free-ranging howler monkeys (Alouatta
pigra Lawrence) at Tikal National Park, Guatemala, C.A. during the
summer of 1978. Approximately 500 hours of observation were ac-
cumulated utilizing focal animal, scan and ad-lib sampling tech-
niques.
   An analysis of the activity budgets indicated the howlers divide
93 percent of their time between three major activities; resting,
feeding and travel. Howlers at Tikal are committed to a general
strategy of energy conservation. This is reflected in morphological
and behavioral features. Furthermore, activities were participated
in differentially by age/sex categories. The adult female fed
significantly more than the adult male. The female was focusing her
energy demands on reproduction, while the male was primarily concerned
with defensive behaviors.

ACKNOWLEDGEMENTS

I am grateful to several persons who helped make this thesis possible.

I would like to thank the members of my thesis committee, Dr. Charline G. Smith, Dr. Dee C. Taylor, and Dr. David Strobel for their patience and willingness to work within the time constraints I placed upon them.

Thanks to Dr. Smith and Dr. Taylor for editing this manuscript. Special thanks to Dr. Smith for her gracious hospitality during my visits to Missoula.

Dr. John G.H. Cant provided me with the opportunity to conduct primate research in Guatemala. His assistance and encouragement in all phases of this research are greatly appreciated. Thanks to John and his wife, Ann Finlinson, for their friendship and company in Guatemala. Thanks to John for providing me with computer access in Colorado.

Special thanks to Janene Caywood, my field partner, for her company and friendship throughout our stay in Guatemala.

I am deeply appreciative of my parents, Don and Alice Cunningham for their neverending support, generosity, and belief in me throughout all phases of my life.

Finally, I would like to thank my friend and husband, Thomas R. Lincoln, for his sense of humor, patience and love throughout my struggles with this research and life in general.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Sociobiology

The last decade of research on the evolution of animal behavior has seen a shift from emphasis on the group to an emphasis on the individual as the unit of natural selection. A common misconception has been that behavioral traits evolve for the benefit of the social group, of the population, or even of the species. Natural selective forces, however, operate on individuals through differential reproduction. Insofar as one can measure benefit or cost at the level of the social group, such outcomes are byproducts of selection maximizing inclusive fitness. Inclusive fitness (Hamilton 1974) comprises individual fitness in the usual sense of re-productive success plus the benefit occurring to copies of an individual's genes that are possessed by close relations. Selection producing behavior that benefits genes in relatives is termed kin selection.

The overall theoretical approach of focusing on indivi-dual's behavior and how it affects inclusive fitness con-stitues the core of "sociobiology" (Wilson 1975). The basic question of a sociobiological analysis is: "How does any particular behavior affect the reproductive success (RS) of

1

the performer and the RS of the performer's genetic relatives?" R.L. Trivers' (1972) elucidation of sexual selection, and the differences between males and females in methods of achieving RS, has proved particularly useful in the evolutionary analysis of behavior.

In sociobiology, analysis of behavior is made in ultimate as opposed to proximate terms. A proximate analysis is concerned with the immediate factors responsible for a particular response, e.g. internal physiology, previous experience or factors in the environment. An ultimate analysis is concerned with the evolutionary factors that bestow selective advantage upon proximate variables. Interpreting a behavior in ultimate terms involves identifying the adaptive significance of that behavior.

Animals are observed to divide their time between activities which allow them to satisfy their basic needs of food, movement, rest and reproduction. The amount of time and/or energy devoted by animals to each of these activities, the time or energy "budget", varies greatly from one taxon to another. Time budgets also vary within a species according to age and sex. Orians (1961) and Schoener (1971) established that the analysis of time budgets is a legitimate approach to the study of behavioral strategies employed by animals.

Objective

The primary aim of this study was to identify the differences in adaptive strategies between males and females

in a small group of free-ranging Guatemalan howler monkeys, Alouatta pigra Lawrence. The research was conducted at Tikal National Park, Guatemala, C.A. during the summer of 1978. Although an abundance of literature is available on primates, including howlers, analyses utilizing a sociobiological perspective are only recently increasing.

Suitability of Study Site and Animal

The vast majority of Alouatta research has been conducted on one species of howler, Alouatta palliata, and from one location, Barro Colorado Island (BCI), Panama. Because of these factors, relatively little is known about other howler species and different howler environments. Tikal afforded an opportunity to examine both an alternative species and environment, and to establish a basis for comparison with studies in other areas.

Studying arboreal animals in a dense forest environment can present many problems to a potential observer. They may include, among others: (1) difficulty in finding the animals; (2) once found, keeping all or even a few of the study animals in view; (3) habituating the animals to the observer's presence; and (4) maneuvering on the ground while following subjects that can travel more quickly through the trees.

Studying howler monkeys at Tikal National Park helped reduce the limitations that some of these factors can impose upon data retrieval. The park provided an area where the animals were protected from hunting, artificial feeding or moles-

tation of any kind. Numerous park trails facilitated movement on the ground and the presence of park personnel and tourists over the years had accustomed the local population of monkeys to humans in their environment. On rare and delightful occasions, vantage points provided by some of the ruins offered excellent views of the animals without the aid of binoculars.

Alouatta receive their vernacular name "howling monkeys" justifiably, by virtue of their well known and voluminous vocalizations. These sounds are among the loudest produced by any animal in the tropical American forests and may resound a kilometer or more. When engaged in such vocalizations, the animals are easily loacted. Howler monkeys typically locomote in slow linear progressions from tree to tree and maintain a relatively condensed group structure during travel. These slow movements and general group cohesiveness make them among the more easily followed arboreal primates.

Population density for howlers at Tikal was low compared to groups in other areas, and they shared their environment with only one other primate species, the spider monkey, Ateles geoffroyi. These factors diminished the amount of inter- and intraspecific contact, thereby placing fewer restrictions on the howlers' utilization of their environment and minimizing displacement of one group by another. This also helped reduce frequent and often confusing distractions to the observer.

Alouatta groups at Tikal were also reportedly small by comparison to group sizes in other areas. Other researchers

in the Tikal area (Coelho et al. 1976, Schlichte 1978, Cant 1977, Bolin 1981) reported group sizes ranging from four to seven animals. The group observed for this study contained five individuals. Since the primary concern of this paper was to elucidate behavioral differences between individuals, this small group size aided in maximizing the amount of retreivable data per individual.

Considering all the factors discussed above, studying howlers at Tikal National Park presented a particularly favorable atmosphere for the investigation of behavior in an arboreal primate.

Classification and Overview

Howler monkeys belong to the order Primates, suborder Anthropoidea, family Cebidae and genus Alouatta. They are among the largest and most conspicuous of the New World primates. Howlers exhibit moderate sexual dimorphism; adult males weigh between seven and nine kilograms with the adult females averaging approximately 80% of the adult male weight. Howlers are highly arboreal, preferring middle and upper levels of the forest canopy. Only very rarely, under unusual or extreme circumstances, are thay seen to travel on the ground. They locomote quadrupedally and use their prehensile tails in travel for extra support.

Alouatta are widely distributed, ranging from the coastal forests of Mexico, through Central America and as far south as the northern parts of Argentina. They inhabit a variety of

forests types including lowland evergreen, highland, swamp, and riparian. At least five species are recognized in the literature. The most geographically widespread and the most commonly studied of these is the mantled howler, _Alouatta palliata_, synonymously referred to as _A. villosa_. This species ranges from Mexico to as far south as the equator and was the subject on Barro Colorado Island, Panama of the pioneering investigation by C.R. Carpenter (1934, 1965). Additional information on BCI has been added by numerous others: Collias and Southwick (1952), Altmann (1959), Berstein (1964), Hladik and Hladik (1969), Chivers (1969), Richard (1970), Hladik et al. (1971), Mittermeier (1973), Mendel (1976), Smith (1977), Milton (1975, 1978-1981), Jones (1979, 1980), Otis (1981), Froehlich (1981) and Young (1981). Other populations fo the same species have been studied in Costa Rica by Heltne et al. (1976), Freese (1976), Glander (1975, 1977, 1978, 1980) and in southwestern Panama by Baldwin and Baldwin (1972). Several subspecies of _A. palliata_ have been indentified.

Studies began on _A. seniculus_, the "red" howler and _A. caraya_ in the 1960's. _A. seniculus_ has been observed in Venezuela by Neville (1972a, 1972b) and Braza et al. (1981), in Colombia by Klein and Klein (1975) and Defler (1981), in Surinam by Mittermeier and Roosmalen (1981) and in the Upper Amazon Basin by Izawa (1975, 1976). _A. caraya_ has been studied in Argentina by Pope (1966) and Malinow (1968). Little is known of _A. guariba_ and _A. belzebul_ (Baldwin et al. 1977).

The last species to be discussed is _Alouatta pigra_ Law-

rence, the subject species of this paper. In addition to this study, A. pigra has been observed by Coelho et al. (1976, 1977), Schlichte (1978) and Cant (1977) at Tikal and by Bolin (1981) in Belize. Except for Cant, whose emphasis was on the sympatric species *Ateles geoffroyi*, the studies were of short duration, four months or less.

Some questions have been raised as to the exact classification of *Alouatta* in the Peten region. Until Smith (1970), Lawrence (1933) had published the only taxonomic review of howlers in Middle America. The monkeys living at Tikal conform to Lawrence's description of A. *palliata pigra*. Smith (1970) believed that this subspecies of A. *palliata* should be given full taxonomic status as a separate species, A. *pigra*.

Howler monkeys are generally considered to be allopatric (nonoverlapping), but Smith discovered two species, A. *pigra* and A. *palliata mexicana* occurring sympatrically in Tobasco, Mexico. He determined that A. *pigra*, unlike A. *palliata mexicana*, was not a subspecies of A. *palliata* based on:
1) differences in cranial and external size
2) differences in the shape of the skull
3) characteristics of the upper molar dentition
4) color and texture of the pelage (1970:361)
Most observable of these in the field was the color of the pelage. Howlers at Tikal exhibited coat hair that was uniformly and entirely black, except for the anogenital region. This contrasts with A. *palliata* that exhibit a characteristic blending of brown or yellowish mantle that extends around the heavy cape on their backs. Furthermore, accurate sexing of

individuals was possible because the testes, in even small male infants, were fully descended and conspicuously white in color. The female gentalia, although similar in color, were clearly distinguishable. This is also in contrast to studies of _A. palliata_ that report difficulty in sexing immature animals (Carpenter 1965).

There also seems to be some ecological segregation of _pigra_ and adjacent populations of _palliata_. _Pigra_ appears to inhabit relatively extensive and undisturbed areas of mesic tropical forest, whereas "_palliata_ apparently thrives in less extensive, subclimax or secondary forest" (Smith 1970:365). The former environment is found in the Peten region, the latter in areas such as BCI and much of Central America inhabited by typical _palliata_.

In conclusion, conditions at Tikal support evidence that the howler monkeys there are a species distinct from _A. palliata_. For the purposes of this paper, they will be considered as belonging to the separate species _Alouatta pigra_ Lawrence.

CHAPTER II

ENVIRONMENT

Study Site

The area of investigation was at Tikal National Park in the northcentral part of El Peten, the lowland area comprising the northcentral section of Guatemala (Figure 1). The park is a 24 kilometer square and was established to protect a major Maya archaeological site which has been, beginning in the 1950's, partially excavated and restored by the Guatemalan government and the University of Pennsylvania. The topography of the site and location of the ruins are well documented and available on detailed maps.

Tikal, 190 air miles from Guatemala City, has become a well-known tourist attraction in Guatemala. Access is possible by unimproved roads passable most of the year. Preferable transportation is provided by air service to an airstrip located within a few kilometers of the central ruins. The elevation of the park ranges from 190 to 350 meters, averaging about 250 m (Cant 1977). The central ruins, consisting of major palaces and temples, are situated on a small ridge system (225 m) and surrounded by "bajos" or flat broad areas. A porous limestone substrate underlying Tikal, and most of the Peten, prevents the formation of streams or permanent water

9
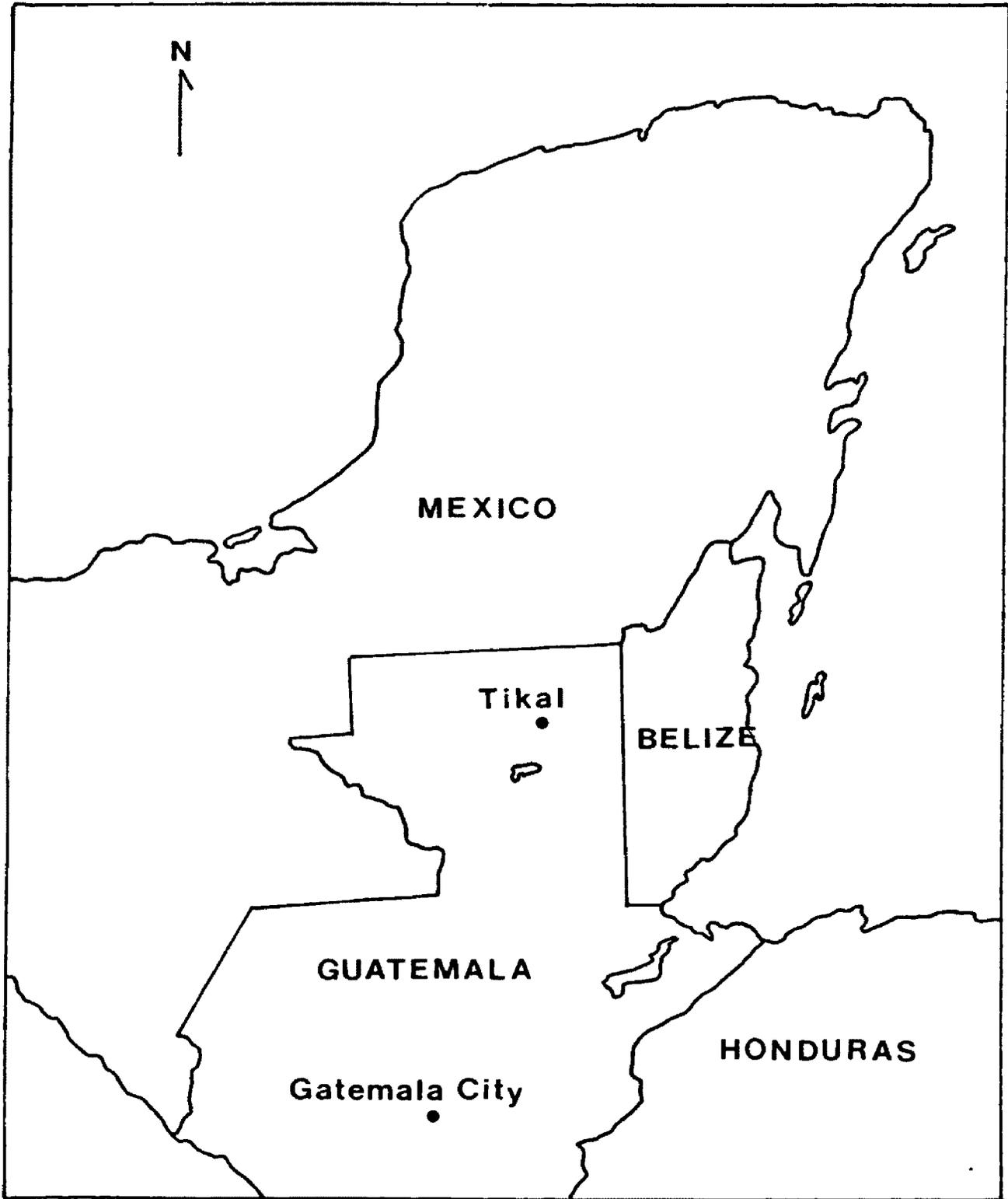
Figure 1   Map of Guatemala showing location of Tikal
           (after Cant 1977)

sources (Coe 1967). The bajos, formed by the conversion of eroded limestone to clays, provide some relief from this water shortage, collecting run-off during the rainy season. The ancient Maya took advantage of this natural condition by digging catchment reservoirs which remain today as an important water source for animals and humans alike.

Climate

Although climatic data for Tikal are incomplete, an adequate summary can be provided. Coelho et al. (1976), utilizing data collected by Smithe (1966) between 1959 and 1963, indicated an average yearly rainfall of 146.0 cm. Cant (1977), using precipitation data complete for six years (1960-1962 and 1966-1968) calculated an annual mean of 137.6 cm. Distinct wet and dry seasons are observable. Calculating from Cant's data (1977:27), the average monthly rainfall for the dry season, December to April, is 4.8 cm. The wet season, May through November, averages 16.1 cm per month.

Tikal's mean temperature varies little throughout the year, with "daily mean minimum and maximum temperatures of 20.9° and 29.0° C for all months of the year combined" (Cant 1977:29). Temperature extremes often occur during the dry months of March and April, but warmest mean temperatures predominate during the rainy season. Many trees flower during the dry season and some defoliation may occur toward the end of the season. May, the beginning of the rainy season, is also the time of onset for production of new leaves and fruit in

many plant species.

Vegetation

The vegetation of Tikal conforms to the general typology
of northern Peten and has been described by Lundel (1934, 1937)
as a quasi-rainforest characterized by the following: (1) an
annual rainfall between 100 and 200 cm per year, (2) prolonged
dry season, (3) a thick, semideciduous forest canopy, and (4)
between three and five stories of vegetation. The descriptive
term "quasi-rainforest" has more recently been replaced by
"tropical dry forest" by Puleston (1973) and Cant (1977) fol-
lowing a classification system for vegetation zones based on
evapotranspiration developed by Holdridge (1967).

The forest at Tikal can be divided into three major and
distinct plant communities: (1) upland forest, (2) escobal,
and (3) tintal. The first of these, upland forest, is charac-
terized by well drained areas on ridges and hills and is the
predominant (55%) vegetation zone at Tikal. Escobal (29%),
named for the abundance of a small armed palm Cryosophila ar-
gentea, and tintal (16%), named for a hardwood tree Haematoxy-
lum campechianum, are found in lower, less well-drained areas
such as bajos (Cant 1977). This field study was conducted in
and around the central ruins (Fig. 2) which are characterized
by upland forest.

Various individuals have described the frequency of
plant species at Tikal. Coelho et al. (1976) used data gath-
ered by timber surveys to list the one hundred most common

Figure 2   Central ruins study site at Tikal, squares are
            500m/side

tree species and their frequencies for the Peten region. Past agricultural practices of the Maya have been found to contribute to the differential distribution of particular plant species. Coelho et al. (1976) found zapote, Achras zapota (6%), and ramon, Brosimum alicastrum (9.4%), two trees extensively exploited by the Maya, to be present in large numbers throughout the Peten.

Schlichte's census (1978) at Tikal found that the 10 most common tree species made up 78% of the 301 trees he counted. Ramon was found to be the most common, preferring upland areas and growing mainly near rocks or ruins.

Cant's survey (1977) of 62 tree species at Tikal found the first 10 most common tree species to comprise 70% of the total and the first three to account for 32%. Again, ramon was found to predominate; however, Cant suggested that frequency alone may not indicate how important trees are (1977). He examined the basal area of trees and found that ramon accounted for 20.8% of the total basal area compared with only 14.3% for its density. The first 10 species comprised 92%, and the first three 36%, of the total basal area.

In addition to ancient horticulture (Lundell 1937), ramon's abundance has also been attributed to its apparent affinity for limestone-enriched soil (Coelho et al. 1976, Cant 1977). Tikal's ruins and naturally occurring limestone deposits provide a particularly suitable environment for Brosimum proliferation.

In general, Tikal's vegetation can be characterized by

by the predominance of a relatively small number of tree species. Of particular interest is ramon, _Brosimum_ _alicastrum_, which provides a major food source for many of Tikal's animals, including the primates.

Animals

Tikal is not only a famous archaeological site, but it is also a government-protected animal reserve. Hunting, artificial feeding, restricting or molesting the animals in any way is prohibited. Smithe (1966) and Smithe and Paynter (1963) have described the avifauna of Tikal; of the 285 species recorded, 209 are resident (Coe 1967). In addition to the two primate species, howler monkeys (_Alouatta_ _pigra_) and spider monkeys (_Ateles_ _geoffroyi_), Tikal exhibits a variety of large and small mammals, reptiles and insects. A partial listing of the mammals, taken from Cant (1977), is presented in Appendix I. Of these, five species of feline (ocelot, margay, puma, juguar and yaguaroundi) and the tayra (a large weasel-like mammal) may be predators of the primates. Other mammals that may share the arboreal habitat of the primates include squirrels, several members of the raccoon family, opossum, porcupine, and three-toed anteater.

CHAPTER III

METHODOLOGY

This research was conducted during the rainy season at Tikal from June 21 to September 11, 1978. Two primary investigators were involved in the collection of data, I and a fellow graduate student, Janene Caywood. Periodic assistance was provided in the field by Dr. John Cant and volunteers from his summer Earthwatch project. Their help in providing observational assistance and keeping track of our howler group when we were unable to do so was of great benefit to this research.

The field methods used resulted from the different objectives of both primary investigators. Because circumstances required that we collect data for one another, data from two types of variable, ecological and behavioral, were collected simultaneously. Ms. Caywood's primary focus was the elucidation of foraging strategies as they were reflected in ecological variables, especially feeding behavior and dietary choice. The primary emphasis of this paper is social behaviors and time budgets of activity variables that illustrate differences between male and female adaptive strategies.

The initial weeks of the study were spent learning the

16

topography of Tikal, identifying plant species and establishing a howler group. Only two groups were contacted in the central ruins area throughout the duration of the study. They were designated according to their proximity to the central ruins as the "North" and "South" groups. Both groups consisted of five animals and were "monogamously" organized. The North gourp was comprised of one adult male, one adult female, and three juvenile males. The South group reflected a greater differene in age/sex categories; one adult male, one adult female, a juvenile male, a juvenile female, and an infant. The South group was chosen as the study group by reason of its greater age/sex diversity. The compositions of both groups remained the same over the three month period.

Each field day was divided into two shifts, morning and afternoon. Observations began at approximately 0600. Since howlers are very diurnal animals, movement before this time (i.e. dawn) was rare. At noon, a time when the animals were frequently inactive, the observer working the morning shift was relieved by the second investigator at a predesignated location. She would then follow the animals until they settled for the night, sometime between 1630 and 1800 hours. This investigator would then take the next morning shift knowing best where she had left the animals. The howlers were seldom found anywhere but where they had last been seen. If the animals were occupying an unfamilar section of the forest, a path was flagged in and/or out from a known point to prevent getting lost and for easy relocation the following day.

Since observations required the use of binoculars, initial attempts were made to record data on tape recorders, thus freeing the observer's hands. However, rain and high humidity frequently rendered the machines inoperable and this proved to be an unreliable procedure. Subsequently, data were recorded into field notebooks. Definitions of the variables were agreed upon by both investigators prior to the onset of data collection. J. Altmann (1974) provided an excellent review of sampling methodology. Among those discussed were three sampling methods used during this investigation. They included focal-animal, scan, and ad-lib sampling.

Focal Animal Sampling

Focal animal sampling (FAS) was used to collect foraging data for primary use by Ms. Caywood. FAS is defined by J. 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 (1974:242).

The ideal field conditions would provide collection of FAS on all members of the study gorup. However, this would require simultaneous observations of each individual over a continuous and indefinite time period and would prove an impossible task for one observer. A single focal animal was therefore required. The obvious candidates were the adult

male and adult female. C.C. Smith (1977) determined from his study on BCI that adult females fed for a considerably longer time period than adult males. Given that feeding behavior is of primary concern in elucidating foraging strategies, the adult female was chosen as the foacl animal. Assuming that howlers behave more or less synchronously as a group, if the adult female feeds the longest, then she would have the greatest potential impact on the foraging activities of the group as a whole.

Foraging variables were recorded for 398 feeding bouts over fifty-six days of focal animal sampling. The variables recorded for each bout included:

1. Bout Start Time - Feeding bouts began when the adult female's hand or mouth came into contact with a food resource or when she was actively searching for food. The bout continued as long as there was no pause greater than three minutes or until she moved from the tree.

2. Bout Stop Time - Feeding bouts stopped when the animal ceased feeding, had a pause greater than three minutes, or changed feeding trees.

3. Plant species being utilized.

4. Plant part being utilized, e.g. fruit, stems leaves.

5. Maturity of plant part utilized, i.e. mature or immature.

In addition, the diameter at breast height (DBH) was measured for each tree the adult female fed in and the trees were numbered sequentially from the onset of the study. When possi-

ble, distances between feeding trees were measured by pacing. The numbered trees were then plotted on detailed topographic maps to aid in determination of daily, weekly, and seasonal ranging patterns.

Scan Sampling

Simultaneous with focal animal sampling, scan sampling was used to determine the activity budgets of each of the five group members. Scan sampling, also referred to as instantaneous sampling, was defined by J. Altmann (1974:258) 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.

Scans were initially set at ten minute intervals, but were subsequently increased to five minute intervals in order to maximize data retrieval. The activity variables recorded by scan sampling included:

1. Feeding - Feeding occurred when any animal was engaged in within-tree foraging or satisfied any of the conditions defined under FAS feeding bouts, e.g. active food search or when hand or mouth was in contact with a food resource.

2. Travel - Travel included "progressive" or directional movement with at least two tree-to-tree transitions and no pause greater than three minutes.

3. Inactive - Inactive occurred during stationary activities such as rest, sleep, auto-play, auto-groom and postural shifts. "Inactive" could not be included within a three minute pause during feeding or travel.

4.   Move - Move applied to movement between loci of a single tree or movement between two trees which did not include shifting between loci in a feeding bout and not travel.

5.   Allogrooming - Allogrooming consisted of social grooming between two or more individuals.

6.   Elimination - Urination and/or defecation.

7.   Roar - "Typical" howler vocalizations made by the adult male, adult female or juveniles in response to or directed at another group or perceived threatening situation.

8.   Sexual Activity - Included sexual solicitation by males or females and any occurrences of copulation.

9.   Missing - When any one or number of members of the group were not observable at the time of the scan.

For a period of 46 almost-continuous days from July 24 to September 8, a total of 500 hours of scan sampling were recorded. If the number of 5 and 10 minute scan instants (5370) is multiplied by the number of group members (5), 26,850 individual states were potentially observable. From this potential, only 8% comprised missing values. Of this value, the proportion for each group member was as follows:

         Adult male........16%
         Adult female......15%
         Juvenile female...20%
         Juvenile male.....22%
         Infant............27%
                           ‾‾‾‾‾
                           100% missing values

These proportions might be expected inasmuch as the adults, by virtue of their size and relative inactivity compared to

the juveniles (Table 5, p. 52) were the most discernable members of the group. Furthermore, with the adult female also being the focal animal, some observer bias may have existed for insuring that she was detectable at any given scan instant.

Ad-Lib Sampling

Much of an observer's field notes may be composed of what J. Altmann (9174) termed "typical field notes" or "ad-lib sampling". Altmann explained this type 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 or a group in which behaviors, individuals and often the times for behavior sessions are chosen on an ad libitum basis (1974:235).

Ad-lib sampling was used to record unusual or infrequent behaviors such as grooming, sexual activity, inter- and intraspecific interactions and any other behaviors that would not be adequately qualified by scan sampling alone. For these occurrences, the entire behavioral "bout" was descriptively recorded. Environmental and situational variables were recorded as well during the course of the day. These would include factors such as changes in the weather, condition of the foliage (wet or dry), planes passing overhead and general states of the animal's health (e.g. botfly infestations).

Recording all the variables available by each of the sampling methods in the field could prove cumbersone, at best. Whenever possible, the variables were numerically coded or abbreviated. Sample entries from the field notebooks might appear as follows:

	AM	AF	JM	JF	I
13:05	2	2	4	4	9
13:10	2	4	5	5	5

13:12 AF Ram#138 imft

13:13 plane overhead - no resp

	AM	AF	JM	JF	I
13:15	2	1	5	5	5

Decoded, this means that at instant 13:05 (scan sampling) the adult male and female were inactive, the juvenile male and female were moving and the infant was missing from view. During the next instant, 13:10, the adult male was still inactive, the adult female was moving and the juveniles and infant were engaged in social play. At 13:12 the adult female (FAS) began a feeding bout on immature fruit in Ramon tree number 138. At 13:13 a plane passed overhead (ad-lib) which illicited no responese from any of the animals. The final scan, 13:15, still shows the adult male inactive, the adult female continues to feed, while the juveniles and infant continue in social play.

Once out of the field, the variables were further encoded to permint computer manipulations of the data. The data for this paper were manipulated on the CDC 6400 at the University of Colorado.

CHAPTER IV

HOWLER DEMOGRAPHY AND RESOURCE UTILIZATION

Population Density

Population densities of howler monkeys vary widely with study area and year. An examination of Table 1 shows the howler population at Tikal's central ruins area to be low compared to values reported for howlers in other habitats. Although this investigation is in general agreement with Coelho's et al's (1976) density estimates for 1973, i.e. five animals per km^2, the average group size had dropped form 6.2 to 5.0 members by 1978. Archaeologists working in the Tikal region have consistenely reported small groupings of howlers, usually between four and seven animals, as far back as the mid 1950's.

Logically, questions are generated as to (1) what limits primate populations in general, and (2) more specifically, why are howler groups small and density low at Tikal when compared to other howler studies.

The first of these questions has become a pertinent issue among primate ecologists. If the assumption underlying most competition paradigms is that populations live at the carrying capacity of their habitat, the disparity in the density values presented in Table 1 cannot be attributed to spe-

24

TABLE 1

COMPARISON OF HOWLER POPULATION DENSITY IN DIFFERENT HABITATS

Observer	Year	Group Avg	Density Animal/km^2	Species	Location
Carpenter	1932	17.3	31.0	A. palliata	BCI, Panama
Collias	1951	8.0	15.0	A. palliata	BCI, Panama
Carpenter	1959	19.0	52.0	A. palliata	BCI, Panama
Chivers	1967	12.8	57.0	A. palliata	BCI, Panama
Pope	1964	7.9	25.0	A. caraya	Argentina
Klein	1967	4.3	11.5	A. seniculus	Colombia
Neville	1972	7.5	114.0	A. seniculus	Trinidad
Coelho	1973	6.2	5.0	A. pigra	Tikal, Guatemala
Bolin	1979	4.4	8.1	A. pigra	Belize

cies specificity. Analogous ideas have been developed by Crook (1970), Denham (1971), Schoener (1971), S.A. Altmann (1974) and others to account for dispersion and group size. S.A. Altmann stated (1974:229):

> Primate group sizes appear to be adaptations to two major classes of selective forces: the distribution and denstiy of essential resources, such as food, water and sleeping sites, and patterns of predator attack and anti-predator behavior.

The extent to which these forces impact any particular primate species or population varies considerably, e.g. open country primates may experience ecological stress in obtaining "safe" sleeping sites as opposed to an arboreal species for which there is no shortage of such suitable sites (trees). Setting aside the predation factor, in forest monkeys, then, availability of sleeping sites would set few constraints on group size or dispersion. Subsequently, food resource availability and distribution becomes a major environmental factor.

Coelho et al. (1976, 1977) suggested that primate populations at Tikal were not limited by food resources. This claim is based on estimates of the available calories from a single food source, ripe fruit of the ramon tree (Brosimum alicastrum), and that "a similar population, up to 170 times larger, could be supported by the productivity of ramon fruit alone" (1977:225). The importance of ramon in the howler diet at Tikal is not disputed. Data from this investigation indicate that ramon contributes 76% of the howler diet (Caywood 1980). Coelho et al. (1976) and Schlichte (1978) reported 86% and 87.6% respectively. Coelho et al's figure is combined for

both howler and spider monkeys. However, both Schlichte (1978) and Cant (1980) demonstrated that Coelho et al's calculations for ripe ramon fruit were erroneous.

Schlichte (1978) noted that during the ramon tree fruiting periods, not all ramon trees bear fruit. Additionally, the amount of fruit is not evenly distributed throughout these periods. Schlichte explained (1978:558):

> If at any time of the fruiting period only ten percent of the ramon would bear fruit, then the number of primates supported by the area, for which Coelho gave the value 42,500, would be less by a facotr of 10.

Cant (1980) criticized Coelho et al. for using a single large tree for calculating fruit availability when, in fact, smaller trees obviously produce lesser quantities of fruit than larger trees. Cant observed in his own studies at Tikal that trees below a minimum size did not fruit at all. Coelho et al's estimates for average <u>Brosimum</u> productivity were based on nonrandomly selected seed-fall sites and "Coelho et al. (1977) added the value of mature fruit pulp to the value of a mature seed. Neither spider nor holwer monkeys consume mature seeds at Tikal" (Cant 1980:540).

Assuming reductions in Coelho et al's (1977) estimates for available ramon resources, Tikal may still appear to be dietarily abundant. However, shortages may take the form of deficits in specific nutritional needs rather than in food volume (Crook 1970). It would be misleading to to regard "forests" as uniform environments. Critical elements may be available in foods that occur, not only seasonally, but at

low density. Many trees do not grow in large stands, but
singly or in small patches. Viewed from a primate's perspec-
tive, the home range of a group of monkeys may contain only
a few of any one tree species. Analysis of dietary composi-
tion for howlers in this study indicate the the second most
frequently utilized resource (capulin 22%, Caywood 1980)
occurs, in fact, at a relatively low density (estimated at .5
trees per hectar, Cant 1977).

Plant Secondary Compounds

Conversely, the presence, rather than the absence of
specific elements in plants may operate as a limiting factor.
All plants contain properties that offer some degree of pro-
tection from predation (Freeland & Janzen 1974). One form
may constitute a set of chemical defenses (secondary com-
pounds). Glander (1975, 1977, 1978a, 1978b) has pioneered the
investigation of the role of plant secondary compounds in pri-
mate ecology. His long term study of mantled howling monkeys
(Alouatta palliata Gray) in Costa Rica has substantiated that
"Plant secondary compounds directly and indirectly affect what
is available as food" (Glander 1978b:571). Glander (1977) ob-
served howlers falling from trees after they ingested leaves
from specific trees. Evidence strongly suggested the animals
were naturally poisoned after consuming toxins contained in
the leaves. Chemical analysis of the leaves indicated the pre-
sence of alkaloids.

Although the specific diet of howlers at Tikal has not

been tested for toxins, the potential for their existence or impact cannot be negated. Furthermore, Tikal's vegetation may contain an increased load of secondary compounds. It was noted above (Chapter 2) that the abundance of ramon trees at Tikal has been attributed to its apparent affinity for limestone-enriched soil. Limestone is comprised primarily of calcium carbonate. When calcium carbonate is dissolved in water, a base solution is formed; such solutions are commonly known as alkalies. Certainly, when plants absorb moisture through their root systems, they also assimilate elements that are soluble in the solution. The degree to which ramon and other vegetation at Tiakl are absorbing alkali solutions and storing alkaloids has not been determined. However, Tikal's howler popoulation exhibited behaviors that may be indicative of avoidance to large quantities of plant toxins.

During the summer of 1978, howlers at Tikal were frequently observed to "sample" resource species. During travel, for example, howlers might take bites from leaves or fruit and then quickly spit out the part. Glander (1978b) suggested this feeding behavior may operate as a strategy to test the suitability of a particular plant species or food part.

Howlers at Tiakl exhibited another unusual behavior, drinking from arboreal water sources. Glander is the only other researcher who reports observing this behavior in field studies of howlers. In not one of the numerous studies conducted at BCI, Panama (see overview, Chapter 1) has this behavior been reported. Likewise, howler studies from other

neotropical areas, such as Colombia, Venezuela, Argentina, and the Upper Amazon, report no observations of drinking. Glander (1978a) observed drinking 38 times, all during the wet season (May through November). Drinking was completely absent during the five-month dry season. Glander (1978a) suggested that there is greater "water stress" during the wet season because of the unavailability of succulant new leaves (high moisture, low alkaloid content) and a corresponding increase in consumption of plant secondary compounds contained in mature leaves (low moisture, high alkaloid content). Therefore, additional water intake may be necessary to flush toxins from the primates' bodies.

By comparison, seven drinking bouts were observed at Tikal during the rainy season of 1978. Schlichte (1978) reported no drinking during his dry-season study conducted there in 1974-75. Although this number of observational bouts may seem small in contrast to Glander's (7 vs 38), the number of animals in this study group was smaller (5 vs 13), and they were observed for only three months. Not all group members were seen to drink in either study. The rate and ability to detoxify ingested substances may be specific to the physiology of the individual, as well as the species, and can be influenced by facotrs (e.g. microsomal enzymes and gut flora) involving "the animal's size, age, sex, and sexual state" (Freeland & Janzen 1974:275). The adult male and infant were not observed to drink in this study. Howlers from all age/sex categories were observed to drink in Glander's study (1978a).

He did not, however, analyze his data by characteristics of these categories. The sample size in this study was too small to draw conclusions based on an age/sex category of the individuals exhibiting drinking behavior.

Caywood (1980) determined that the howler diet for this study was comprised of only 8% leaves; of this value, 31% were mature, 69% immature. Since plant secondary compounds are generally considered to concentrate at their highest levels in mature leaves (Morton 1973, McKey 1974), it is surprising that howlers at Tikal were observed to drink at all.

Howler Diet and Physiology

Howlers are viewed as the most folivorous of the New World primates (Eisenberg et al. 1972), taking all their food from the first trophic level and spending approximately 40% to 90% of their daily feeding time consuming leaves (Milton et al. 1979). However, howlers do not exhibit the same type of digestive specializations that their Old World counterparts (colobines and indriids) posses. Milton suggested (1978:537):

> ...that a distinction be made between those primates that have highly specialized gastro-intestinal features associated with leaf-eating, which I call anatomical folivores, and those primates that lack such specializations, which I would call behavioral folivores.

The term "generalist herbivore" (Freeland & Janzen 1974) may be a more appropriate classification for howlers since their diet, as well, is not nearly as specialized as true Old World folivores.

Caywood (1980) provided an extensive analysis of the

dietary composition utilized by Tikal's howlers during the summer of 1978. In Table 2 (1980:30), she gives a breakdown of dietary percentages by plant part utilized during the wet season from Tikal and two other areas, BCI (Smith 1977) and Costa Rica (Glander 1975). A superficial analysis of the high percentage of fruit at Tikal may suggest that howlers there are unusually frugivorous. However, a breakdown of the fruit by its level of maturity reveals that barely half, 52%, was mature fruit. The remaining, 47%, was immature (green) fruit and primarily ramon. Of the ripe fruit utilized, 79%, was capulin, not ramon. This would indicate that howlers at Tikal are not consuming a diet of ripe ramon on a continuous basis.

Food choice by animals can be difficult to explain without some idea of how they digestively process it (Bell 1971). Briefly, leaves can be equated dietarily with protein and fruit with sugar (i.e., ready energy). Howlers may be restricted physiologically to the amount of fruit they can consume without trading off nutritionally. Milton (9181) conducted tests on howler (herbivorous) and spider (frugivorous) monkeys to obtain estimates of food passage rates. Both primate species were fed similar diets and both showed differential rates of food passage. Howlers showed the same rate of passage whether they were consuming a diet high in fruit or high in leaves.

Howlers passed the bulk of a given meal within 30 hours after initial feeding, spider monkeys within eight hours. Subsequently, spider monkeys can process considerably more food

TABLE 2

DIETARY PERCENTAGES BY PLANT PART IN THREE STUDIES*

Food Part	(%) Composition of Diet/Wet Season		
	Tikal 1978	Smith (BCI)	Glander (Costa Rica)
Fruit	72	32	16
Leaves	8	66	57
Seeds	16		
Flowers		3	20
Other	4		6

*(Caywood 1980:30)

per unit time than howlers. Milton (1981) deduced that since (1) the type of fruit (ripe) that howlers eat is low in protein, (2) their gut physiology permits only a slow passage rate, (3) they probably cannot process a sufficient volume of fruit to satisfy their protein requirements and therefore, (4) they must eat some leaves.

By comparison, if spider monkeys, whose digestive strategy appears one of rapid food passage, were put on a primary diet of leaves, they would not be able to meet energy demands. Milton concluded by stating (1981:503):

> Once a particular digestive strategy has evolved, with its attendant morphological, physiological, and behavioral adaptations, diet switching, at least over the short run in evolutionary time, does not seem possible.

Caywood's analysis of the nutritional variables involved in Tikal's howler diet indicated that immature fruit was (1980: 35):

> ...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 <u>Alouatta</u> species in different areas.

Howlers at Tikal may be consuming large quantities of immature fruit because it represents the "best" dietary alternative to leaves that are, to a large degree, inedible. The extent to which immature fruit may contain plant secondary compounds is unknown. The suitable "abundance" of this resource has not been measured at Tikal and therefore, its impact on the howler population cannot be determined. However, it can be established from the preceeding discussion that the

parameters which define "resource abundance" constitute a highly complex set of interacting variables. Coelho et al. (1976, 1977) has certainly failed to sufficiently demonstrate that the howler population at Tikal is not restricted by adequate resource availiability.

Predation and Disease

Predation on howlers by mammals other than man does not appear to play a significant role in limiting howler density (Glander 1975). Only in some areas does human predation contribute to depletion of free-ranging primate popoulations (Neville 1974). Howlers at Tikal are protected from hunting and Guatemalans, in general, do not appear to be interested in primates as a food source. Of the five feline species reported at Tikal, the puma and jaguar are both large cats and primarily ground dwellers. Since howlers are among the largest of New World primates, the smaller cats (ocelot, margay, and yaguaroundi) probably find more suitable prey among smaller mammals. No one at Tikal has ever reported a cat attack on howlers. Carpenter (1965) observed occasional attacks by ocelot on young howlers. The cats, in turn, became the object of aggression by the howler adult males. It is unlikely that cats affect howler populations to any appreciable degree.

There is little evidence to show that predatory birds attack howlers. However, large birds and planes were occasionally observed to elicit responses from howlers at Tikal. Their complete lack of interest at other times, though, would

suggest that predation by birds does not pose a serious threat.

Disease bearing microorganisms also act in a predatory manner. In tropic areas, recurring epidemic diseases play a role in cyclical reductions of primate populations (Bramblett 1976). The fluctuations in howler density on BCI, Panama (Table 1) resulted from a yellow fever epidemic there is 1949 (Collias & Southwick). Glander (1975) reported that evidence is available for the effects of yellow fever on his Costa Rican population and both Tikal's primate populations were decimated by yellow fever in 1958 (Coe 1967). Primates are susceptible to numerous other diseases, many of which are shared with humans as can be evidenced by the prolific use of primates in medical research. Cross-infection may occur naturally between primates and man in some areas (T-W-Fiennes 1972).

Howler monkeys appear to be natural hosts for bots, the larvae of flies of the family Cuterebrinae (Shannon & Greene 1926). The botfly eggs are laid on the underside of mosquitos' abdomens and hatch in response to the warmth of the howler's body when the mosquito takes a blood-meal (Smith 1977). Sign of infection is an inflamed swelling (cyst) with a pore. "Secondary infections by bacteria entering through the pore may occur and may be more serious than the primary infection since the bot eventually matures and leaves the host" (Ruch 1959:508).

Carpenter (1965) observed that howlers on BCI were seriously annoyed by botflies and that some young individuals appeared to be sick from larval infections. Glander (1975) ob-

served only one botfly cyst on one animal during the course of his study in Costa Rica and reported the absence of bots from more than 80 howlers captured in his study area. He is of the opinion that healthy animals are "probably not heavily infested with botflies" (1975:80). Smith (1977) reported bots on howlers in his study on BCI in 1967-1968. Of three monkeys found dead, two were too badly decomposed to determine the extent of parasitism. The third, a juvenile, was found barely alive and had been infected with 25 botfly larvae. Many of the holes were secondarily infested with larvae of other fly types and these were eating through the body wall, the peritoneum and even the liver. Smith felt that there is a causal relationship between botfly infections and poor health in howlers and the "botflies limit howler population both through adult mortality and reduced reproductuve success" (1977:116). Howler density does not appear to be a contributing factor. Baldwin and Baldwin (1972) found "healthy" populations at 12 times the density in southwestern Panama.

Schlichte (1978) observed bots on howlers in his study at Tikal. All but one of the animals in our study group was observed with botfly infestations. The number of cysts increased with the progression of the rainy season. The juvenile male and infant were the most seriously infested. At one time, the infant's entire left side was covered with large cysts, many with larvae exit holes in them. The degree of secondary infection was not known and the study was terminated before many of the cysts had disappeared.

Spider monkeys, the sympatric primate species in this study, did not appear to be infected by bots. Cant (1977) reported no bots on spider monkeys at Tikal for an observation period of more than a year.

Grooming, or the lack of it, is not an indication that parasites are present. Grooming is a social activity with obvious hygienic benefits (T-W-Fiennes 1972). Howlers are known for their relative absence of allo-grooming (Carpenter 1934, Moynihan 1976). For approximately 500 hours of observation, we observed only 24 bouts, totalling just under 22 minutes (Appendix II) of allo-grooming. Glander (1975) and Neville (1972b) reported varying degrees of allo-grooming in Costa Rica and Venezuela, respectively. Others (Carpenter 1965, Smith 1977, Milton 1980) from BCI reported none at all. The presence of bots does not appear to be correlated with allo-grooming activity. In fact, grooming itself may be "hazardous for the groomer, since it exposes the performer to the exudate and infected tissue surrounding a lesion" (Bramblett 1976:248).

Auto-grooming also occurs at a comparatively low frequency in howlers. The type of observations made at Tikal consisted primarily of scratching, shaking and passing of a limb around the periphery of the body. The hands of howlers are modified for grasping branches, "the first two fingers of each hand are set apart from, and opposable to, the other three" (Moynihan 1976:59). This does not facilitate delicate forms of manual dexterity.

The indidence of disease in primates is probably most highly related to the distribution of disease carrying vectors, such as mosquitos. Many ectoparasites (e.g. botflies) and arboviruses (e.g. yellow fever, malaria) are carried and transmitted by mosquitos. It has been supposed for many years that different mosquito species are "layered" in the forests, just as arboreal primates are, and that vertical mixing does not occur (T-W-Fiennes 1972). Studies have shown this to be only partially correct. Some canopy species have a diurnal rhythm, feeding in the upper canopy levels during the day, and descending to the ground at dusk. However, Downs et al. (1955) found no yellow fever virus in 118,000 ground-living mosquitos which they caught, and none in the 120 canopy species caught at ground level. Moynihan (1976) suggested the last two expected epidemics of yellow fever on BCI did not occur because (1976:64):

> The epidemics used to come from the Darien in eastern Panama. Much of the forest between Darien and Barro Colorado has been cut down as the countryside has been settled and developed. This has interrupted the movements of the insect vectors of the disease.

Just as with the evaluation of resource abundance, the parameters involved with predation and disease are complex and interacting. Unless direct evidence is available, it is difficult to measure the degree of impact of these factors on limiting primate populations. The discussion in this chapter has concerned itself with factors that are primarily "proximate" in nature. In the following chapter, I will try to discuss variables in a more evolutionary perspective.

CHAPTER V

ACTIVITY BUDGETS AND SOCIAL RELATIONS

Social Organization

Alouatta groups may be unusual in that they appear to
alternate between multimale and unimale social arrangements,
depending upon aspects of the population density as a whole
(Wilson 1975). Alouatta palliata in both Panama and Costa
Rica live in multimale groups averaging from 14 to 20 indivi-
duals (Milton 1980). Reports on A. seniculus from Trinidad,
Venezuela, and Argentina (Neville 1972a, Braza et al. 1981)
indicte smaller groups, averaging from 6 to 8 individuals, in
both unimale and multimale groups. Furthermore, Braza et al.
(1981) found 6 of 141 groups surveyed to contain one each of
an adult male and adult female. A. caraya in Argentina live
in multi- and unimale groups, averaging from 5 to 7 indivi-
duals (Pope 1966).

Carpenter (1934) coined the term "socionomic sex ratio"
to refer to the average ratio of adult males to adult females.
The sex ratio is a characteristic of a specific population.
The socionomic sex ratio for A. palliata on BCI has ranged
from a low of 1:1.8 (Chivers 1969) to a high of 1:3.8 (Collias
& Southwick 1952). Neville (1972a) reported sex ratios for
A. seniculus (Trinidad and Argentina) and A. caraya (Argentina

40

and the Chaco) at roughly 1:1. More recently, Milton (1980) indicated sex ratios for A. palliata (Panama and Costa Rica) and A. seniculus (Peru) to be around 1:2.5. The ratio does not suppose that a greater number of adult females than males will be present in any specific multimale group.

Table 3 presents the history of population variables and social organization for A. pigra at Tikal over the last decade. As much detail as is known about the age/sex categories for these groups is presented in Appendix III. The studies are in general agreement that the population density equals approximately five animals per km^2 and the sex ratio is 1:1. However, the table indicates a gradual decrease in the number of animals observed in the area and a lowering of average group size. Coupled with this has been a shift from multi- and unimale groups to exclusively one adult male/one adult female groups.

It is known that Cant (per. comm.) and Schlichte (1978) observed the same multimale group, based on the discription of a readily identifiable "old" male and the same composition for the remaining group members. This "old" male was not present in either of the two groups contacted in this study and it is believed that at least one female perished from the group designated "North". This group contained one adult male, one adult female, two medium-sized juvenile males, and one small juvenile male. Twins are not known to occur in howlers and since two of the juvenile males were essentially indistinguishable, it is highly probable that the mother of one had

TABLE 3

HISTORY OF HOWLER POPULATION AND SOCIAL ORGANIZATION AT TIKAL

Study	Composition					
	Total Observed	No. of Groups	Group Mean	Multi-Male	Uni-Male	1-Male 1-Female
Coelho 1973	25	4	6.25	2	2	-
Schlichte 1974-75	11	2	5.5	1	1	-
Cant 1975-76	11	2	5.5	1	-	1
Cunningham/Caywood 1978	10	2	5.0	-	-	2
Bolin 1978-79	NA	3	NA	-	-	3

died. This group occupied a range similar to Schlichte's study group, and may have been the remnant of the group he observed.

In addition to the social groups, solitary males were observed in all studies at Tikal except that of Coelho et al. (1976). Solitary males are generally reported for other howler studies (Carpenter 1934, 1965; Collias & Southwick 1952; Neville 1972a; Pope 1966; Glander 1975; Otis et al. 1981; and others). Neville (1972a), Schlichte (1978) and Glander (1975) reported sightings of solitary females, or adult females with a juvenile, as well. Explanations for solitary females have not been given. Solitary males are believed to be young adults leaving their natal groups and trying to transfer into another group (Wilson 1975, Otis et al. 1981). We observed one such attempt during the summer of 1978; however, after being followed for a period of rapid travel (about 20 min.), the adult male in our group severely rebuffed and chased the other male out of the area.

The changes seen in the social arrangements of groups at Tikal (Table 3), are most interesting when viewed in the light of evidence presented by Bolin (1981). Bolin (1981) moved her study on howlers from Tikal to Belize (Dec. 1978 to March 1979) because of greatly improved visibility at the latter site. She made observations on 13 groups, totaling 55 howlers, in a 7 km^2 study area. Population density was estimated at 8.14 animals per km^2 with an average group size of 4.4 and 1:1 sex ratio. Of these 13 groups, 11 were mated monogamously. Of the remain-

ing two groups, one was multimale, the other unimale. No other studies have been done on A. pigra in this area. This appears highly unusual, since throughout most of the literature (Carpenter 1934, 1965; Altmann 1959: Neville 1972a and others), Alouatta is considered to mate polygamously.

Mating Strategies

Principles developed by Darwin indicate that natural selection operates on individuals through differential reproduction. Methods of achieving reproductive success are inherently tied to parental investment. Triver's (1972) defined parental investment as any behavior toward offspring that:

> ...increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring (1972:139).

The kind and degree of parental investment, particularly the ratio of male to female contributions, varies with the type of mating system. The major systems include (Wilson 1975):

(1) monogamy - a reproductive unit of one male and one female.

(2) polygamy - in the broad sense, covers any form of multiple mating; within polygamy are three general categories:

(a) polygyny - one male bonds with more than one female.

(b) polyandry - one female bonds with more than one male.

(c) promiscuity - a mating system where no units or bonds are formed; this does not imply that choice is not a factor (i.e., it is not random).

Ultimately, natural selection causes an individual to make the best decision "for its own maximum fitness and not necessarily that of a prospective partner" (Barash 1977:149).

Females are considered to have the greatest parental investment in offspring because they produce a small number of large gamates (eggs), for which they may incur the costs and risks associated with pregnancy, birth, and lactation (Barash 1977). In contrast, the male's contribution consists of quantities of small gamates (sperm) which are readily replaced.

Animals are fundamentally polygamous (Wilson 1975). Polygamy is found where cooperation of both parents is not needed to insure the success of their offspring. Theoretically, polygyny and promiscuity would be the mating systmes preferred by males since they can maximize their reproductive success by inseminating as many females as possible. A major component of the male strategy is competition with other males for sexual access to females. The strategy of a female would depend largely on maximizing her own investment in her offspring and choice of a male with whom to mate (Barash 1977). Females would gain by mating with the "best" male available, even if they mated with other females. If a polygynously mated male helps produce offspring that would themselves be more likely to experience reproductive success, the fitness of females who adopt this strategy is better insured. Alternatively, females may be more interested in the quality of resources controlled by a male, than by the male himself (Orians 1969).

Monogamy appears to be secondarily derived (Barash (1977). In monogamous systems, one finds nearly equal parental investment and is selected for when reproduction requires the cooperation of two committed adults. Monogamy may serve in facilitating defense of a scarce and valuable resource (Wilson 1975). Females would generally be most fit if mated monogamously, since they would profit from the assistance of a committed male.

The literature on howlers generally agrees that adult males display a high degree of tolerance toward infants, but show little active participation during interactions (Altmann 1959, Baldwin and Baldwin 1972, Carpenter 1965, Neville 1972b). Males are known to actively interfere in the case of danger (Carpenter 1965). Bolin (1981) delineated from her observations on A. pigra at Tikal and in Belize, that males generally showed more tolerance, accommodative and protective behavior than is reported for other species of Alouatta. However, she found the degree of male parental behavior to vary considerably between groups. She found the average percentage of male-infant interactions (16.4% frewuency, 7.4% duration) to be low when compared to reports from the literature on strictly monogamous primates (e.g. tamarins, night monkey, gibbon, siamang).

The preceeding discussion indicates that howler populations do not appear to be "fixed" by a specific mating system, Evidence from this study at Tikal, and groups observed by Bolin (1981) and Braza et al. (1981) indicate, that monogamy exists in addition to polygamy as a strategy for mating in

howlers. Milton suggested that "features of social organiza-
tion cannot be considered apart from the total ecology of the
species in question...one is ultimately asking questions re-
lated to demography" (1980:145). Factors which may influence
demography were discussed in the preceeding chapter. What
appears evident, is that howlers have adapted a strategy of
"flexibility" towards mating. This allows individuals par-
ticipating in social groups to adjust their patterns of mating
to maximize their reproductive success in response to prox-
imate changes within their environment.

Activity Budgets

Since an animal cannot generally perform more than one
activity at a time, the relative amount of time an individual
spends in different activities may be a good indicator of the
role it plays in an organism's game-plan for adaptation.
Wilson (1975) presented two generalizations that relate eco-
logy to the time-energy budgets of animals. The first of
these he called the "principle of stringency: time-energy bud-
gets evolve so as to fit the times of greatest stringency"
(1975:142). This suggests that although an animal may appear
to be living in the midst of plenty, their time-energy bud-
gets have been adjusted to see them through periods of food
shortage. "Maximum consumers", or genotypes that are commit-
ted to rapid growth and reproduction, may derive advantages
during periods of resource surplus, but may experience set-
backs, possibly even extinction, when times are difficult.

The second generalization that Wilson (1975) proposed
is termed the "principle of allocation".

> This states that the major requirements of animals
> differ greatly in the amounts of time and energy
> that is profitable to devote to them in the cur-
> rency of genetic fitness. Furthermore, as a rule
> these requirements descend in importance as follow:
> food, antipredation, and reproduction (1975:143).

If one priority is easily satisfied by a generous environment,
more time and energy may be shifted to activites of the other
priorities.

In Table 4 are comparisons of the average daytime adult
activities from this study (calculated from Table 5), with
three other howler studies: Schlichte (1978), Glander (1975),
and Chivers (1969). The four studies were considered to be
more or less comparable based on similar methodologies. Al-
though Schlichte also studied howlers at Tikal, he employed
five-minute scans on the group as a whole, not individuals.
The discrepancy between his values and those of this study
can be attributed to asynchrony of activity between indivi-
duals. This was found to exist, especially, in feeding be-
havior. When compared to Glander and Chivers, the lower per-
centage of time spent feeding in this study is attributed to
the overall high proportion of fruit consumed by howlers at
Tikal (Chapter IV).

Table 4 shows a great emphasis on the behavioral cate-
gory "inactive". This low level of activity appears to be
related to the general foraging strategy employed by howlers.
Westboy (1974) proposed that the objective of the foraging

TABLE 4

COMPARSION OF AVERAGE ADULT DAYTIME ACTIVITY
BUDGET FOR FOUR HOWLER STUDIES

Activity	(%) Time of Activity			
	Tikal 1978	Schlichte (Tikal)	Glander Costa Rica	Chivers (BCI)
Feed	17	22	23	21
Inactive	65	66	64	59
Travel	11	12	12	9
Move	4			11
Soc Play	1		1	
Misc	3		1	

strategy for a large generalist herbivore is to optimize the best nutritional balance within a given total food volume, rather than to maximize the energy consumption for time spent foraging. Howlers at Tikal appear to be employing a similar strategy. It was noted earlier that howlers at Tikal appeared to have an abundance of ripe fruit (high energy) at their disposal. However, it comprised only 38% of their total diet. The remainder was composed of primarily low-energy foods (e.g., immature fruit, leaves) which may have been necessary to balance nutritional requirements. Physiologically, howlers do not show a lowered standard of metabolism when compared to other primate species (Milton 1979), and Milton (1978) determined that howlers were no more "active" when they were eating a high proportion of fruit. This is supported by data collected at Tikal, which indicates the howler level of "inactivity" is well within the range reported for studies in other areas (Table 4).

Howlers appear to have developed a strategy of energy conservation. Howlers exploit energy-rich foods when they are available (Caywood 1980, Milton 1980), but do not correspondingly increase their levels of activity. This may permit howlers to build up energy reserves (fat) to use when high-energy foods are scarce. In general, this is a reflection of Wilson's principle of stringency".

If an animal evolves a general foraging strategy of "energy conservation", other behavioral and/or morphological features should reflect this as well. In addition, an exam-

ination of activity budgets by age/sex categories should il-
luminate differences in individual adaptive strategies.

Table 5 presents the activity budgets for each indivi-
dual observed in this study. The figures are percentages.
The miscellaneous category represents activities observed,
primarily, in ad-lib sampling (e.g., grooming, elimination,
sexual activity).

What should be noted in Table 5 is the greater percent
of time spent feeding by the adult female (19%) compared to
the adult male (15%). For a 33-day sample of complete days,
the adult female fed more than the adult male on 29 of these
days. Utilizing the T-test, this day-to-day difference was
significant at the .001 level. C.C. Smith (1977) found a sim-
ilar differnece between adult males and females on BCI with
respective percentages of 14% and 18%. Since howlers are sex-
ually dimorphic (males are larger than females), this differ-
ence may seem unusual. Smith (1977) also found females with
infants to spend about 1.5% more of the day feeding than fe-
males without infants. The first of these patterns appears to
be common among several primate species, e.g. indri, gelada,
siamang, and vervet (Clutton-Brock 1977). Clutton-Brock sug-
gested that (1977:545):

> Males might be expected to feed for less time per
> unit 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 fe-
> males 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...

TABLE 5

PERCENT TIME SPENT BY INDIVIDUALS IN
MAJOR ACTIVITIES DURING DAYLIGHT HOURS

Activity	(%) Time of Activity				
	AM	AF	JF	JM	I
Feed	15	19	17	16	11
Inactive	66	63	59	58	67
Travel	11	12	11	12	12
Move	3	4	6	7	9
Soc Play	<1	1	7	7	2
Vocalization	3	1	<1		
Misc	1	<1	<1	<1	

A = adult, M = male, F = female, J = juvenile
I = infant

The first of these (a), was certainly evident for howlers at Tikal. However, there did not appear to be a differential access to food availability (b). The howlers maintained a relatively condensed group at all times, and feeding was done in close proximity to one another. The last variable (c) did not appear to apply to the howlers, but feeding rates for males and females were not measured. Feeding differences between the juveniles and adults may be attributed to the increase in energy demands for growth and more activity. The latter is represented by the greater amount of social play (7%) for both juveniles.

Morphology

Certain features of howler morphology may operate to conserve energy. It has been noted that howlers are among the largest of Neotropical primates. Kleiber (9161) found decided advantages to a relatively large body size when measured by the kilocalaries required per unit weight for basal maintenance. Surface-to-volume ratio decreases as animals become large; this in turn reduces heat loss and lowers metabolic costs.

Milton (1980) demonstrated that, although howlers lack extensive hindgut enlargement chatacteristic of many primate folivores, the howler hindgut (caecum + colon) is larger than other non-leaf-eating primates. This permits howlers to retain quantities of food in the hindgut for longer periods (food passage rates, Milton 1981), and therefore increases

the efficiency of absorption of nutrients.

Howlers have a greatly enlarged hyoid bone, the reson-
ating feature of the voice, which enables them to produce
their distinctive vocalizations, i.e., roaring or howling (Moy-
nihan 1976). These vocalizations appear to function as an in-
ter-group spacing mechanism (Carpenter 1934, Chivers 1969) by
(1) announcing the location of a group, thereby inhibiting the
intrusion of one group upon another; (2) reducing the chance
of inadvertant inter-group contact; and (3) settling inter-
group contacts by primarily vocal, rather than physical bat-
tles (Milton 1980). Thus, howling provides an energetically
conservative means of avoiding and dealing with inter-group
conflict.

Although aggressive physical interactions are known to
occur between howlers (Collias & Southwick 1952, Carpenter
1965, Glander 1975 and others), it appears to be the exception.
No direct physical aggression was observed at Tikal during this
study. Levels of aggression within a species are often con-
sidered to be reflected in the amount of allogrooming that
occurs (Sparks 1967, Jolly 1972). If high levels of aggression
exist within groups, then it tends to exist between groups as
well. Species such as macaques and baboons are known for their
high levels of inter- and intragroup aggression (Berstein &
Gordon 1974). Grooming operates to reinforce dominance hier-
archies and to reduce tensions between group members (Sparks
1967). It was stated previously that allogrooming among how-
lers is rare; 24 bouts were reported for our group (Appendix

II) totaling only 22 minutes of the total observation time. Grooming is not generally reported for groups at BCI (Carpenter 1934, 1965; Collias & Southwick; Smith 1977), but has been reported in other areas (Neville 1972b, Glander 1975, Bolin 1981).

Howlers at Tikal did not exhibit the typical "dawn chorus" reported by studies at BCI (Carpenter 1965, Chivers 1969 and others). Roaring bouts occured throughout the day in response to, or initiated by, proximity to the other howler group. For a 48-continuous-day survey, howling occured on only 20 days. The longest continuous period with absence of howling was seven days. This is, no doubt, partly attibutable to the low population density of howlers at Tikal. The howlers occasionally roared in response to drenching rain. It is not known if they were responding to the thunderous noise of the downpour, or the discomfort of being soaked, perhaps both.

Home Range

For the 56 days of observation, home range for our group at Tikal was calculated at 47 hectars (Caywood 1980). Schlichte (1978) reported about 125 hectars for the group he observed there in 1974. Home range sizes may vary considerably from one study group or area to another. Range sizes change constantly and may reflect differences or changes in season, resource availability, population density, and group size (Clutton-Brock 1977). Estimates may be biased by the method used for calculating range sizes. Glander (1975) noted that

the concept of home range may have limited application to arboreal primates, since the concept was originally developed for terrestrial species.

> Terrestrial primates have essentially a flat, i.e.,
> two dimensional habitat. An arboreal primate's home
> range is three-dimensional. Two-dimensional concep-
> tulizations do not provide accurate estimations of
> the true nature or size of the habitat (1975:71).

Distances traveled daily varied from approximately 100 meters to more than 250 meters (Caywood 1980). Caywood (1980) delineated that our howler group followed a ranging pattern similar to one described by Milton (1980) in which the group makes use of various "core" resource areas. This implies that the resources may be distributed unevenly in both time and space, and that the best pattern of travel should be "goal-directed". Our howlers were observed to use the same arboreal pathways and feeding trees at different times. This indicated their foraging was not random and, therefore, energy conservative. "Travel could be minimized by a search strategy that maximized the probability of finding preferred foods in relation to the distance traveled" (Milton 1980:98).

Since travel was usually associated with feeding, the time spent feeding and traveling together should give a good indication of the time spent foraging (Milton 1980). Feeding and travel together accounted for an adult average of only 28.5% of the total time budget. Therefore, despite the uneven distribution of food resources, the howlers were able to meet their dietary requirements in an average of 3.1 hours of foraging per day.

It is a common feature for animal groups to show strong affinities for specific areas (Chivers 1969). Home range is defined as the area traversed by a group carrying out its activities during a specified period and may, to varying degrees, overlap supply areas used by one or more conspecific groups (Jewell 1966, Chivers 1969). Brown and Orians (1970) defined "territory" as a supply area which can be successfully defended. Chivers (1969) demonstrated that howlers are not territorial by this definition. They use their vocalizations as a way of buffering themselves from other groups, but these interactions may occur in any part of the home range without reference to any specific location, i.e., territorial boundary. "... it is a reaction of intolerance to the close proximity of a conspecific group at any place or time" (Chivers 1969:78).

The costs and benefits of defending resources from conspecifics have been examined by Brown (1964), Brown and Orians (1970) and Schoener (1971). The benefits result in having exclusive use of resources, the costs in patrolling the area and repelling invaders. Schoener (1971) predicted that when a preferred resource is abundant (i.e., there is enough to support more than one group), it would not be profitable to defend it because it would be costly both in terms of energy expenditure and in loss of opportunity to seek other required resources. On the other hand, if desirable resources are scarce, animals may be less selective (e.g., eat more undesirable foods) and conserve energy by reducing time spent traveling. Since howler's resources are often patchy in both time and space, de-

fending only the space presently occupied would be more cost-efficient than defense of an entire supply area.

Roaring provides howlers with a "cheap" mechanism of this type of defense. Another examination of Table 5 indicates differential participation in vocalization. The adult male did the most howling: three percent of his total activity budget. By contrast, the adult female participated in howling for only one percent of her total activity budget. This "division of labor" (Milton 1980) would help conserve energy for females who are already faced with the demands of pregnancy and lactation. Our adult female generally remained inactive or fed while the adult male participated in inter-group encounters. She became involved only during relatively intense and persistent encounters. Any behavior that could generally be performed by the adult male would be beneficial to her by lowering her energy demands and focusing them on re-production. This in turn increases her chances for reproductive success. If she is successful, than the male who insemi-nated her would also realize success.

Ad-Lib Behaviors

Ad-lib sampling was utitlized to record the occurance of allogrooming, drinking, roaring, and sexual behavior. All of these have been discussed except the latter. Only one copulation was observed during this field study and was significant because the adult female in our group was still lactating. This particular incidnet is described in detail in Appendix

IV, but will be summarized briefly. Our study group had been in close proximity to the other central ruins group for several days. Two or three times a day, roaring bouts would occur. On the day of the observed copulation, the adult males of both groups had been roaring at each other on and off all afternoon, with our adult female and juvenile female occasionally joining in. Our adult male had left the tree in which the other group members were resting to chase the male from the opposing group. After our male returned, the adult female walked to the end of her branch and stopped. She presented to her group male, who had followed her down the branch, and a 45 second copulation took place with presumed ejaculation. Although the adult male in our group appeared to monitor the adult female's sexual state (Appendix IV) by occasionally sniffing her genitals or urine, she was still nursing. This would indicate she was lactating and therefore, not in estrus. The copulation may have operated to affirm the bond between the adults and maintain the mating unit.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Examination of animals from a sociobiological perspective provides a framework for synthesizing the morphological, physiological and behavioral parameters that operate to facilitate animals in achieving successful adaptive strategies.

From June 21 through September 11, 1978 fieldwork was conducted on a group of free-ranging howler monkeys (<u>Alouatta pigra</u> Lawrence) at Tikal National Park, Guatemala, C.A. Approximately 500 hours of observation were accumulated. Field methods included focal animal, scan and ad-lib sampling. Data on ecological and behavioral variables were collected.

The species of howler at Tikal represents one which has been little studied previously. Although howlers at Tikal have a distinctively unique diet high in fruit, a majority of their total diet represents "low energy" foods, similar to diets of howlers in other areas. In general, their foraging strategy is that of a generalist herbivore, seeking to meet a nutritional balance with minimization of energy expenditure.

The population density of howlers at Tikal appears low by comparison to other study areas. Factors were discussed which may limit populations; primary theory suggests that animals are limited by essential resources and predation.

Howlers at Tikal exhibit behaviors, such as "sampling" and "drinking", which indicate they may be responding to a dietary environment high in plant secondary compounds. Disease was discussed as a form of predation.

Howlers are generally known to oganize in multimale and unimale social groups of varying sizes. At the time of this investigation, both groups in Tikal's central ruins area were monogamously mated. This probably resulted from a decrease in the population, but was interesting in light of the evidence presented by Bolin (1981) on A. pigra in Belize, where she found a high degree of monogamy. Methods for achieving reproductive success were discussed within the framework of mating systems. Monogamy and polygamy were viewed from both a male and female adaptive perspective. Howlers exhibit a "flexibility" in their mating selection which enables them to employ the best strategy when proximate variables change.

An anlysis of activity budgets indicate that howlers at Tikal divide 93% of their time among three major activities: resting (65%), feeding (17%) and travel (11%). These percentages are comparable to the same activities in other howler studies. The great percentage of resting indicates howlers are committed to a strategy of "energy conservation". They exhibit morphological and behavioral features which reflect this strategy.

Morphological features include large body size, slow rates of food passage, and enlargement of the hyoid bone enabling them to make loud vocalizations. Roaring provides an

energetically "cheap" means of maintaining inter-group spacing.

Just as in other areas, howlers at Tikal are not "territorail". They defend only the space they currently occupy within their home range, and most inter-group conflicts are resolved through vocal, rather than physical battles.

Howlers at Tikal participate in a form of "division-of-labor". The adult female, although smaller than the adult male, fed significantly more. This was in response to the increased energy demands of pregnancy and lactation. Alternatively, the adult male performed more "defensive" behaviors (e.g. roaring) than the adult female. This would benefit the female by allowing her to focus her energies on reproduction, and the male by protecting his access to a reproductive female and desirable habitat resources.

The one incident of sexual copulation observed was considered highly unusual since the adult female was still lactating. It was suggested the copulation served to reaffirm the mating bond between the adult male and female during a time of intense conspecific interaction.

Ideally, field studies should be conducted for a minimum of one annual cycle, preferably, several years. This would illuminate seasonal differences, as well as changes from year to year. Although the collection of baseline data for Tikal is advancing, future research would be warranted. There are still many questions about the primates and their environment that remain only partially explained.

REFERENCES CITED

Altmann, Jeanne
    1974 Observational study of behavior: sampling methods.
           Behavior 49:227-267.

Altmann, S.A.
    1959 Field observations on a howling monkey society.
           Journal of Mammalogy 40:317-330.

    1974 Baboons, space, time and energy. American Zoologist
           14:221-248.

Baldwin, J.D. and J.I. Baldwin
    1972 Population density and use of space in howling mon-
           keys (Alouatta villosa) in southwestern Panama.
           Primates 13:371-379.

Baldwin, L.A., T.L. Patterson and G. Teleki
    1977 Field research on callitrichid and cebid monkeys: an
           historical, geographical and bibliographical list-
           ing. Primates 18:485-507.

Barash, David P.
    1977 Sociobiology and Behavior. New York: Elservier.

Bell, R.H.
    1971 A grazing ecosystem in the Serengeti. Scientific
           American 225:86-93.

Bernstein, I.S.
    1964 A field study of the activities of howler monkeys.
           Animal Behavior 12:92-97.

Bernstein, I.S. and Thomas P. Gordon
    1974 The function of aggression in primate societies.
           American Scientist 62:304-311.

Bolin, Inge
    1981 Male parental behavior in black howler monkeys (Alou-
           atta palliata pigra) in Belize and Guatemala. Pri-
           mates 22:349-360.

Bramblett, Claud A.
    1976 Patterns of Primate Behavior. Palo Alto, CA: Mayfield
           Publishing Company.

Braza, F., F. Alvarez and T. Azcarate
    1981 Behavior of the red howler monkey (Alouatta senicu-
           lus) in the llanos of Venezuela. Primates 22:459-473.

Brown, J.L.
    1964   The evolution of diversity in avian territorial sys-
            tems. Wilson Bulletin 6:160-69.

Brown, J.L. and G.H. Orians
    1970   Spacing patterns in mobile animals. Annual Review of
            Ecology and Systematics 1:239-62.

Cant, John G.H.
    1977   Locomotion and social organization of spider monkeys
            (Ateles geoffroyi). Ph.D. dissertation, University
            of California, Davis.

    1980   What limits primates. Primates 21:538-544.

Carpenter, C.R.
    1934   A field study of the behavior and social relations of
            howling monkeys (Alouatta palliata). Comparative
            Psychological Monographs 10:1-168.

    1965   The howlers of Barro Colorado Island. In, Primate
            Behavior. I. DeVore, ed., Pp. 250-291. New York: Holt
            Rinehart & Winston.

Caywood, Janene
    1980   Ecology of Guatemalan Howler Monkeys (Alouatta pigra
            Lawrence). M.A. thesis, University of Montana,
            Missoula.

Chivers, D.J.
    1969   On the daily behavior and spacing of howling monkey
            groups. Folia Primatologica 10:48-102.

Clutton-Brock, T.H.
    1977   Some aspects of intraspecific variation in feeding
            and ranging behavior in primates. In, Primate Eco-
            logy. T.H. Clutton-Brock, ed., Pp. 539-556. London:
            Academic Press.

Coe, Willian R.
    1967   Tikal, A Handbook of the Ancient Maya Ruins. Univer-
            sity of Pennsylvania: The University Museum.

Coelho, A.M., C.A. Bramblett, L.B. Quick and S.S. Bramblett
    1976   Resource availability and population density in pri-
            mates: a socio-bioenergetic analysis of energy bud-
            gets of Guatemalan howler and spider monkeys. Pri-
            mates 17:63-80.

Coelho, A.M., et al.
    1977   Ecology, population characteristics and sympatric
            association in primates: a socio-bioenergetic analy-
            sis of howler and spider monkeys in Tikal. Yearbook
            of Physical Anthropology 20:96-135.

Collias, N.E. and C.H. Southwick
    1952 A field study of population density and social organ-
          ization in howling monkeys. Proceedings of the Ameri-
          can Philosophical Society 96:143-156.

Crook, J.H.
    1970 Socio-ecology of primates. In, Social Behavior in
          Birds and Mammals. J.H. Crook, ed., Pp. 103-166. Lon-
          don: Academic Press.

Defler, Thomas R.
    1981 The density of Alouatta seniculus in the eastern
          llanos of Colombia. Primates 22:564-569.

Denham, Woodrow W.
    1971 Energy relations and some basic properties of primate
          social organization. American Anthropologist 73:77-
          95.

Downs, W.G., T.H.G. Aitken and C.R. Anderson
    1955 Activities of the Trinidad regional virus laboratory
          in 1953 and 1954, with special reference to the yel-
          low fever outbreak in Trinidad, BWI. American Journal
          of Tropical Medicine and Hygiene 4:837-843.

Eisenberg, J.F., N.A. Muckenhirn and R. Rudran
    1972 The relation between ecology and social structure in
          primates. Science 176:863-874.

Freeland, W.J. and D.H. Janzen
    1974 Strategies of herbivory in mammals: the role of plant
          secondary compounds. American Naturalist 108:269-289.

Freese, C.
    1976 Censusing Alouatta palliata, Ateles geoffroyi and
          Cebus capucinus in the Costa Rican dry forest. In,
          Neotropical Primates: Field Studies and Conservation.
          R.W. Thorington and P.G. Heltne, eds., Pp. 4-9. Wash-
          ington: National Academy of Sciences.

Froehlich, J.W., R.W. Thorington and J.S. Otis
    1981 The demography of howler monkeys (Alouatta palliata)
          on Barro Colorado Island, Panama. International
          Journal of Primatology 2:207-236.

Glander, Kenneth E.
    1975 Habitat and resource utilization: an ecological view
          of social organization in mantled howling monkeys.
          Ph.D. dissertation, University of Chicago, Illinois.

    1977 Poison in a monkey's Garden of Eden. Natural History
          86:34-41.

Glander, Kenneth E.
1978a Drinking from arboreal water sources by mantled howl-
ing monkeys (_Alouatta palliatta_ Gray). Folia Prim-
tologica 29:206-217.

1978b Howling monkey feeding behavior and plant secondary
compounds: a study of strategies. _In_, The Ecology of
Arboreal Folivores. G.G. Montgomery, ed. Pp. 561-
574. Washington, D.C.: Smithsonian Institution Press.

1980 Reproduction and population growth in free-ranging
mantled howling monkeys. American Journal of Physical
Anthropology 53:25-36.

Hamilton, W.D.
1974 The genetical theory of social behavior: I and II.
Journal of Theoretical Biology 7:1-52.

Heltne, Paul G., D. Turner and N. Scott
1976 Comparison of census data on _Alouatta palliata_ from
Costa Rica and Panama. _In_, Neotropical Primates:
Field Studies and Conservation. R.W. Thorington and
P.G. Heltne, eds., Pp. 10-20. Washington: National
Academy of Sciences.

Hladik, A. and C.M. Hladik
1969 Rapports trophiques intre vegetation et primates dans
la foret de Barro Colorado (Panama). Terre Vie 23:
25-117.

Hladik, A., et al.
1971 Le regime alimentaire des primates de l'ile de Barro
Colorado (Panama). Folia Primatologica 16:85-122.

Holdridge, L.R.
1967 _Life Zone Ecology_. San Jose, Costa Rica: Tropical
Science Research Center.

Izawa, K.
1975 Foods and feeding behavior of monkeys in the Upper
Amazon Basin. Primates 16:295-316.

1976 Group sizes and compositions of monkeys in the Upper
Amazon Basin. Primates 17:367-399.

Jewell, P.A.
1966 The concept of home range in mammals. Symposia of the
Zoological Society of London 18:85-110.

Jolly, A.
1972 _The Evolution of Primate Behavior_. New York: Mac-
millan.

Jones, Clara B.
    1979 Grooming in the mantled howler monkey, Alouatta pal-
          liata Gray. Primates 20:289-292.

    1980 The functions of status in the mantled howler monkey,
          Alouatta palliata Gray: intraspecific competition for
          group membership in a folivorous neotropical primate.
          Primates 21:389-405.

Kleiber, M.
    1961 The Fire of Life. New York: Wiley

Klein, Lewis L. and D.J. Klein
    1975 Social and ecological contrasts between four taxa of
          neotropical primates. In, Socioecology and Psychology
          of Primates. R.H. Tuttle, ed., Pp. 59-85. The Hague:
          Mouton.

Lawrence, B.
    1933 Howler monkeys of the palliata group. Bulletin of the
          Museum of Comparative Zoology 75:313-354.

Lundell, C.
    1934 Preliminary sketch of the photogeography of the Yuca-
          tan Peninsula. Carneigie Institute, Washington 436:
          257-321.

    1937 The vegetation of Peten. Carneigie Institute, Wash-
          ington No. 478.

Malinow, M.R., ed.
    1968 Biology of the Howler Monkey (Alouatta caraya). Basel:
          S. Karger AG.

McKey, D.
    1974 Adaptive patterns in alkaloid physiology. American
          Naturalist 108:305-20.

Mendel, F.
    1976 Postural and locomotor behavior of Alouatta palliata
          on various substrates. Folia Primatologica 26:36-53.

Milton, Katharine
    1975 Urine-rubbing behavior in the mantled howler monkey
          Alouatta palliata. Folia Primatologica 23:105-112.

    1978 Behavioral adaptations to leaf-eating by the mantled
          howler monkey (Alouatta palliata). In, The Ecology
          of Arboreal Folivores. G.G.Montgomery, ed. Pp. 535-
          549. Washington, D.C.: Smithsonian Institution Press.

    1979 Factors influencing leaf-choice by howler monkeys: a
          test of some hypothesis of food selection by general-
          ist herbivores. American Naturalist 114:362-378.

Milton, Katharine
    1980 The Foraging Strategy of Howler Monkeys A Study in
           Primate Economics. New York: Columbia University
           Press.

    1981 Food choice and digestive strategies of two sympa-
           tric primate species. American Naturalist 117:496-
           505.

Milton, Katharine, T.M. Casey and K.K. Casey
    1979 The basal metabolism of mantled howler monkeys (Alou-
           atta palliata). Journal of Mammalogy 60:373-376.

Mittermeier, R.A.
    1973 Group activity and population dynamics of the howler
           monkey on Barro Colorado Island. Primates 14:1-19.

Mittermeier, R.A. and M.G.M. Roosmalan
    1981 Preliminary observations on habitat utilization and
           diet of eight Surinam monkeys. Folia Primatologica
           36:1-39.

Morton, E.S.
    1973 On the evolutionary advantages and disadvantages of
           fruit eating in tropical birds. American Naturalist
           107:8-22.

Moynihan, Martin
    1976 The New World Primates. Princeton University Press.

Neville, M.K.
    1972a The population structure of red howler monkeys (Alou-
           atta seniculus) in Trinidad and Venezuela. Folia
           Primatologica 17:56-86.

    1972b Social relations within troops of red howler monkeys.
           Folia Primatologica 18:47-77.

    1974 "Carne de monte" and its effect upon simian popula-
           tions in Peru. Paper read at the 73rd meeting of the
           American Anthropology Association, Mexico City.

Orians, G.H.
    1961 The ecology of blackbird (Agelaius) social systems.
           Ecological Monographs 31:285-312.

    1969 On the evolution of mating systems in birds and mam-
           mals. American Naturalist 103:589-603.

Otis, J.S., J.W. Froehlich and R.W. Thorington
    1981 Seasonal and age-related differential mortality by
           sex in the mantled howler monkey, Alouatta palliata.
           International Journal of Primatology 2:197-205.

Pope, B.L.
    1966 The population characteristics of howler monkeys
          Alouatta caraya) in Northern Argentina. American
          Journal of Physical Anthropology 24:361-370.

Puleston, D.E.
    1973 Ancient Maya settlement patterns and environment at
          Tikal: implications for subsistence models. Ph.D.
          dissertation, University of Pennsylvania.

Richard, A.
    1970 A comparative study of the activity patterns and be-
          havior of Alouatta villosa and Ateles geoffroyi.
          Folia Primatologica 12:241-263.

Ruch, T.C.
    1959 Diseases of Laboratory Primates. London: W.B. Saun-
          ders Company.

Schlichte, Hans-Jorg
    1978 A preliminary report on the habitat utilization of a
          group of howler monkeys (Alouatta villosa pigra) in
          the National Park of Tikal, Guatemala. In, The Eco-
          logy of Arboreal Folivores. G.G. Montgomery, ed. Pp.
          551-559. Washington, D.C.: Smithsonian Institution
          Press.

Schoener, T.W.
    1971 Theory of feeding strategies. Annual Review of Eco-
          logical Systems 2:369-404.

Shannon, R.C. and C.T. Greene
    1926 A botfly parasitic in monkeys. Zoopathologica 1:285-
          290.

Smith, C.C.
    1977 Feeding behavior and social organization in howling
          monkeys. In, Primate Ecology. T.H. Clutton-Brock,
          ed., Pp. 97-126. London: Academic Press.

Smith, James D.
    1970 The systematic status of the black howler monkey,
          Alouatta pigra Lawrence. Journal of Mammalogy 51:
          258-369.

Smithe, F.B.
    1966 The Birds of Tikal. Garden City: Natural History
          Press.

Smithe, F.B. and R.A. Paynter
    1963 Birds of Tikal, Guatemala. Bulletin of the Museum of
          Comparative Zoology, Harvard 128:245-324.

Sparks, John
    1967   Allogrooming in primates: a review. In, Primate Eth-
            ology. D. Morris, ed. Pp. 148-175. London: Weiden-
            field and Nicolson.

Trivers, R.L.
    1972   Parental investment and sexual selection. In, Sexual
            Selection and the Descent of Man. B. Campbell, ed.,
            Pp. 136-179. Chicago: Aldine.

T-W-Fiennes, R.N.
    1972   Ectoparasites and vectors. In, Pathology of Simian
            Primates Part II: Infectious and Parasitic Diseases.
            R.N. T-W-Fiennes, ed., Pp. 158-176. Basel: S. Karger.

Westboy, M.
    1974   An analysis of diet selection by large generalist
            herbivores. American Naturalist 108:290-304.

Wilson, E.O.
    1975   Sociobiology, the New Synthesis. Cambridge: Harvard
            University Press.

Young, O.P.
    1981   Chasing behavior between males within a howler mon-
            key troop. Primates 22:424-426.

APPENDIX I

MAMMALS OF TIKAL*

Canidae
> Urocyon cineroargenteus - gray fox

Cervidae
> Odocoileus virginianus - white-tailed deer
> Mazama americana - brocket

Dasypodidae
> Dasypus novemcintus - nine-banded armadillo

Dasyproctidae
> Cuniculus paca - paca
> Dasyprocta punctata - agouti

Didelphidae
> Didelphis marsupialis - Central American opossum
> Philander opossum - opossum
> Caluromys derbianus - opossum

Erethizontidae
> Coendou mexicanum - tree porcupine

Felidae
> Felis pardalis - ocelot
> Felis wiedii - margay cat
> Felis concolor - puma
> Felis onca - jaguar
> Felis yaguaroundi - yaguaroundi

Mustelidae
> Eira barbara - tayra
> Galictis allamandi - grison

Myrmecophagidae
> Tamandua tetradactyla - three-toed anteater

Primates
> Alouatta pigra - howler monkey
> Ateles geoffroyi - spider monkey

Procyonidae
> Procyon lotor - raccoon
> Nasua nasua - coati
> Potos flavus - kinkajou
> Bassariscus sumichrasti - ring-tail guayu

71

Sciuridae
     Sciurus _deppei_ - squirrel
     Sciurus _yucatanensis_ - squirrel

Tapiridae
     Tapirus _bairdii_ - tapir

Tayassuidae
     Tayassu _tajacu_ - collared peccary
     Tayassu _pecari_ - white-lipped peccary

*Summarized from Cant 1977:44-47

APPENDIX II

ALLOGROOMING

7-22
14:17   Adult male grooms adult female 1 min.

7-26
13:50   Adult male grooms adult female 1 min., adult
         male moves away

7-27
09:27   Juvenile male grooms adult female 1 min.
14:13   Juvenile female grooms adult female 1 min.

7-30
13:10   Juvenile female grooms adult female 1 min.

7-31
13:02   Adult female tail-hangs within reach of adult
         male, solicit grooming? Adult male grooms her
         1.5 min.
13:05   Adult female continues to tail-hang, juvenile
         female grooms adult female 30 sec.; adult fe-
         male tail-hangs until 13:10, inactive

8-2
10:45   Juvenile female grooms juvenile male 1 min.
16:40   Adult male grooms infant 30 sec.

8-13
13:20   Adult male grooms adult female 15 sec.

8-16
06:25   Juvenile (unknown) grooms adult female 3 min.
06:35   Juvenile (unknown) grooms adult female 30 sec.

8-22
13:09   Juvenile female grooms juvenile male 30 sec.

8-30
15:29   Juvenile female grooms juvenile male 30 sec.

9-31
10:26   Juvenile male grooms tail-hanging adult female
         1 min.

9-4
13:10   Juvenile female grooms juvenile male 1.5 min.

73

9-5

08:40   Adult female tail-hangs for juvenile female who
        then grooms her 30 sec.
08:44   Adult female solicits grooming via new tail-hang
        from juvenile male who then grooms her 1 min.
13:31   Adult male grooms adult female less than 1 min.

9-6

10:58   Juvenile female grooms adult female (infant rest-
        ing with adult female) 1 min.

9-7

11:18   Adult female grooms juvenile female 30 sec.
12:17   Juvenile female grooms adult female 1 min.

9-8

08:12   Juvenile female grooms juvenile male who is tail-
        hanging less than 1 min.

total = 24 grooming bouts observed

      = 1315 sec. (21.9 min.): avg bout duration = 55 sec.

received: 77% adult female   gave: 46% juvenile female
            19% juvenile male   30% juvenile male
            02% juvenile female   22% adult male
            02% infant   02% adult female
            _____   _____

            100%   100%

HISTROY OF AGE/SEX COMPOSITION

Coelho: June – August 1973
       4 groups totaling 25 howlers
       min. 6 per group
       max. 7 per group
          2 multimale groups: one = 2 AM, 1 AF, 2 J, 1 I
          2 unimale groups: one = 1 AM, 2 AF, 2 J, 1 I

Schlichte: October 1974 – January 1975
       2 groups totaling 11 howlers
       study group = 2 AM, 2 AF, 2 J, 1 I
       north of study group = 1 AM, 2 AF, 1 J
       sighted 1 solitary AM, 1 solitary AF with JF

Cant: March 1975 – April 1976
       2 groups totaling 11 howlers
       Schlichte's study group (same "old" male), other members
            equaled same composition
       group to south = 1 AM, 1 AF, 1 JM, I (born spring 1976)
       transit = 2 groups of 2 animals each and 1 solitary AM

Cunningham & Caywood: June – September 1978
       2 groups totaling 10 howlers
       study group "south": occupied range south of Schlichte's
            study group = 1 AM, 1 AF, 1 large JF, 1 JM, 1 IM
       "north" group: occupied range similar to Schlichte's
            study group, could be remnant
            = 1 AM, 1 AF, 2 med JM, 1 small JM
       3 sightings of solitary AM, unknown if same animal

Bolin: December 1978 – March 1979
       Tikal = 3 groups, all monogamous; age/sex categories or
            number of group members unknown
       Belize = 13 groups totaling 55 howlers
            min. 3 per group
            max. 7 per group
            avg. = 4.4 per group
            11 groups monogamous
            1 multimale group = 2 AM, 2 AF, 1 J, 2 I
            1 unimale group = 1 AM, 2 AF, 2 J, 2 I
            2 sightings of solitary AM

SEXUAL ACTIVITY

7-23
10:53   Following an inactive period by both adults, adult male approached adult female and sniffed her gentals; adult female moved away, adult male then sniffed/licked branch she was sitting on; both animals moved from view
10:55   Next instant, both adults inactive

7-26
15:55   Following group elimination, adult male sniffed adult female's genitals; adult female moved away
16:00   Next instant, both adults feeding

8-5
12:33   Following adult male inactive/adult female move, adult male inspected adult female's genitals
12:35   Next instant, both adults inactive

9-3
13:17   "North" group began to roar (our group seemed to be moving in their general direction)
13:23   Adult male began roar, facing direction of north group
13:28   Adult female joined male in roaring
13:38   Adult female ceased roar
13:40   Adult male ceased roar
13:43   North group ceased roar
14:43   Adult male began roar, north group responded, north group seemed close, but not visible
14:47   Adult female joined male in roaring, both faced direction of north group
14:55   North group ceased roar
14:56   Adult female ceased roar
15:00   Adult male from north group very close, two trees away
15:02   Adult male from north group approached, breaking branches as he came
15:04   Adult male urinated/defecated, chased lone north male out of tree, others stayed behind; both males were grunting and howling at each other
15:09   Adult male returned, continued to roar; north group continued roaring, but had moved away
15:17   Adult male ceased roar

76

interim: Feeding, snacking, moving, inactive but no sleep
          north group heard roaring faintly, light rain

16:37 Adult male began roar, north group responded
16:45 Adult female joined adult male in roar
16:53 Adult female ceased roar
16:58 Adult female walked to end of branch towards north
       group and presented to her group male who had fol-
       lowed. He then copulated with her, approximately
       45 sec. with several thrusts and assumed ejacula-
       tion (male tensed)
17:00 Male roaring, female inactive
17:05 Adult male continued roaring
17:11 Adult female joined roar
17:14 North group sounded farther away, still roaring
17:18 North group ceased roar, adult female ceased roar
17:28 Adult male ceased roar

9-4

16:20 Adult female urinated/defecated, adult male sniffs
       branch