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THE COSTS AND BENEFITS OF NOCTURNALITY FOR AOTUS TRIVIRGATUS (THE NIGHT MONKEY)

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THE COSTS AND BENEFITS OF NOCTURNALITY FOR AOTUS TRIVIRGATUS (THE NIGHT MONKEY)

by

PATRICIA CHAPPLE WRIGHT

A dissertation submitted to the Graduate Faculty in Anthropology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1985

This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree Doctor of Philosophy.

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Abstract

THE COSTS AND BENEFITS OF NOCTURNALITY FOR AOTUS TRIVIRGATUS (THE NIGHT MONKEY)

by

Patricia Chapple Wright

Adviser: Professor Warren G. Kinzey

The purpose of this research was to document the behavior and ecology of the only nocturnal monkey in two different natural habitats to understand better the cost and benefits of nocturnality for Aotus.

First, Aotus trivirgatus and Callicebus moloch (a diurnal monkey with similar body weight, group size, and monogamous social system as Aotus) were compared and constrasted in the same undisturbed tropical rain forest in Manu National Park, Peru, for 15 months. Differences were found in (1) diet (in the dry season Aotus frequented large-crowned fruit trees and nectar sources, while Callicebus increased leaf-eating); (2) choice of sleeping sites (Aotus used only five habitual obscure sleeping sites over an annual cycle, while Callicebus used 30 relatively open sleeping sites annually); (3) timing of exit from and entrance into sleeping sites (Aotus exit and entrance times were consistently correlated with sunset and sunrise, while Callicebus entrance and exit times varied); (4) loud calling behavior (Aotus called once a month when

the moon was near full, while *Callicebus* called frequently each month); and (5) attacks by predators (*Aotus* was never attacked but *Callicebus* was attacked five times). These data suggest that the behaviors could have been influenced by nocturnal and diurnal differences in interference competition and predators.

To confirm these two benefits of nocturnality, I studied *Aotus* five months in Paraguay in a habitat where diurnal eagles were rare, large nocturnal great horned owls were common, and potential competitors (capuchin and spider monkeys) were absent. During this study, many aspects of *Aotus* behavior were similar to the behaviors of *Callicebus* in the rain forest. *Aotus* in the Paraguayan Chaco habitat was highly folivorous in the months of scarce resources. *Aotus* in Paraguay also used a variety of sleeping sites (42 different trees in 5 months), varied the timing of entrance into and exit from sleeping trees, traveled and fed from one to three hours in daylight, and avoided the great horned owls. In this very specialized habitat where diurnal predation pressure and interference competition from large monkeys does not occur, the night monkey was active during daylight as well as at night.

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Many people have generously contributed to the completion of this project. First, I'd like to thank my committee for their advice and patience. *Warren Kinzey* has given enthusiastic support from the very beginning to the final stages of this dissertation. This thesis would never have been started or completed without his advice and understanding. Warren's expertise, especially concerning *Callicebus* has enlightened this manuscript.

John Oates gave me my formal training in primate behavior, methods, and ecology. His careful criticism, excellent advice, and guidance have greatly enriched this dissertation. I appreciate John carrying earlier versions to Africa to critique. John Oates brought an Old World perspective to a New World project.

John Terborgh initially suggested that I do my ecological comparision of *Aotus* and *Callicebus* in Manu National Park. Discussions with John Terborgh helped inspire some of the theoretical frameworks for this project. His ecological expertise was always helpful at Cocha Cashu.

Eric Delson persuasively advised me to finish this dissertation as soon as possible.

Special thanks to *John Fleagle* for his enthusiastic support, encouragement, and advice at all stages of this work. Without his help, the field work would not have begun

in 1980. In addition, he maintained my captive Aotus throughout my field work in Peru and Paraguay.

At Cocha Cashu my work was enriched by the scientists diligently recording behavior and ecology of other species of plants and animals. Special thanks to Charles Janson for his ecological expertise, fountain of ideas, and thought-provoking discussions. I am grateful to CJ for first introducing me to the Manu National Park in 1979. Our dissertation projects coincided at Cocha Cashu in 1980-1981, allowing us to compare and contrast two monogamous and two polygynous species at the same time. My project was enriched by our discussions and comparisions as well as by CJ's generous sharing of data, including fruit trap and insect abundance information.

Many thanks to Louise Emmons for teaching me useful techniques for trapping and marking nocturnal mammals and for helpful discussions about tropical night life.

Special thanks to Robin Foster for sharing with me his vast knowledge of tropical botany. RF taught me to identify the plants at Cocha Cashu and helped identify fruits eaten by the monkeys I studied. His patience and understanding helped me through the trials of beginning a field project. This field work on Aotus was greatly helped by the use of the Varo Noctron IV image intensifier borrowed from RF.

Anne Wilson Goldizen contributed many group sightings and counts, sleeping tree locations, and solitary animal locations of Aotus and Callicebus at Cocha Cashu. AWG's ardent dedication to monkey-watching is appreciated and I thank her for many wonderful discussions at Cocha Cashu, especially during the rainy season of 1981.

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Cirilo Lujan Munares was my Perivuan assistant during the first Aotus study, and I am grateful to him for his help, both in June, July, and August, 1980, and at Cocha Cashu in December, January, and February, 1981. CLM's skills at following night monkeys, coupled with his cheerful nature and good sense of humor made him invaluable in the field.

I appreciate the help of *Curtis Freese* in expediting permissions for me to study *Aotus* in Paraguay when a war had prevented me from entering the Argentine Chaco.

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Many thanks to *Linda Taylor* who typed the final drafts, combining her editorial expertise and her knowledge of primate behavior to improve the final product. Jorg Ganzhorn kindly helped with statistics.

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In 1976 it was Mrs. Nancy Mulligan who funded my first expidition to find out what those monkeys do in the night. Barbara Maines provided me with wisdom and advice in dark moments and to her I am very grateful. Wilson McCagg gave me help so that I could begin graduate school.

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Doing field research at a remote site and writing up a dissertation is not easy for a single parent. I very much appreciate the friends and relatives who cared for Amanda throughout various stages of this project: Betty and Jim Wright, Edward and Julie Chapple, Jill and Bob Parliament, Christopher and Maureen Chapple, Rosa Wehr of Peru and all the Cocha Cashu scientists.

And to Amanda, my daughter, who spent her elementry school years waiting for her mother to complete her Ph.D., I dedicate this thesis and thank her for her patience and cheerfulness at Cocha Cashu and in the United States.

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CHAPTER I

INTRODUCTION

A. Scope of the Problem

Aotus is the only nocturnal primate in the Neotropics and the world's only nocturnal monkey. Nocturnal prosimian primates (*e.g.*, lorises, mouse lemurs, tarsiers, and galagos) live in Asia and Africa, but *Aotus* stands alone as the only nocturnal anthropoid primate. It is unusual that this one instance of nocturnality arose during the evolution of otherwise diurnal monkeys and apes. Trends in the evolution of anthropoids (Le Gros Clark 1959) are those reinforced by daytime activity cycles. In anthropoid primates, emphasis on olfaction is decreased and replaced by emphasis on vision, especially color vision. Diurnal monkeys locate ripe fruits at a distance by keen color vision, and often travel directly from one fruit tree to the next. Because a great deal of ripe fruit may be present at a single site, large numbers of animals may feed together; opportunities for increased sociality arise. The increased brain size relative to overall body size in higher primates is attributed, in part, to the interrrelationships of frugivory, increased sociality, and large home range size (Milton and May 1976; Clutton-Brock and Harvey 1977b, 1978; Harvey *et al.* 1980). All of these factors are responses to the demands of a diurnal life style.

A nocturnal life style, on the other hand, makes different demands. The main disadvantage of nighttime activity is the difficulty of clear vision in low light. Low light levels may restrict an animal's ability to travel, to locate ripe fruit, and consequently group size and degree of sociality. Nocturnal prosimian primates adapt to these problems by having small home ranges, small group size, and by dependence on olfaction and audition rather than vision (Charles-Dominique 1975,1977; Clutton-Brock and Harvey 1977a).

Morphological evidence indicates that the ancestor of _Aotus_ was diurnal. The eye of _Aotus_ has no trace of a _tapetum lucidum_, the reflective structure behind the photoreceptors, found in nearly all nocturnal mammals and all nocturnal strepsirhines (Jones 1965; Jacobs 1977a, 1977b; Pariente 1978, 1980). _Aotus_ does have a duplex retina with both rods and cones, resulting in poorly-developed color vision (Jacobs 1977a, 1977b). _Aotus_ has a typical platyrrhine nose; the olfactory bulbs in the brain are no larger than those of other small New World primates (Hershkovitz 1977). In every aspect of morphology, _Aotus_ is a true cebid. The only anatomical specializations for a nocturnal life style exhibited by the genus are increased eye size and fewer cones with more tightly packed rods than are found in other cebids (Jacobs 1977a).

Molecular evidence corroborates the morphological evidence of a close affinity between Aotus and other Cebidae (Goodman 1976; Baba et al. 1980). Aotus is not a `missing link' between prosimians and anthropoids, (Hanson and Montagna 1962; Perkins and Meyer 1980), but rather, a monkey probably most closely related to Callicebus (Rosenberger 1979).

The evolution of nocturnality in Aotus is a paradox. Why would its cebid ancestor, equipped with color vision and lacking a strepsirrhine nose necessary for acute olfaction, become active primarily at night? At first glance, the selection pressures to remain diurnal appear great, and yet night monkeys are found throughout South American forests. In evolutionary terms, Aotus is a success. There must be advantages in the nocturnal way of life for this genus.

Prior to the collection of data presented in this thesis, little was known about the behavior and ecology of night monkeys. Moynihan (1964) described behavior patterns based mainly on observations of captive specimens. Thorington et al. (1976) placed a radio collar on a young male Aotus and followed it for nine days in a Panamanian forest. Wright (1978) followed one group of night monkeys during a nine-week pilot study in Puerto Bermudez (Peru). Previous work has shed little light on the costs and benefits of nocturnality for the only extant night-living monkey.

To understand more clearly Aotus behavior and ecology, I began my research in the rain forest of the Manu National Park (Peru). I chose to observe also Callicebus moloch to provide comparative data because the two monkeys have in common body size, monogamous mating system, and group size, and because the two species may be closely related (Rosenberger 1979). The ecology and behavior of the two sympatric species were studied for 15 months at the same site. Comparisons were made concerning diet, sleeping sites, ranging patterns, aggression between groups, and intergroup calling. There were marked differences in the behavior of the two species. The data suggest that there are two main benefits derived from being nocturnal for Aotus:

1) absence of interference competition from diurnal monkeys; and

2) avoidance of diurnal raptors.

I then hypothesized that if these two selective pressures were eliminated, Aotus activity patterns would reflect the difference. Aotus does occur in a habitat where there are no large competing monkeys and few, if any, large hawks or eagles...the Chaco of Paraguay. Furthermore, a large nocturnal predator, the great horned owl (Bubo virginianus), is common in the Chaco. This owl occurs rarely in the rain forest. I predicted Aotus would be active during the day in this environment because of the different set of selective pressures inherent in it. I observed *Aotus* in the Chaco for four months to test the hypothesis.

B. Review of the Literature on *Aotus trivirgatus*: Morphology, Geographic Range, Taxonomy, Behavior, and Ecology

1. Morphology

Aotus is a member of the Family Cebidae (Napier and Napier 1967). It is specifically identified by its large eyes and black and white facial markings. Above the eyes are two white to buffy semilunes outlined by three black stripes, two lateral and one medial, all three converging on the crown. The exact pattern of the stripes varies individually and subspecifically. The dorsal coat varies from brown to grey to reddish, but in general has a grizzled, agouti appearance due to the banding of each hair. The ventral coat differs among populations, ranging from bright orange, to yellow, to buff-white. Hershkovitz (1949) comments that *Aotus* from high altitudes have more muted coloration and longer hair. The non-prehensile tail is nearly as long as the body and its distal half is usually black. Aotus has small rounded ears; hands and feet with prominent tactile pads; and true nails (Hill 1960; Biegert 1961). Hanson and Montagna (1962) describe the extensive glands in the sternal and subcaudal areas of Aotus. Hill (1960) describes a "felted mat" of thick hair on an oblong glandular field on the ventral aspect of the base of the tail I've observed an elongated grooming nail on the index toes of Aotus, a structure which may be likened to the grooming claw found in prosimians. The combined length of head and body ranges form 240mm to 475mm, while the length of the tail ranges from 220mm to 418mm (Hill 1960; Napier and Napier 1967). Body weights of adults range from 780 gms to 1249 gms (Hill 1960; Napier and Napier 1967). There is no marked sexual dimorphism, although Kinzey (1972), Orlosky (1973), and Swindler (1976) report significant sexual dimorphism in the buccolingual diameter of upper canine teeth of 5%, 11.5%, and 7.7% respectively. Kinzey (1972) also reports 10% dimorphism in unworn maxillary canine height.

Anatomical specializations in relation to diet

Limbs and tail

Stern (1971) describes Aotus as a quadrupedal leaper without prehensile tails. The long tail is used for balance during locomotion and terminal branch feeding.

Digestive system

The digestive system includes a simple stomach, a capacious and broad caecum, and a medium-sized colon in comparison to other New World monkeys (Hill 1960; Chivers and Hladik 1980). Sacculated stomachs are found exclusively in folivorous Old World primates. Large caeca are found in many New World monkeys, including *Callicebus*, *Aotus*, *Ateles*, *Cebuella*, and *Alouatta* (Hill 1960; Chivers and Hladik 1980; Milton 1981). The function of the caecum may be the decomposition of cell wall materials (Bauchop 1980), and/or fermentation of fruit pectins (Milton 1981). The ascending colon of *Aotus* is narrower than that of *Callicebus* and contains well-defined sacculations and taeniae that are absent in *Callicebus*. Transverse and descending colons are similar in the two genera (Hill 1960). It should be noted that the gut is not extremely short as seen in highly insectivorous genera like *Saimiri*, *Saguinus*, and *Tarsius*, nor is it especially elongated as seen in the leaf eating specialists *Indri*, *Propithecus*, or *Lepilemur* (Chivers and Hladik 1980). No differences in gross gut morphology have been demonstrated between *Aotus* and *Callicebus* which would suggest that one is more insectivorous or folivorous than the other.

Tooth morphology

The canines of *Aotus* shows little sexual dimorphism, and barely protrude beyond the tooth row.

Although *Aotus* has slightly longer canines than *Callicebus*, they are not effective in opening fruit with thick husks or tough ectocarps.

Molars: The quadritubercular molars suggest a highly frugivorous diet. *Aotus* has a less pronounced *cristid obliqua* and a more bunodont talonid basin than *Callicebus*, indicating that the molars are better adapted for frugivory than folivory (Kinzey 1978). Kay (1974) has demonstrated that among primates, more folivorous groups are distinguished from more frugivorous groups by having well-developed molar shearing structures. Kinzey (1978) describes *Callicebus* molars as having elongated shearing blades (*cristid obliqua*) which could facilitate shearing leaves.

Mandibular corpus depth: The mandible of *Aotus* is not deep like that of *Alouatta* and *Callicebus*, implying that there is less specialization for leaf eating (cf. Ankel-Simons 1983).

2. Range

Aotus trivirgatus is the most widespread species of primate in South America. It is found in forested areas from about 81° W in Panama (the Azuero Peninsula), south to the Gran Chaco in Argentina and Paraguay, and as far east as the Paraguay River. The genus has been found from sea level up to about 2770m altitude (Napier 1977). Although its range includes the Amazon drainage south to Mato Grosso do Sul and east to the Amazon's mouth, *Aotus* has not been found in the Guianas (Cabrera and Yepes 1957; Muckenhirn *et al.* 1976; Mittermeier 1977) nor in the eastern coastal forests of Brazil.

3. Taxonomy and Genetics

Since 1949 most authors have recognized only one species in the genus *Aotus*, *Aotus trivirgatus* (Hershkovitz 1949; Napier and Napier 1967; Thorington and Vorek 1976). However, the genus contains a number of distinct forms. Elliott (1913) listed 15 which he considered full species; Hill (1960) recognized ten subspecies; Napier and Napier (1967) listed nine subspecies. Hershkovitz (1949) examined and reclassified all specimens found in the British Museum (London) and the Musie de L'Histoire Naturelle (Paris), retaining only five subspecies. Hershkovitz is currently revising the taxonomy of *Aotus* and has provisionally divided *Aotus* into nine species (Hershkovitz 1983). Thorington and Vorek (1976) studied the coat color, permanent tooth eruption, craniometry, and sequence of epiphysial union and described three different phenotypes, but they continued to recognize only a single species.

Recent cytogenetic studies have shown that *Aotus* populations vary in chromosome number and morphology. DeBoer (1971, 1971, 1974), Brumback (1973, 1974), Brumback *et al.* (1971), and Brumback and Willenborg (1973) found three different chromosome numbers. On the other hand, Ma *et al.* (1976, 1978) described nine karyotypes from five major areas in South America. In addition to these, Yunis *et al.* (1977) described natural hybrids found in Colombia. Thorington and Vorek (1976) suggested that these chromosome numbers vary clinally, a view consistent with the single-species argument. Ma (1981) also agreed with the single-species approach. In this dissertation, I shall use the five subspecies of Hershkovitz (1949), with recent reclassifications by Hershkovitz (1983) noted in brackets.

The population I studied in Peru belongs to *A. t. nigriceps* [*A. nigriceps*] chromosomal group VII (females 2n=52; males 2n=51). The Paraguayan population belongs to the *A. t. azarae* [*A. azarae*] group (females with 2n=50; males 2n=49)(Ma 1981; Colillas personal communication). Both populations are classified in the red-necked species group described by Hershkovitz (1983).

4. Ecology and Behavior of Wild Aotus

Much of the published information on the ecology and behavior of *Aotus* in the wild has come from anecdotal reports by early naturalists, *e.g.*, Azara (1801), Humboldt (1812), Rengger (1830), Wallace (1853), Bates (1863), Miller (in Allen 1916), Kreig (1930), Mann (1930), Walker (1941), and Sanderson (1957). Brief studies of *Aotus* were conducted on Barro Colorado Island (Panama) by Chapman (1929, 1938) and Enders (1930, 1935). General on *Aotus* may be found in Cruz Lima (1945), Cabrera and Yepes (1957), and Hernandez-Camacho and Cooper (1976). The Hladiks (Hladik *et al.* 1971) made inferences about the diet from examining the stomach contents of *Aotus* on Barro Colorado Island. Moynihan (1964) reported incidental observations of wild *Aotus*, also on Barro Colorado, over a five-year period.

There are also some comments about behavior and ecology in the many census reports on *Aotus* from various parts of South America. Struhsaker *et al.* (1975), Cassidy (1976), and Green (1978) included *Aotus* in their surveys of Colombian primates; Heltne (1977) censused *Aotus* in northern Columbia and later in Bolivia (Heltne *et al.* 1975). Neville *et al.* (1976) referred to *Aotus* in their survey of Peruvian primates, while Rathbun (1980) determined population density in Argentina's eastern Formosa Province and northeastern Chaco Province.

The first systematic attempt to document the behavior and ecology of *Aotus* in the wild was conducted by Thorington *et al.* (1976). A young male *Aotus* was released into a forest in Panama and then radiotracked for nine days to determine home range and behavior. Later Wright (1978) followed a group of two adults and two juveniles for nine weeks in Puerto Bermudez (Peru), while gathering data on home range, activity patterns, and general behavior. Prior to the study reported here, these were the only documented reports on the behavior of Aotus in its native habitat.

5. Behavior of Aotus in Captivity

Two studies have been done in captivity on weight gains, dental eruptions, and birth weights of Aotus in captivity (Hall et al. 1977; Rendquist pers. comm.). Dixson et al. (1981) described the onset of puberty in male Aotus and Hunter et al. (1979) was the first to document accurately the gestation period of Aotus at 133 days. Studies of infant development and parental behavior have been by done English (1934), Dixson and Fleming (1981), and Wright (1981, 1984). Moynihan (1964) produced a major work on the behavior patterns of Aotus with special emphasis on vocalizations.

6. Mating System

The data, based on both captive and wild animals, agree that Aotus has a monogamous social system, with a pair remaining together for a number of years. One infant is born each year; each infant remains with the family group until it is two and one half to three years of age (Wright 1984). The male assumes most of the parental care (carrying, playing, instructing in feeding, protecting from danger) from the first week after birth throughout the first year of the infant's life. The father stops carrying the infant when it is four months old. The mother nurses the infant until it is seven or eight months old. This biparental care system is found in half of the species of New World primates, including *Callicebus moloch* (Kleiman 1977; Fragaszy *et al.* 1982; Wright 1984).

CHAPTER II

STUDY SITES AND METHODS

A. Description of Study Sites

1. Cocha Cashu (MNP), Peru

The behavior of both *Callicebus moloch brunneus* and *Aotus trivirgatus nigriceps* was studied for a total of 15 months (September 1, 1980 - August 15, 1981; October 1, 1982 - December 8, 1982) at the Cocha Cashu Biological Research Station in the Manu National Park (MNP), Department of Madre de Dios, southeast Peru (71° 22'W; 11°W 52'S)(See Fig. 1). This isolated park contains 15,000 km^2 of virgin forest. The research station is at 400m elevation in "tropical moist forest" (Holdridge 1967), with an annual rainfall of approximately 2000mm. Cocha Cashu is located on rich, alluvial floodplain soil which supports a high diversity of plants and animals. There are 13 sympatric species of monkey, ten of which are common. This is one of the highest counts in any area of the Neotropics (Table 1).

The research station is located near an oxbow lake, from which it takes its name (Cocha Cashu). The area surveyed by trails is 2 km^2. The main study area is located between the banks of the meandering white water Manu River and the shoreline of the oxbow lake. A mosaic of habitats exists within this study area (see Terborgh 1983), including a well-drained, rarely-flooded primary forest; poorly-drained floodplain forests; swamps containing stands of *Ficus trigona* trees; secondary forest with large numbers of *Cedrela* and *Ficus insipida* trees; and, river edge habitat containing *Cecropia sp.*, *Tessaria sp.*, *Gynerium sp.*, (*Cana brava*). (Fig.2)

2. La Golondrina Ranch, Presidente Hayes, Paraguay

The behavior of *A. t. azarae* was studied for four months (May, 1982 - September, 1982) at the ranch, La Golondrina, owned by Diane and Anthony Espinoza. It is located in the department of Presidente Hayes, north of Asuncion, between the Rio Confuso and Rio Pilcomayo, Paraguay (24° 25'S; 58° 40'W).(Fig.1) This study site was located in the Chaco on an undisturbed five hectare "habitat island" of dry, subtropical forest (Holdridge 1967) surrounded by palm savannah. The study site is approximately 200m above sea level. Average precipitation for Asuncion, 70 km south, is 1340mm of rain per year during a forty year span. The Chaco is the most southern and southeastern extension of the range of *Aotus*; the only sympatric nonhuman primate at the study site is *Alouatta caraya* (the black howling monkey). This site was chosen because hunting has not been allowed on the ranch for 50 years, and that area of the ranch is relatively undisturbed.

B. Methods in Peru

Methods used to sample both species were similar, but due to differences in habitat preferences and circadian activity patterns, methods had to be somewhat altered as discussed below.

1. Censuses of Aotus and Callicebus

Censuses of both Aotus and Callicebus were conducted at the beginning of the study in September, 1980, and again in October, 1982, to determine population density, group composition, and age of offspring in each group. At the beginning of the study, I selected a group on which to focus my observations, a focal group, for each species and mapped the location and group composition of neighboring groups. The focal Aotus group was Group I (the River Group), which lived along the river's edge (Fig. 3); the focal Callicebus group, Group II (House Group), lived along the lake's edge (Fig. 4). An additional Callicebus group, Group I, which had a territory that overlapped with that of Aotus Group I, was followed for six months (from September through October 1980 and May through August 1981 [Fig. 5]).

Trail censuses were conducted over three nights in September, 1980, for Aotus, and for ten days in September, 1980, for Callicebus. For each census, I traversed 6km of trail, within an area of a square kilometer. Each census required four to five hours. When an individual was sighted, I recorded all animals in view, location, number and size of individuals in the group, as well as information on any infants being carried. Because individuals within a group of *Callicebus* and/or *Aotus* may travel 1 to 10 meters apart in MNP, I could usually count all group members if I waited and watched the same area for 10-15 minutes. Individual characteristics, such as scars, short tails, or ringed tails, distinguished members of some groups. Recognition of these distinctive individuals and knowing ages of juveniles and infants made it possible to distinguish and identify groups, as well as individuals.

During the censuses of *Callicebus*, I could see about 25 meters on either side of the trail. The distance of each monkey sighted from the trail was noted. The day censuses began at 07:00 hours. On the sixth through tenth censuses I did not encounter any new groups of *Callicebus*. Thereafter, I conducted a monthly census to determine group size, dispersal of subadults, births, and infant development for each group. The same 6 kilometers of trails were censused repeatedly.

Night censuses of *Aotus* were less successful. They began at 18:30 hours. Most nights I detected one group, during only one census did I hear two or perhaps three groups. When I learned later (October 1980) that ten groups occupied the area censused, I decided that night trail censuses were of little value and terminated them.

In place of the trail censuses of Aotus, I developed a more valid method for censusing at night which I have termed the vocalization census. This is based on the knowledge that Aotus emits loud calls during the week before the full moon. During this time, a loud call is given constantly for periods of an hour or more in the early evening, usually between 18:00 and 21:00 hours (Chapter 3). Because these long distance vocalizations (which can be heard by humans over a distance of 500m) are contagious, accurate counts of the number of groups in an area can be obtained on those evenings. I used this method on October 18 and 27, 1981, and on January 22, February 13, March 16 and 19, 1982. The main problem with the vocalization census is that it is impossible to predict on which night of about 7 the animals will be vocalizing; also there is no certainty that all groups will call. Thus, the census yields a minimum number of groups per area.

Using the same method, counts of Callicebus groups were tabulated from compass readings of their dawn calls. Callicebus was thus censused on 16 mornings: January 10,11,12; February 4,6; March 3,6; April 4,6,7,27; May 1,2,3; June 5; and July 5, 1981. However, because all groups did not always call during "call" days, this also provides a minimum count for the number of groups estimated to populate an area. Unless one can run quickly from group to group, this type of census does not provide data on group size or timing of dispersals and births.

In addition to my observations, I obtained many counts of group size, size of infants, location of sleeping trees, and location of groups, from the observations of other primatologists and ecologists working in MNP. (See Acknowledgements).

2. Study Groups and Sampling Periods

The ideal plan was to conduct monthly a 5-day sample on one *Callicebus* group, followed by a 5-day sample on an *Aotus* group, providing they had overlapping home ranges. I chose 5-day periods for sampling for two reasons: 1) other researchers (*e.g.*, Chivers 1974; Struhsaker 1975; Kinzey 1977) used five or six-day periods for sampling; and, 2) five days is about the limit of my physical endurance for continuous 12-hour samples without a day's break or without help from an assistant. I did succeed in obtaining at least four full nights of data on *Aotus* per month, although it was not always possible to obtain these data on consecutive nights. Because of the frequent use of a single sleeping tree by *Aotus*, finding the group at dusk was seldom a problem. *Aotus* groups at Cocha Cashu were not intimidated by my presence, and allowed me to follow underneath them from the first night of observations. All data presented on *Aotus* in this thesis will be those collected from the focal group

(River, I) except where indicated (*e.g.*, intergroup encounters, loud calls, and census information).

The *Callicebus* group (Study Group I) that had an overlapping home range with the focal *Aotus* group, could be followed only during September and October, 1980; May-August 1981; and October-December, 1982. During the period from November, 1980, until May, 1981, this group fled into a vine tangle whenever I was near.

In January, 1981, I began to follow a group of *Callicebus* (Study Group II) which had been studied for a eighteen days by Kinzey (1978) and an additional week by Janson and Terborgh (Terborgh 1983). I obtained a minimum of four consecutive full day samples on this group for eight months (January-August) in 1981, and then for an additional three months in 1982 (October-December). Data presented on *Callicebus* will be data collected from Study Group II, except where indicated.

During May-August (1981) and again in October-December (1982), I obtained data on each of the two groups of *Callicebus* for three-five consecutive days during the same month. Comparisons between the two groups were useful for several reasons: 1) differences in ecology and behavior that were idiosyncratic or due to individual variation could be distinguished from more typical *Callicebus* behaviors, and, 2) ecological variability between the lake and river habitats (in fruit availability, interference competition, and sleeping tree availability) could be measured and the Callicebus response to this variability could be observed.

3. Territory Size

If the supplying area of a group of animals is successfully defended against use by another group of animals in the same species (Brown and Orians 1970), when the group has exclusive use of the resources in an area, the area used exclusively and/or defended is called a territory (Burt 1943). To determine the territory of the focal Aotus group, I mapped all path lengths of the group for the year of study. I then drew a line around the outside of the area, forming a convex polygon. Next, I mapped all aggressive encounters with other groups of Aotus for that year. Exclusive use of fruit trees is difficult to document at night, but five to ten nights each month were spent censusing the focal Aotus group's territory to determine if other groups were feeding in it. The same methods were used to determine territory size for Callicebus Groups I and II.

4. Weather

Daily measures of rainfall, and minimum/maximum temperatures were taken by resident personnel at the station. Every hour during the sampled days (or nights), I recorded weather conditions, including information on cloud cover; wind; location, phase and visibility of the moon; humidity; temperature; fog; mist; rain; and storms.

5. Plant Phenology and Botanical Censuses

Cycles of fruiting, flowering, and leaf production have been documented at Cocha Cashu in 1976-1977 and 1980-1981 (Janson *et al.* 1981; Janson 1983; Terborgh 1983; Terborgh *et al.* in press). From July 1980 to December 1981, Janson measured production of fruits and flowers in the forest by means of fruit traps. Each trap consisted of a plastic bag (0.32cm diameter) slung from a hoop raised 0.40m off the ground (Fig. 8). One hundred bags were located throughout the forest at 25 meter intervals. Contents of these traps were tabulated at the end of every two week period. During my study I divided the number of traps containing fleshy fruit, seeds, or flowers eaten by *Callicebus* and *Aotus* by the total number of traps set, to obtain the percent of traps containing edible fruit for the sampling period. Wind-dispersed seeds were not included in the calculations because monkeys were never observed to eat these.

Fruit traps provide an overall estimate of fruit and flower productivity in the forest. However, I also wanted an estimate of individual variation of productivity and timing of fruiting of certain species. I therefore maintained records of phenology of 176 trees of 44 species on which monkeys fed. Once monthly these trees were visited, observed on all sides with the aid of binoculars, and scored by amount of fruit, flowers, and new leaves. Scores ranged across a scale of 0-5: 0 = no ripe fruit (leaves or flowers); 1 = few ripe fruits (new leaves or flowers); 2-4 = gradients in between; 5 = abundant ripe fruit. A fruiting period usually lasted two weeks, so that occasionally fruiting periods were missed in the monthly censuses. Therefore, it would have been better to have conducted phenology censuses at one or two week intervals. Due to time limitations, this was not possible.

Density and numbers of different plant species in the territories of the study groups were determined by transect enumerations. Eighteen species which were most often used by monkeys were selected and censused five meters on each side of the 10 meter-wide path for 1000 meters of trail within the territory of each main study group (2000m in all). Five hundred meters of trail in each territory was near river or lake edges, 500 meters were located in upland forest. All individual trees were counted.

Additional transects were made to determine forest structure in two different 10 hectare territories. I recorded the number of lianas per tree, tree height, trunk diameter, crown diameter, and crown depth for all trees over two meters tall, in a total of one half hectare ($5000m^2$). Fifty meter stretches of trail were randomly selected and censused, 5 meters on each side (10 m total), for a total of

5000 m^2 (one half hectare) per territory. The total census included an entire hectare out of the combination of the two territories (20 hectares).

Basic data were recorded for every tree or vine which *Aotus* or *Callicebus* exploited. Identification of species, estimation of numbers of fruits available during each feeding session, height of tree, crown diameter and depth, and location of each tree were recorded. Identification of plants was done by Robin Foster during the three months from September 1980-December 1980. For the remainder of the study period, plants were identified by collecting fruits, flowers, and leaves for comparison with copies of herbarium specimens brought from the Field Museum of Natural History by Foster. Six bound volumes, containing descriptions of over 1000 species, were available for comparisons. Unidentified plants were collected and sent to the Field Museum for identification.

6. Insect Availability

Three different ecological projects were developed to quantify insect availability. These were:

a) Light Trap Method: Janson constructed a fluorescent light trap (powered by a 12 volt car battery and solar panel) which was located directly above a large bucket and white sheet (Terborgh *et al.* in press). Before dawn on sample nights, all insects were collected from the sheet and out of the bucket. Insects were sampled six nights per month: three nights on the rising half moon and three on the waning half moon. Insects were counted, identified by class, and then weighed. Insects captured included specimens of Lepidoptera (moths), Coleoptera (beetles), and Orthoptera (cicadas, crickets, grasshoppers, and katydids), all of which are eaten by Aotus. Data gathered by this method were therefore particularly useful.

b) Substrate Search: Brecht and Munn (Terborgh et al. in press), who were studying insectivorous forest birds, quantified insect availability by sampling native substrates for 20 hours each month during the period from June 1981 through January, 1982. These data included insects not attracted by night lights and which were also important prey items of Aotus. Locations of insects were recorded by substrate class: "under leaf, under bark, on trunk, or on leaf", as well as distance from the substrate (pers. comm). This technique fails to account for those insects which live in the forest canopy, and it therefore has limited applicability to my research. It is also very labor intensive.

c) Habitat Scans: I sampled insects during sessions of nighttime observations. Throughout the night on the hour, I shone a light around the area near the monkeys. I then counted all moths, beetles, spiders, cicadas, and grasshoppers. I moved the light in circles at heights of 1, 10, and 20 meters while remaining in the same position. Insects with eye shine, like moths and spiders, could be detected accurately 25 meters away, whereas counts of cicadas, and other insects without eye shine, were less precise. This technique was used as a way to obtain rough estimates of actual insect prey available when the monkeys were foraging. The limitation of this method lies in the fact that many insects, especially those high in the forest canopy, could not be seen and therefore, could not be counted.

7. Animal Trapping

To identify specific individuals radio collars were to be placed on the animals in the study group. I attempted to trap both *Aotus* and *Callicebus* individuals. Platforms were constructed 10 to 15 meters above the ground, in the trees near known travel routes of both genera. Four Tomahawk traps (squirrel and racoon size) were placed on the platforms. Traps were baited with bananas. During 56 nocturnal trapping sessions, spaced across a year, no *Aotus* or *Callicebus* were caught using this method. In a previous study in Puerto Bermudez (Wright 1978), a captive adult male *Aotus* was imported from the United States to decoy wild *Aotus* to the traps. During the 10 nights it was placed as a decoy, the captive animal failed to attract any conspecifics, even though they ranged within a few meters of the site. On six occasions, a wild-caught *Aotus* juvenile female was used as the decoy in her own home territory. She too failed to attract any other *Aotus* to her. Neither *Aotus* nor *Callicebus* has been successfully trapped in MNP or Puerto Bermudez in the Peruvian rainforest by using any form of decoy or food bait.

8. Data Recording

A field notebook was used to record data. The right hand page was prelabeled and marked off for five-minute samples. The left page was reserved for continuous notes. Unusual or rare behaviors, copulations, fighting, loud calls, grooming, and playing were all described in detail here.

9. Nightly Behavioral Sampling

Because darkness limited what I could see at night, I could not quantify *Aotus* activity patterns with the same precision as I did those for *Callicebus*. For the most part, I had to rely on my sense of hearing. Therefore, individuals often could not be identified, especially when there was no moon. Because of size differences, in full moon and at dawn/dusk, I could occasionally distinguish the youngest juvenile and infant from the adult male and female. But for activity patterns, I decided to give one score to the group as a whole using the following categories: 1) Feeding; 2) Traveling; 3) Resting; 4) Other (including playing, calling, and fighting). Because monogamous primates appear to coordinate their activities within groups (Chivers 1974; Kinzey et al. 1977; Wright 1981), I felt confident that scoring was reliable within limitations. I could hear when most of the animals were traveling, because they travel noisily, and I could count areas of fruit dropping to determine how many monkeys were feeding above me (one monkey per drop zone). The greatest inaccuracy occurred in the category resting. Because I could not hear leaf-eating or insect-foraging at night, these categories were probably subsumed under rest. My general group activity score for Callicebus was most probably comparable to the general group activity score for Aotus, with the exception that insect-foraging, grooming, and leaf-eating could not be scored.

a) Traveling: The monkeys could be heard leaping from branch to branch. I measured group spread by estimating the distance between the first animal and the last animal. However, progressions in which I could distinguish individuals could only be documented at dawn and dusk and in the bright moonlight. Then I could differentiate individuals by size.

b) Feeding: Fruits, flowers, and nectar that fell from a tree Aotus entered were noted. The tree was then checked for the eyeshine of marsupials or procyonids. Rate of ingestion of fruits and flowers was scored, if possible, by counting seeds, husks, fruits, or half eaten flowers dropped in one site for a given time period. All feeding trees were labeled with plastic flagging tape and later mapped. Fruit samples were collected for later chemical analysis (see Section D on diet, Chapter III). I returned to all feeding trees in the morning and estimated height, crown diameter and depth, and number of fruits or flowers in the tree. These measurements were impossible to do during the night.

c) Resting: If the group was stationary with no fruit or flowers falling, and no other behavior such as calling or fighting was noted, it was scored as resting. Leaf-eating and some insect-foraging can be silent; it is therefore possible that resting scores also included these activities.

d) Other Behaviors: Calling, playing, and fighting were recorded. I was unable to observe grooming bouts at night. However, *Aotus* rarely allogroom in captivity (Moynihan 1964; Wright 1981). Both calling and playing could be heard at night. These behaviors were noted during time samples and all details recorded in continuous notes.

Calling: A group was scored as calling only when it was giving the 'hoot call', the loud call. *Aotus* hoot calls consist of a continuous series of groups of two-six hoots. These calls were counted. Monkeys moved between hoots, and I tagged the path of the vocalizer every 10 minutes as I followed underneath (tags were labeled with date and time). I paced off and mapped each calling route the next day because it was too difficult to take compass readings while listening for and tape recording hoot calls. Location, number of hoots, and description of hoots were noted for all hoot calls from other groups as well. The phase, cloud cover, and angle of the moon were noted at the beginning and throughout the series of hoots. Fruiting trees along the route were also noted. None of the intragroup calls or the fight calls of <u>Aotus</u> were scored as 'calling'.

<u>Playing</u>: Active play was easy to identify because branches and leaves rustled loudly as the monkeys tumbled through the trees. At dawn and dusk, and in the full moon, silhouettes of the monkeys could also be seen in chases and play, etc.

<u>Fighting</u>: Intergroup encounters which involved ifghting wre called agonistic encounters. Fights could be identified by two signs: 1) jumping and fierce activity in the trees, and; 2) the aggressive 'resonant whoop' (Moynihan 1964) was heard.

The 'resonant whoop' was given by at least two, if not four, monkeys 4-20 times in the space of about 15 minutes. Fights occurred only in the nearly full moon, so chases could actually be seen. The group was scored as fighting if any member of the group was actively chasing any member of the other group, of if any member of the group was retreating or engaged in actual physical combat with any member of another group. Intragroup interactions were not scored as fighting. As soon as fighting was recognized, continuous sampling was begun and data on heights, interindividual distances, calls, attacks, etc., were taken.

10. Behavioral Sampling of *Callicebus*

Because I was collecting data on *Callicebus* to compare with data on *Aotus*, I first noted a 'general group activity' score at five minute intervals. The categories scored were those used for *Aotus* and did not include activities that I could see but not hear, *e.g.* leaf-eating or grooming. Sixty seconds after I recorded the comparison score, I scan sampled the group (Altmann 1974) noting activity of each group member in view. Because there were only four or five individuals per group, and visibility was usually good (about 75% of the time I could see all group members), individuals were easily identified.

Callicebus activities are defined below. Fruit-feeding begins when an individual enters a fruit tree and begins feeding on fruit, and ends when an individual exits the tree. Once begun, fruit-feeding was a continuous process. However, neither species remained in any fruit tree for more than 60 seconds after feeding ceased. Time spent traveling to and from fruit trees is not included in fruit-feeding scores.

Leaf-feeding includes each time a monkey reaches for and puts leaves, buds, petioles, and/or apical stems of plants into the mouth, chews, and swallows.

Insect-feeding and foraging includes the time an individual spends scanning for insects in addition to the time an individual spends hunting for, capturing, and ingesting insects. Because scanning time is included in the time, insect-feeding scores are over-represented in the samples. The actual intake of insects is much less than indicated by the foraging time scores (see Appendix IV for Fecal Analysis). Inclusion of scanning and hunting time differs from the method used by Terborgh (1983) and Kinzey (1972) because these authors included scanning for insects in the category 'rest'.

11. Additional Data taken for Both Aotus and Callicebus

a) Sleeping trees: All sleeping trees used by both species were labeled and mapped. Notes were taken on height of tree, habitat, height and diameter of sleeping bough, and distance from trunk that monkeys slept. Each sleeping bough was rated as to whether I could see the monkeys sleeping or not and whether or not there was dense foliage overhead. This information was used in estimations of effectiveness of defense against predators.

b) Ranging: Location of animals was noted every five minutes. I stayed under the animals, paced the distance moved using a stride of known length, and took compass readings when the monkeys strayed more than 25 meters from a trail. Both Callicebus and Aotus groups often traveled in single file along the same route, making mapping of their movements easy and accurate. The distance the group actually traveled was defined as 'daily path length'. If animals did not travel in single file, I followed under the lead animal and mapped the route accordingly. I chose the lead animal because this minimized chances of my losing the group. Because of territory size, well marked trails, and slow rates of travel, my figures for 'daily path length' are accurate to within 50 meters or less per group per day. The location of all fruit trees was accurately mapped.

c) Interference Competition: If another animal interfered with the activity of either Aotus or Callicebus by causing Aotus or Callicebus to exit a fruit tree, flee rapidly, or hide, I noted this behavior as 'interference'. I recorded the species of interfering animal, distance from the study animal, reaction of the study animal, identity of tree from which it was displaced, distance chased, and time/location of the interaction.

d) Predation Incidents: Any incident of a study animal being attacked was recorded. Data were collected on time, location, predator, reaction of study animal, success of predator, etc.

e) Forest Level Usage: Every five minutes I estimated the height above the forest floor of every study animal and recorded these figures in my field notebook.

12. Data recorded ad libitum

a) Fruits: Information on fruits included identification by species, height, crown diameter and depth, approximate numbers of fruit, and location of the fruit tree. Each individual monkey's rate of ingestion of fruit was scored. These data were necessary to quantify individual differences in feeding rate (*e.g.*, male versus female), as well as comparison of feeding rates for the same individuals at different times of the year and stages of life (*e.g.*, lactating versus non-lactating females).

b) Leaves: Leaves and vegetation were identified by species whenever possible. Vegetation was classified into the following headings: vine-leaf; vine-tip; new-leaf from mature tree (leaf flush was identified by color - either light green, red, or even white - and texture [shiny, often], and by being uncurled), the white, tender shoot found at the base of bamboo leaves; mature-leaf; or leaf-petiole. All these categories were exclusive, but in the end I lumped vine-tips and vine-leaves together as vine-leaves, and lumped leaf-petiole with mature-leaf, which resulted in the following four categories: vine-leaf; flush-leaf; bamboo-shoot; and, mature-leaf.

c) Insects: Size and type of insect eaten were noted when possible. Height of the individual and method of capture (*i.e.*, two-handed grab; one-handed grab; unroll leaf and capture in mouth; grab leaf with two hands and capture in mouth; etc.) were recorded.

d) Feces: I collected feces from *Aotus* and *Callicebus* opportunistically during the months of April through August, 1981. These fresh feces were examined within 12 hours of collection under a ten power magnifying glass. The contents of each fecal sample were classified into three categories: (1) leaves and leafy vegetation; (2) fruits including seeds; and (3) animal remains. Each sample was rated on a five point system on the quantity of category per sample, with 0= none and 5= entire composition of sample (See Appendix IV).

Vegetation was distinguished by the color of the feces (green), and the large amount of fiber present (leaf veins and petioles). Fruit could be identified by seeds (*Cecropia* and *Ficus*), color and texture of the undigested ectocarp (*Sloania*, *Clarisea*, and *Jacaratea*) by the brown color and loose consistency. I had determined from experiments with captive *Aotus* that animal remains such as chitin, feathers, and teeth were not digested. Therefore, each fecal sample was checked for animal remains. The number of pieces of chitin were counted. Percentage of insect remains in both species samples (<u>Aoltus</u> and <u>Callicebus</u>) were underestimated because soft insects such as pupae, larvae, and spiders were not indistinguishable in fecal samples.

<u>e) Calls</u>: All intergroup loud calls were sampled continuously and timed to the nearest whole second. Particular attention was paid to the height of all individuals, distances between individuals, duration and intensity of call, timing, and activities of the study group after calling ceased. Tape recordings were made of loud calls whenever possible. Tape recordings were made with a Sony TCM 5000 tape recorder and a Sennheiser ME-88 ultradirectional microphone. No playback experiments were conducted. The timing, frequency, location, and direction of loud calls given by other groups were noted.

<u>f) Play</u>: Height, location, duration, and participants in play bouts were recorded.

<u>g) Fights</u>: Height, interindividual distances, associated calls were noted as well as any details on the opponents.

<u>h) Grooming</u>: Only social grooming (versus selfgrooming) was scored. Grooming bouts were timed for <u>Callicebus</u>. A bout began when one individual groomed another and ended when that same individual stopped grooming.

i) Progressions: Order of traveling animals, entering and exiting fruit trees, and fleeing from other monkeys were recorded throughout the year.

j) Nursing: Nursing bouts were timed and data recorded on height, type of substrate used, and location of father and juveniles. Any conflicts between mother and infant were described.

k) Infant carrying: Carrying bouts were timed to the minute. The individual carrying the infant was identified whenever possible. The context of carrying (*e.g.*, during flight from *Cebus*, during a big jump between two trees, when frightened by loud calls, etc.) was given. Any conflicts between infant and carrier were described.

l) Copulation: Data were taken on precopulatory behavior, timing, duration, number of thrusts, vocalizations, height of activity, location of juvenile and infant, postcopulatory behavior, and frequency.

13. Special Problems in Observation of Aotus

Visibility problems are inherent in all studies of rainforest primates. Even the most habituated monkeys disappear into the leaf cover or vine tangles for varying periods of time each day. Problems of visibility reach the acute stage, however, when observing a nocturnal primate. Night monkey silhouettes can be seen for about 15 minutes at dawn and again for about 15 minutes at dusk. In bright moonlight, silhouettes can be seen traveling and feeding, backlit by the moonlight. By standards applicable to studying diurnal monkeys, conditions for observation of _Aotus_ are far from ideal.

Methods used for studying nocturnal prosimians in Africa and Madagascar (Charles-Dominique 1977; Charles-Dominique _et al._ 1980; Bearder and Doyle 1974) have included trapping, marking, and radiocollaring animals. I had two problems applying these methods to _Aotus_: 1) I had no success in catching _Aotus_ in traps (see discussion of trapping above) and I did not feel the risk in darting such a small animal was worth the risks involved. 2) I wanted data on _Aotus_ to be equivalent to those on _Callicebus_ for comparative purposes. It was with standards for studying diurnal monkeys in mind that I developed the _Aotus_ sampling methods.

There are several idiosyncrasies of _Aotus_ behavior that made following them possible without radio collars. 1) _Aotus_ jumped noisily through the trees, providing auditory cues to their location. 2) _Aotus_ gave a low call whenever they detected me throughout 11 of 12 months of the first year of study, and throughout the additional 3 months of 1982. Because the monkeys continued to feed or travel when they gave this call, the vocalization acted like a built-in radio transmitter. It was on dark nights, when they may not have been able to see me, that they stopped calling and I had to rely only on the sounds of jumping monkeys and dropping fruits. 3) _Aotus_ used the same sleeping trees habitually. Even if I lost the group during the night, I could always find them in the half hour before dawn as they approached their sleeping tree. 4) Aotus habitually followed the same routes in its small territory (10 hectares). Every time the group stopped traveling, I labeled the tree with plastic flagging tape. On this, I wrote the date and time with indelible marker. I used solid white or red and white striped flagging tape because it was readily visible in the beam of my headlamp at night, and because it was nearly invisible during the day, and therefore, perhaps less offensive to diurnal scientists.

The use of habitual arboreal pathways also made it possible for me to follow Aotus through Heliconius swamps. These broad-leafed plants created an impenetrable ground cover 3-4 meters tall. Not only were monkeys invisible to me as they passed over or through these low areas, but the noise made by my movements caused me to lose track of the traveling monkeys. The morning after the group passed over such an area, I cut a trail with a machete up to the last flag (the point where I last was certain of the monkey's location). That night I had no difficulty following them as they traveled over the trail I had cut, but I lost them about 50 meters beyond it. The next morning, I cut another 50 meters of trail through the Heliconius. I did this day after day, until I had cut a trail completely through the swamp beneath the study group's arboreal pathway. After that, I never lost the group over the Heliconius. This technique would not have been possible if the monkeys had not been faithful to certain routes.

14. Special Equipment for Observation of Aotus

Headlamp: To light my way through the forest at night, I used a headlamp, powered by 4 D-size alkaline batteries. After alkaline batteries were depleted, I relied on rechargeable D nickle-cadmium batteries recharged from a solar panel via a 12-volt car battery. I shone this light to check fruit trees for kinkajous, olingos, and marsupials. Unlike these animals, *Aotus* did not tolerate bright light shined in their eyes. Later, I tried a red acetate filter over the lens because *Aotus* is reported to have poor vision in red light (Jacobs 1977a), but reduced intensity made the filter impractical. I preferred to rely extensively on sounds and to shine lights on them infrequently to avoid disturbing the behavior of the study groups.

Image Intensifiers: For 6 months in 1981 (February-August), and three months in 1982 (October-December), I used two image intensifiers.

Varo Noctron IV: I mounted this machine on a pistol grip and carried it in a waterproof shoulder bag. This machine had the advantage of a magnifying lens. Its disadvantages were weight (1 kilo) and accuracy limited to only high light levels (*i.e.*, in bright moonlight). Further, it was monocular and therefore tiring to use over extended periods of time (cf. binocular viewing).

ITT Pocketscope: This small image intensifier had an infrared light source that was helpful at distances of 3-15 meters, even on the darkest nights. This machine was lightweight and compact (6 inches long), and therefore, easy to carry. It's disadvantages were lack of magnification and a monocular lens. Again, eyestrain was created by prolonged use.

C. Methods in Paraguay

I tried to standardize methods between the two sites as much as possible. In this section, I will explain only those methods which differ from those used in Peru.

1. Censuses

My assistant (Patrick Daniels) and I censused four habitat island forests on the Golondrina Ranch and chose one for the study site. Groups were located during the day in their sleeping tree. Because of the openness of the forests and collaboration between two observers, I am confident of the accuracy of group size counts, especially since *Aotus* sleeps only six-eight meters high in the trees on open branches. Night censuses were not as successful since *Aotus* travels quietly here and sits facing away from headlights. 'Vocalization' censusing was used to locate groups in nearby forests. Counting the 'hooting' groups is an accurate minimum measure within limits, especially if it is followed with a diurnal census the next morning.

2. Plant Phenology and Botanical Census

The only difference between methods used in Paraguay and those in Peru was in numbers. Forty fruit traps were placed 25 meters apart along trails instead of 100 meters apart. Phenology records of only 25 trees were kept. Species diversity in this area was low and only those species important to Aotus were chosen for sampling.

3. Insect Availability

Tape recordings of night sounds were made 3-5 times monthly. Orthopterans and amphibians sing when active. Sonagraphs of the tapes were made with a Kay Elemetrics Sonagraph, Model 6061B. Comparisons of noise amplitude were made to calculate relative amounts of prey insects available to Aotus throughout the seasons.

4. Mammal Trapping

To detect competition for food, I set four Tomahawk live traps, baited with fruit, at five locations 100 meters apart in the forest. Traps were open for 10-15 nights each month. Six white-bellied opossums (Didelphis albiventris), six four-eyed opossums (Philander oppossum), and one tree mouse (Orizymys sp.) were trapped, weighed, measured, and marked with reflective bead collars. The marsupials were released after being collared and were then followed to ascertain their ranging patterns and feeding behaviors.

5. Collection and Examination of Owl Pellets (Boluses)

Daily, during the four month period from June to September, 1982, I collected crop pellets regurgitated by a pair of owls (Bubo virgineansus) and their two chicks resident in the study site. Clearly identifiable bones are contained in these pellets. Collection and examinations were made to clarify this species' prey items in this part of Paraguay.

6. Sampling Techniques for Activity and Behavior

a) Sampling regime: Originally, I had planned to do five monthly samples of Aotus. However, because of the diurnal life style of Aotus in this area, I decided that documentation of diurnal behavior was of utmost importance in light of the nocturnal life style exhibited elsewhere. The monkeys were followed all night for three-five nights monthly, and followed for 12 hours during the day for 6-15 days per month. On four occasions the Aotus were followed for consecutive 24 hours, with my assistant and I working successive six-hour shifts.

b) Animal visibility: Our ability to detect animals during the night was greatly improved at this study site. Because the trees were short (10-15 meters) and the canopy was relatively open, the monkeys could be seen except on the darkest nights. Many of the trees were defoliated during June, July, and August, which contributed to our ability to see the monkeys in them during these months. Although visibility was increased, loss of leaves decreased acoustic clues. It was more difficult to hear the monkeys move through the trees that were leafless. Group size of two (compared to four-five at Cocha Cashu) also added to stealth of movement. This group of Aotus did not call unless we shone the light directly in their eyes, unlike the group at

Cocha Cashu. An added problem was the density of bromeliad ground cover. We could not walk off the cleared trail system without making loud rustling noises which impaired our ability to pick up acoustic cues.

We could not rely on habitual sleeping trees to locate _Aotus_ at this site. This was indeed a handicap because _Aotus_ seemed to sleep randomly in many trees each day.

7. Special Equipment

a) Image Intensifier: The Varo Noctron IV image intensifier was much more useful at this site because light levels were so much higher in the open, short forests than they were in the rainforest. With the aid of the image intensifier, the monkeys could be kept in sight continually during the night - an impossibility in the rainforest. We were not able to obtain the ITT Pocketscope for use in Paraguay.

CHAPTER III

RESULTS IN PERU

A. Population Densities and Life History Parameters

1. Population Densities/Aotus

The population density of Aotus at Cocha Cashu was 36-40/km^2. This is a complete count of groups observed in the study area during 1980-1981 (Table 2). Aotus were found in all habitats, including well-drained primary forest, poorly-drained primary forest, and secondary growth caused by blowdowns, changing river courses, etc. (Figs. 2,3). Most groups were found living in a variety of habitats, which may account for the minor differences in population density found in different areas. Size of the annual area used by each family group averaged 9.2 hectares (range 7.0-14 hectares; N=7) (Table 4). Home range size for the study group was calculated at the end of 12 months. All areas where the River Group was sighted were counted as its home range. Other groups were followed for two-five hour intervals and censused throughout the study period. Home ranges were estimated from this information. Because each home range was used nearly exclusively by one group, and because these areas were defended from conspecifics, these home ranges are also called territories (see Sections I and J, this chapter).

2. Population Densities/*Callicebus moloch*

The population density of *Callicebus*, calculated from a complete count of groups in a one square kilometer area, was 20-26/km^2 (Table 4). *Callicebus* groups were not found in all habitats of the Cocha Cashu study site (Fig.4). *Callicebus* groups ranged in viney, dense vegetation, usually along lake or river edges, and bamboo patches. Inland, areas on well-drained soil did not contain dusky titi monkeys. The population density reported here is much lower than that reported by Mason (1966;1968) and by Robinson (1979) in Colombia. Differences may be attributed to extensive secondary growth and edge habitats in the other study sites, and lack of interference competition by larger monkey species (the biomass of competing primate in the Cocha Cashu is much greater). Size of home ranges averaged 6.9 hectares (range=6-8 hectares; N=6) (Table 4). Home ranges of Group I and II were calculated from data collected over the 15 month study period. All areas which the group were seen entering was considered as part of their home ranges (Fig. 4). Home range size for groups III through VI were estimated from a) one-two hour observation periods throughout the study period; b) my census data, and; c) sightings and group counts by other researchers working in the area (see Acknowledgments). Because each home range was used nearly exclusively by one group, and because the home range was defended against the intrusion of conspecifics, a home range qualifies as a territory (see Sections I and J, this chapter).

3. Life History Parameters/*Aotus*

Group size for those groups censused ranged from two-five individuals, including infants carried by the adult male. (Tables 2, 4). Group size varied during the year for each family, dependent on timing of births and subadult dispersals. All evidence corroborates the suggestion that *Aotus* live in monogamous pairs, give birth once yearly to a single offspring, and migrate from their natal group at two-three years of age. Spacing of births suggests two birth peaks per year (Table 5), one at the end of the dry season (September-October), and another in the middle of the wet season (January-February). The absence or delay in births in some groups (*e.g.*, River Group 1982 and North Group 1982) may be due to predation and/or infertility. In most groups, a two year-old subadult migrates permanently from its natal group shortly after the birth of its second sibling (Table 5). Consequently, group size often reached five individuals.

4. Life History Parameters/*Callicebus*

Group size of groups censused ranged from two-five animals (Table 3). Family membership varied during the year, depending on time of births and departure of subadults. As seen in other sites (Mason 1966; Kinzey *et al.* 1977; Robinson 1979, 1981), dusky titis live in monogamous pairs, give birth once yearly to a single infant which emigrates from the family group at two-three years of age. In most groups at Cocha Cashu, as in the case of *Aotus*, a subadult left permanently its natal group after the birth of its second sibling (Table 5). Although births may occur from July through November, there was a birth peak in September (Table 5). The interbirth intervals of Callicebus Group II (Lake) were precisely one year (Table 5). Copulations of the adult pair in Group II observed on April 7 and 8 (1981) suggest a gestation of approximately 160 days. Infant suckling continued for eight months. The father no longer carried the infant when it was four months old. The mother did not carry the infant on her back except momentarily during three-minute nursing bouts, beginning one week postpartum (Wright 1984).

B) Climate, Botany, and Invertebrates in Peru

The Neotropical rain forest is a more complex and less uniform environment than was once supposed (Foster 1980). Areas of different botanical compositions (swamps, river succession, blowdown edges, high ground forest, etc.) exist within the rain forest. The timing and production of fruits can differ from zone to zone within the forest (Foster 1973; 1982; Rodman 1978; Terborgh 1983). Inherent in zonal variation are annual fluctuations in food availability in the forest as a whole. There is evidence that rainfall and temperatures trigger the seasonality of resource availability (Chivers and Raemakers 1980). Rainfall and temperature at Cocha Cashu vary from year to year. Climatic events are often unpredictable. For example, in July (1975) a cold spell with temperatures of 8°C lasted for three days at Cocha Cashu (Terborgh 1983). In 1982, at the end of the dry season in MNP, torrential rains dropped 36mm of rain in 36 hours, causing some of the most severe floods in a decade. The far-reaching consequences of such events include changes in insect populations and changes in timing and production of fruit and new leaves. Furthermore, the Neotropical rain forest has not been uniform in extent over tha past few thousands of years (Haffer 1969; Prance 1973; Kinzey 1979).

In this chapter, seasonal variations in climate, dispersion of fruit trees, phenology of trees, seasonal variation in fruiting, insect availability and leaf flushing are presented for the 12 months from September, 1980, to September, 1981. Next, the data concerning feeding behavior are superimposed on this background to determine effects of seasonal variation on the two species of monkeys studied.

1. Climate/Temperature

The temperature at Cocha Cashu during the time period from September, 1980, to September, 1981, ranged from 11°C on July 19 and 21 (1981) to 33°C on October 22 (1980) (Table 6). September, October, and March were the hottest months (28°C mean daily high temperature), whereas July was the coldest (18°C mean daily low temperature). In general, temperature remains relatively constant throughout the year with average daytime temperature fluctuating only about 5°C (Fig. 6).

2. Rainfall

Approximately 2000 millimeters of rain falls yearly at Cocha Cashu (Table 6). There is annual variation in monthly distribution (Fig. 7). In general, the wet season begins in late October and persists into June. At the end of June, the dry season begins. July and August are the driest months. In 1981, only 25mm of rain fell in July, most of it on only three days. February received the most rainfall (256mm), with November, December, January, and May all exhibiting high rainfall totals.

3. Botany/Species Diversity: Results obtained from botanical surveys of 100 m^2 plots confirmed that the MNP study site had a high diversity of plant species.

4. Phenology Census

Fruit trap results showed that production of fruit at Cocha Cashu was seasonal (Fig. 9). Fruit eaten by monkeys was produced in large quantities in the wet season, October through May, but fruit was scarce in the months of June through September. Fruit production peaked in February as did precipitation, conversely fruit and rainfall were least abundant in the month of July. The monthly census of 176 trees of 44 species revealed that most trees fruited only once each year (except *Trichilia poepiggii* which fruited at six month intervals), and that most trees of a given species fruited synchronously (within a two-three month span), except *Ficus* species. However, each species may be triggered by different stimuli because fruit is available throughout the wet season. Figure 10 shows the number of species fruiting each month. It is interesting to note that March and May are peak months for numbers of species in fruit, and yet, January and February are the peak months for greatest percentage of fruit eaten by monkeys contained in the traps. The phenology census also revealed that leaf flush was highest in September and October, at the beginning of the wet season, and that flower production began in April, peaking in July and August, the height of the dry season.

5. Tree species diversity

South American forests contain few trees with wind-dispersed seeds. Those species that are wind-dispersed are either along river edges (*e. g.*, *Guazuma sp*.) or are emergent trees high above the continuous canopy (*e. g.*, *Calicophyllum sp*.). In general, this means that nearly every mature tree has the potential to provide fruit eaten by animals. Because different species fruit asynchronously, but within a species-specific 2-3 month period, species diversity is important to any animal with a small home range (*Aotus* and/or *Callicebus*, for example). A high species diversity implies year round fruit availability.

6. Diversity of tree crown size

In the phenological census, trees with big crowns were filled with large amounts of fruit for a 4-5 week period. Small-crowned trees (crown diameter of less than 10 meters) had few fruits as a rule, and those ripened a few at a time across a 2-5 month span. Trees with very large crowns are relatively rare. Because large-crowned trees fruit for a brief period and are widely scattered in the habitat, animals which rely on them for food will have to travel long distances between fruit feeding sites.

7. New Leaves

There is a peak of availability of new leaves in September through November. Few trees put out new leaves in the colder, drier months of June and July. Leaf production rises slightly in August.

8. Flowers and Nectar

Although there was constant tree flowering throughout the year, flowering peaked in July and August, during the dry season. One family, the Bombacaceae, has especially large, nectar-filled flowers in vast quantities. *Ceiba pentandra*, *Quararibea cordata*, and *Ochroma pyrimadale* also produce many large, nectar-filled flowers during the dry season. It should be noted that most representatives of the Bignoniaceae family in the Neotropical rain forest are vines, not trees. These vines flower asynchronously throughout the year, and do not peak in the dry season (cf. data from Paraguay). Not all trees produce large, showy flowers designed to attract avian or large insect pollinators.

9. Insect Availability

Night Light Results: Although there appears to be seasonal fluctuation in insect availability, the results are not as marked as the differences in fruiting seasonality (Fig. 12). There is indeed a peak of maximum abundance in the early wet season (September - November), and a period of scarcity at the beginning of the dry season (May-July). This appearance of insects may be triggered by or coordinated with the appearance of new leaves. Most insects caught in light traps eat new leaves in either the larval or adult stage. Insects caught in light traps are primarily winged insects, including moths, beetles, cicadas, katydids, grasshoppers, ant termites, and leafhoppers.

Substrate Search: The prey biomass captured using this method consisted of 68% Orthoptera (katydids, grasshoppers, praying mantis, etc.) (Martha Brecht, personal communication). Insect availability according to the search method peaks in October, with the lowest amounts occurring during the dry season months of June and July (Fig. 13).

Both methods of insect sampling revealed an overall trend of greater insect abundance at the beginning of the wet season and scarcity in the dry season. It should be noted that insects are available year around, and periods of arthropod scarcity are not as dramatic as are periods of fruit scarcity. Even when the density of prey is at its lowest level, an insect eater may increase the amount of time devoted to insect foraging and thereby, still provide for its needs (Terborgh *et al.* in press).

10. Summary:

Although there was some variability from year to year and variation between habitats, there were several consistent trends in climate, botanical phenology, and arthropod abundance. A period of high rainfall extended from October until May or early June. Fruit, flower, new leaf, and arthropod abundance was high throughout this period. During the dry months of June and July, fruit (except figs) was extremely scarce, insects are few in number, and few trees flush new leaves. However, flowering reaches a peak at this time. The flowering peak was followed by an insect and new leaf peak, possibly triggered by October rains. The peak of fruiting occured two months later. These data point out that the most difficult time of year at Cocha Cashu was June and July. The time of year when most protein was readily available was September through December, when insects were abundant and new leaves were flushing. In the next section, I will discuss how <u>Aotus</u> and <u>Callicebus</u> adjust their feeding and reproductive patterns to fit this overall pattern of resource.

C. Diet of Aotus and Callicebus

Introduction

The feeding behavior of Aotus and Callicebus is compared across an annual cycle. General feeding patterns are first reviewed. Each of the two monkey species is then discussed under specific categories (fruit-feeding, leaf-eating, insect-foraging, and flower- and nectar-feeding). In the next section, ecological differences are suggested for the differences observed. Temporal partitioning of resources, interspecific competition for resources, including interference competition, and differences in resource availability during night and day are discussed.

1. Diet of Aotus

a) Fruit: The focal Aotus group averaged three hours of nightly fruit-feeding year around. Approximately 60% of the total feeding minutes were devoted to fruit consumption. Aotus groups at Cocha Cashu were observed to eat about 70 species of fruits. These 70 species are distributed among 24 families (Appendix III). The families most frequently represented were: Moraceae (17 species), Annonaceae (9 species), Leguminosae (5 species, Bombacaceae (4 species), and Sapindaceae (4 species). Of the flowers and fruit eaten by Aotus, 7 species (10%) were from vines, 58 (83%) from freestanding trees, including one palm species, 3 (4%) from strangler figs, and 1(1%) were from a hemiepiphyte. Of the top ten fruits and nectar resources ranked by number of feeding minutes (Table 7), #1 was Guatteria acutissima, a large freestanding tree, #2 was Combretum assimile, nectar from a vine. Fruits from large-crowned trees ranked from third to seventh. A large-crowned hemiepiphyte ranked eighth, a common vine ninth, and tenth was a species of Lauraceae, a medium sized freestanding tree.

Although Aotus fed in five species of fruit trees per night (range 1-8), a group spent over half of feeding minutes on one or two species. About 50% (range 26-95%) of all feeding minutes were on species ranked number one for that day. About 70% of all feeding minutes were spent on species ranked #1 and #2 (see Table 8). The number of fruit species used per sample varied from a low of two in July, to a high of 18 in March. The mean number of fruit species used per sample was nine. During every month, the bulk of the feeding minutes was spent feeding on only two species.

Figs are an important part of the Aotus diet, especially during times of fruit scarcity, when primarily the large fig trees are fruiting. Three species of fig are in the top twenty fruits eaten; Ficus kilipii ranked #4 for Group I. It should be that the most popular figs were small and red or yellow in color (13% of total feeding minutes). Although

Aotus did eat the figs that were large and green when ripe (Ficus regularis, Ficus sp.), the total number of feeding minutes spent on these figs was only 2%.

The only palm fruit that Aotus was seen eating was the white, meaty ectocarp of the Iriartea ventricosa palm (the fruit is 2cm in diameter).

The data on fruit characteristics are represented in Table 9. The salient features are:

Size - Fruits ranged from 5 mm to 20 cm, but most were small;

Color -Aôtus ate fruit ranging in color from orange-red to green. Color preferences were not obvious;

Taste - We taste-tested the fruits eaten by Aotus and found that most were bland and mealy (figs and the like) (47%), 39% were sweet, and 14% were either spicy, acid, or bitter. When feeding minutes for species ranked #1 through #10 were pooled (Table 7), they indicated that Aotus fed on sweet fruits 60%, bland fruits 24%, and acid or bitter fruits 16% of the time.

Aotus eats very little unripe fruit as observed from half-eaten fruit discarded by the monkeys. During a week of returning to the same tree, the number of feeding minutes and feeding rate increased as the fruit on the tree ripened.

Milk seeds (embryos) of a few species were eaten (Sapium aereum, and Trichilia poepigii). The only seeds of ripe fruit that were chewed and ingested were the seeds of

Brosimum alicastrum, the ramon nut. Brosimum alicastrum seeds were not eaten by Group I, but occasionally were eaten by Group II. Seed predation by Aotus is rare. When eating most fruit, night monkeys spit out the seeds. However, exceptions include Celtis, Ficus, and Cecropia seeds which were eaten whole and defecated intact.

b) Leaves and Vegetation

It is difficult to see leaf-eating in the dark, and quantitative data on leaf-eating could not be collected. None of the feces analyzed (N=64) contained leaf veins or leaf refuse. Aotus did not spend time in bamboo patches or edges where Callicebus eats leaves. Aotus was observed at twilight or in the bright moonlight to eat a vine leaf occasionally. This information suggests that leaf-eating was not extensive (an estimated 5-10% of feeding time).

c) Nectar and flowers

Aotus relied on nectar as a main food item in July and early August when fruit is scarce (Fig. 15). During the July observations, 94% of the feeding minutes were nectar-feeding on Combretum assimile, a vine which flowers 20-30 meters high in the canopy. During August, 40% of the feeding minutes were spent on Quararibea cordata nectar. This tree in the family Bombacaceae (silk cotton) produces cauliflorous, large blossoms filled with nectar. Few nectar resources are available from September to June. Aotus Group I was not observed to feed on flowers, however, Group VI ate legume flowers in January.

d) Animal Protein

Invertebrates: I could not collect quantitative data on insect-foraging for Aotus, but estimations of percent of feeding time spent insect-foraging were 15-20% of total feeding time. Insect-foraging was observed at dusk and dawn, and in the bright moonlight. Aotus does not sit and scan for insects, but rather moves methodically along branches, grabbing the insect with one hand from the air or from the branch. Night monkeys rarely miss. They ate Lepidopterans (moths 2-8cm), Orthopterans (katydids and grasshoppers 6-10cm), Coleopterans (beetles 2-4cm), and spiders. There are two advantages to insect foraging at night: 1) Large Orthopterans and edible Lepidopterans are active then and moving objects are easier to detect than stationary ones; and, 2) Orthopterans call at night, facilitating location.

Approximate insect-foraging time was estimated by a combination of the following methods: 1) Observation of the type of tree and correlation with diurnal primate insect-foraging. Large, older trees are used extensively for insect-foraging by the diurnal monkeys Callicebus, Saguinus, and Cebus. 2) Examination of descending debris during foraging; debris may contain parts of prey species, like wings. 3) By feces estimate. Feces were collected from Aotus and Callicebus (see Methods, Chapter II). In the

June sample, insect-foraging accounted for 20% of the Callicebus feeding time, and 14% of the Callicebus feces collected contained insect fragments; 64% of Aotus' scats contained these remains. To derive an estimate for the amounts of invertebrates in the diet of Aotus, I assumed similar digestive morphology and insect processing (see Morphology Section). Two additional factors that must be considered are relative insect catching efficiencies and insect abundance. Aotus is a more efficient hunter than Callicebus (personal observation of free ranging night monkeys in North America and observations of Aotus in Paraguay). In addition, the number of prey items active at night increases above daytime levels (Janzen 1973; Windsor 1978). The estimate of percent of time insect-foraging ranged from 20% in the wet season to 10% in the dry season (Fig. 16).

Vertebrates: Bates (1863) and Sanderson (1957) describe Aotus eating bats, small birds, eggs, and lizards. In 1500 hours of observation in Peru, I observed neither feathers, egg shells, bat wings, etc., discarded by Aotus, nor did I find vertebrate parts in their feces. Catching vertebrates is probably a rare occurrence for night monkeys.

2. Diet of Callicebus moloch

a) Fruit

Fruit was an important part of the Callicebus diet

(Fig. 17). Study Group I averaged 102 fruit feeding minutes per day, while Group II spent a yearly mean of 143 fruit feeding minutes per day. Group I fed on fruits 40% of all feeding minutes and Group II spent 52% of total feeding time on fruit consumption. There was seasonal variation in fruit feeding. Fruit constituted a greater proportion of the diet in the wet season.

Fruit Sources: The titi groups fed on over 100 species of fruit and flowers (88 of which have been identified by genera or species (Appendix I). Differences in species of plants eaten may be attributed to differences in the availability of the resource in each territory, and not to individual variation in taste. Thirty of the 88 species were found in the territories of both *Callicebus* study groups. The 88 species were distributed among 37 plant families. The families most represented were: Moraceae (14), Leguminosae (8), Annonaceae (7), Meliaceae (6), Myrtaceae (6), and Sapindaceae (5). Of the flowers and fruits eaten by *Callicebus*, 16 species were on vines (18%), 68 species from freestanding trees (76%), two from strangler figs (2%), and one (1%) was an epiphyte. *Celtis iguanea*, a vine, was the species with the highest number of feeding minutes. *Ficus erythrosticta*, a strangler fig, ranked second in number of feeding minutes (Table 10).

Figs: Although only four species of figs were eaten by *Callicebus* (Appendix III), these fruits were very important in terms of overall feeding minutes. The second most important fruit for Group II was Ficus erythrosticta. Both Ficus kilipii and Cecropia sp. were major fruit sources for Group II. It should be noted that titis ate small, red or yellow figs, rarely the large, green-when-ripe variety.

Palms: Palm nuts were not a preferred food item in the diet of Callicebus. In fact, the only palm nuts observed to be eaten were the outer meats of Iriartea. On only one occasion was Callicebus seen feeding on palm fruits, for a total of five minutes.

Although Callicebus ate an average of six fruit species per day (range 3-10; Table 11), the groups concentrated most of their time feeding on one or two species (Table 8). A mean of 48% of all feeding minutes was spent feeding on the species ranked number one that day (range 33-80%). About 70% of all feeding minutes were spent on species ranked #1 and #2. Even though Callicebus may enter and sample a few fruits from many tree species, they obtain the bulk of their diet from one or two species each month. The number of fruit species used per sample varied from a low of eight in January to a high of 23 in March, with an annual mean of 14. The number of species used was directly correlated with the number of species with fruit in a group's territory.

Callicebus fed primarily in trees with crown diameters of less than ten meters (Tables 12 and 13). Group I fed in these small trees 82% of the time and Group II spent 93% of its feeding minutes in them. Most of these trees ripened a few fruits each day for several months. These predictable resources were indeed a mainstay for *Callicebus*. It should be noted that numbers of crown diameters of trees available were correlated with numbers of crown diameters of feeding trees used (Table 14).

Characteristics of Fruit Eaten by Callicebus:

Table 9 presents the data on fruit characteristics. Briefly, these are:

Size - fruit ranged in size from 5mm to 20cm, 80% were 2cm or less in size;

Color - *Callicebus* ate fruit of various colors without showing any obvious preference;

Taste - About 44% of the species eaten had sweet fruit, 43% were bland and mealy, while 13% were spicy, acid, or bitter. When feeding minutes for species preference ranked 1-10 were pooled, they show that *Callicebus* fed on sweet fruit 29% of the time, bland and mealy fruit 56% of time, and bitter fruit only 15% of the time.

Callicebus ate some unripe fruit. Before a tree had any ripe fruit, *C. moloch* would partially eat a few unripe fruits from the tree. If there was a choice between ripe and unripe fruit on a tree, the ripe fruit was invariably preferred. Feeding minutes spent in the same tree increased over a week's time as more fruits became ripe in the tree.

The small seeds of *Cecropia* and *Ficus* were ingested and defecated. Medium-sized and larger seeds were spit out. However, there was variability between the two groups in seed ingestion. Group I ingested the seeds of *Celtis* (5mm) and defecated whole seeds 3-4 hours later. Group II mouthed the pulp of *Celtis* and spit out the seeds. In both groups *Celtis* seeds were not predated. The only seeds eaten and chewed were those of *Brosimum alicastrum* (ranked sixth in feeding minutes).

b) Leaves and Vegetation: Every day they were sampled, the two study groups ate leaves or vegetative plant parts. Group II ate plant parts one hour per day (23% of feeding minutes) during the wet season (October-May). In the dry season, leaf-eating increased to two hours daily (40% of feeding minutes). In Group I, leaf-eating increased from 28% in the wet season, to 66% in the dry season. (Fig. 17)

Ninety-five percent of the leaves eaten by *Callicebus* were young and mature vine leaves (Appendix III). New leaves of successional plants such as *Miconia aulocalyx* and *Acalypha sp.* (both small trees), and of large trees were occasionally eaten. Mature leaves of trees were not eaten. The leaves of at least two species of bamboo (*Bambusa sp.*) were pulled from their sheaths and the tender white shoot at the base was eaten. Group II fed on bamboo leaf bases during 55 of 67 days, or 82% of all observation days. From January to August, in the late wet season and the dry season, the monkeys fed on bamboo for 53% of leaf feeding minutes. The territory of Group I contained no bamboo, and therefore, during this period of time Group I did not eat bamboo.

Seasonal variation in leaf-eating: Both groups of *Callicebus* showed pronounced seasonal variation in time spent eating leaves and plant parts (Fig. 17). In the wet season, Group I spent 28% of feeding time on leaves, and this increased to 64% of feeding time in June through August. Group II spent 22% of feeding time on leaves during the wet season, which increased to 39% during June through August. There was little variability in the abundance of vine leaves and bamboo growth throughout the year. There is an increase of flush leaves in August and September (mature trees), which may have influenced those samples. Increased leaf flush does not explain the exponential increase in leaf-eating in June and July. There is a scarcity of fruit in June through August. Because there is a negative correlation between the time spent eating leaves and the number of fruits available, there is evidence that *Callicebus* eat leaves when less fruit is available.

Comparisons between the two groups also point to the same direction. The territory of Group II had more fruit available than that of Group I during June through August.

During that time, Group II spent 39% of feeding minutes on leaves, while Group I spent 64% of feeding minutes on leaves. Regardless of the season, leaves were eaten every day. When energy-rich fruit was not available, Callicebus increased leaf-eating accordingly.

Location of leaf resources: Although leaves were eaten at all levels of the forest and often fed on opportunistically, there were definite patches where palatable leaves were abundant throughout the year. Bamboo was distributed in dense patches at intervals of about 100-150 meters within Group II's territory. Vine leaves were abundant in low, backwater successional areas containing few fruit trees. Vine leaves were also abundant along the lake edge and at edges of blowdowns.

Leaf-eating strategy: The Callicebus strategy for leaf-eating is to browse through patches of vines or bamboo uniformly and to alternate these patches in such a way as to allow for renewal of the resource. Because these edge or successional plants grow quickly, they provide a predictable, palatable year around resource.

c) Nectar and flowers: Callicebus fed on flowers 2% of all feeding minutes. The petals of the flowers were eaten and the nectar and pollen consumed coincidentally. The monkeys did not feed on all flowers available in the forest, but specialized on the flowers of certain families, mainly Bignoniaceae and Leguminosae. They never fed on the nectar of Combretum assimile (Combretaceae), nor on the nectar of Quararibea cordata (Bombacaceae), although these nectars were a major food resource for most other monkey species during the fruit scarcity of July and August.

d) Animal Protein

Invertebrates: The two titi study groups foraged for insects every day we observed them. They spent an average of 37 minutes per day foraging for insects from December through August, 15% of total activity minutes (Fig. 16). Group II increased the average time to 73 minutes per day in October and November. In these two months, 27% of the feeding minutes and 7.5% of total activity minutes were spent foraging for insects. Insect availability varied throughout the year (Figs. 12, 13). Foraging success correlates positively with availability. Eating insects appears to be a preferred method of obtaining protein, because at the time of leaf flush (October and November), Callicebus are spending less time eating leaves than at other times of the year, and more time eating insects (Fig. 17). It should be noted that due to low capture efficiency, insects are not a significant portion of their diet during most of the year.

Callicebus fed on various insects, including Lepidoptera (moths, caterpillars, chrysalises), Formicida (ants), Coleoptera (beetles), Orthoptera (grasshoppers, katydids), and unidentified insect larvae and Arachnida (spiders) in cocoons on leaves. It was often difficult to discriminate between cocoons of spiders and those of insects, and many of the small insects caught by Callicebus were unidentifiable. There was seasonal variation in types of insects available. Those caught in January through August were small (<1cm), soft-bodied insects and spiders; both had minimal chitin. Immobile cocoons and ants were also taken. In October and November, I observed the capture of large Orthoptera (6-10cm long), large Coleoptera (3-6cm long), and ants.

Callicebus grab flying insects out of the air, using one or both hands, unroll dead or green leaves that contain silk of caterpillars or spiders, and mouth insects off branches or trunks. They do not tear open bark or branches to get at insects like Cebus, nor do they put their hands in knotholes like Saguinus. Titis often pick up and eat ants one at a time from trunks or branches. They frequently fail in their attempts to find or capture insects.

I examined 56 scat samples in April through August to determine what percent contained chitin. Only 13% were found to contain insect parts. Each fecal sample that contained chitin had few pieces (range 1-12 pieces per sample) (see Appendix IV). Although the number of fecal samples collected is small, and collected only during a five-month period, there is some evidence from my analyses that insects do not constitute a large part of the Callicebus diet.

Vertebrates: There are no data, either from observations or fecal samples, that titi monkeys ever take vertebrate prey.

D. Comparison of Aotus and Callicebus Diets

The diets of both species of monkeys are qualitatively similar, but are quantitatively different. Both eat small fruit which is available within their territory. The data suggest that the fruit is not discriminated against because of taste or color. However, Callicebus spends more time in trees with unripe fruit than does Aotus, suggesting that a difference in ripeness is more important than any other difference in fruit type. Vegetation is part of the diet of both monkeys, yet the data suggest that Callicebus consistently eat more leaves; whereas Aotus derives more of its protein from insects.

1. Percentage of Activity Budget Spent in Feeding

The activity budget of both Aotus and Callicebus, as in many other primates taxa, consists of traveling to food, feeding, resting, and participating in social activities such as grooming, playing, fighting, and calling (Fig. 14). Fifteen to forty percent of the time budget of these two species is spent traveling to food. About 40% is spent feeding/foraging on fruits, insects, and leaves. There are fluctuations in the proportion of time allotted to each category, dependent on availability of these resources. During the wet season, when these three resources are abundant, traveling time decreases and time spent in social behavior increases. Time spent feeding does not change, but composition of the diet does.

2. Annual Feeding Trends

The mainstay of the diet of both species is fruit fluctuating from 100% to 60% per month in Aotus (Figs. 15, 16), and from 66% to 18% per month in Callicebus (Fig. 17). This frugivorous diet is supplemented with insects, flowers, nectar, and leaves. Approximately 50% of Callicebus feeding time was spent eating fruit and nectar. The annual average of leaf-eating for this species was 31%, less than 20% of feeding time was spent foraging for insects. Quantitative data for leaf and insect feeding by Aotus could not be gathered. Estimations of feeding minutes by item yielded 15-20% of total time devoted to insect-foraging and 5-10% to leaf-eating. Although the diets of the two study species are quite similar during the wet season when food is abundant, the diets diverge in the dry season when food is scarce.

E. Competitors for Food

Competition for food is difficult to quantify, especially in a habitat with high species diversity, such as Manu National Park. Terborgh (1983) has suggested that fruit is the food item most competed for by primates in the rain forest. The biomass of diurnal frugivores has been estimated at 822 kg/km^2 at Cocha Cashu, while the biomass of nocturnal frugivores has been estimated at 298 kg/km^2 (Terborgh 1983). It has been suggested that *Aotus* became nocturnal to avoid the high biomass of diurnal frugivores, mostly monkeys and birds. This explanation is confounded by the fact that only a certain quantity of fruit is ripe in any 24-hour period, and thus, in reality the nocturnal frugivores are competing with diurnal frugivores for the crop. Ripening rates are more rapid in the daytime, and therefore diurnal frugivores have the advantage of more fruit, and the disadvantage of competing with more species for that fruit.

1. Diurnal competitors

a) Fruit: There are eight diurnal monkey species, at Cocha Cashu other than *C. moloch*, which are direct competitors for the fruit produced by small-crowned trees. *Callicebus* avoid all other primates whenever possible. Other primates can profit from the careful monitoring of fruit trees by titis. For example, *Saimiri*, with a 250 hectare home range, may not know specifically where fruit is ripe within that area and take advantage of the fruit-finding skills of monkeys with smaller home ranges (Janson 1983; Terborgh 1983). However, for Callicebus such parasitism can be disastrous. Large groups of quick-moving squirrel monkeys travel into the small-crowned trees first and deplete the fruit crop. The titi family is then faced with trees empty of fruit. Therefore, avoidance of all other primate species is important to them, as is maintenance of small group size for utilizing small-crowned trees. Callicebus effectively avoids Saimiri by hiding in vine tangles or by reversing travel directions several times when Saimiri calls have been heard.

There is also direct competition for fruit in large-crowned trees. Callicebus were chased out of fruit trees by Cebus apella, C. albifrons, Ateles paniscus and/or Saimiri sciureus, at least once every day of observations (Fig. 19). Monkeys with large group size and overlapping home ranges travel sequentially from one large-crowned fruit tree to the next (Janson 1981; Terborgh 1983). Because Callicebus feeds on both large- and small-crowned trees, being expelled from a large-crowned tree in the wet season may be inconvenient, but not critical. The dusky titis can return to the big tree later in the day. In the dry season, a different situation exists.

During the dry season, fruit is scarce. If there are no large-crowned fruit trees available in the titi territory, as was the case in June, 1981, the monkeys with large ranges are elsewhere and are not present to share the few fruits available. But, when there is a large-crowned fruit tree in a *Callicebus* territory full of ripe fruit during the dry season, as was the case in July 1981, the larger monkeys cluster at the tree. When only scattered figs were ripe in the tree, the *Callicebus* group fed from 65 to 165 minutes in this tree per day (Fig. 20). As more figs ripened, the dusky titis progressively spent more feeding minutes per day in that tree. On 7 July (1981), the titi group entered the fig tree just after dawn. After feeding for approximately ten minutes, they were expelled by groups of *Ateles* and *C. albifrons*. The titis retreated to a vine tangle 50 meters from the fig tree and waited. The tree was continually occupied by other groups of monkeys until dark. Although *Callicebus* made several attempts to reenter the fig tree, they were always chased away. Because they could not enter the tree to feed, they ate bases of bamboo leaves, *Calatola* (a bitter fruit not eaten by other monkeys), and leaves. The following day, squirrel monkeys and *Cebus* entered the fig tree before the titis left their sleeping tree. *Callicebus* were chased from the tree each time they attempted to enter it. They did not feed in this tree for at least the next three days, and probably for the next two weeks (I had switched to sampling *Aotus*, however, after the three days mentioned.) *Callicebus* fruit feeding minutes were as low or lower than the month of June. *Callicebus* relied on leaf eating for 40% of its feeding minutes for both June and July. However, in August, most of the figs in the tree were overripe, and the monkeys with large group size monopolized a new tree bearing a large amount of ripe figs about 700 meters north. Again, the titi family fed in the same *Ficus*. Feeding minutes per day ranged from 50 to 100 in August (Fig. 20), even though most of the ripe figs were widely scattered throughout the crown.

b) Nectar: IN MNP, *C. albifrons*, *C. apella*, *S. sciureus*, and *Saguinus* all feed on the nectar of *Combretum assimile* in July and on that from *Quararibea cordata* in August (Janson *et al.* 1981). Neither *Alouatta seniculus* nor *C. moloch* fed on nectar. Both species increase their leaf eating during the time of fruit scarcity. The dichotomy between nectar feeders and non-nectar feeders is explained by differences in digestive system anatomy, by threat of predation in exposed canopies (*Callicebus*) or by interference competition (larger monkeys do chase *Saguinus* from nectar sites). Because avian predators are asleep, *Aotus* can afford to feed exposed in the canopy at night. *Aotus* and *Potos flavus* (kinkajou) feed together on nectar resources, and there is no interference competition from larger monkeys. It is unknown if digestive system differences between *Aotus* and *Callicebus*/*Alouatta* make nectar a viable food for only *Aotus*.

c) Leaves and vegetation

Mammals: There are three species of primates in MNP, in addition to *C. moloch*, that include leaves in their diets - *Ateles paniscus* (MacFarland in press), *Alouatta seniculus* (Milton 1980), and *Lagothrix lagotricha* (Ramirez 1980). These monkeys rarely feed on leaves at less than ten meters above the ground. This is a consequence of the large size of all three genera (Table 1). In contrast, 50% of leaf eating by *Callicebus* is at heights below ten meters. This provides some evidence that competition for leaves between titis and other monkeys is minimal. There are two species of sloth in MNP. However, sloth population densities are not high (Terborgh 1983), and competition for leaves is therefore negligible.

Birds: There are few species of leaf eating birds in the Neotropics (Meyer de Schauensee 1970). Hoatzins feed on leaves both day and night and have high population densities at lake and stream edges. However, this potential competitor for vine leaves is chased from leaf resources by the titi monkeys.

Insects: The main leaf predators are insects (Windsor 1978). However, because titis eat both insects and leaves, insects are not considered as important competitors for leaves.

d) Insects: During the day, insectivorous birds from about 200 species compete with *Callicebus* for insects.

There are also six species of insectivorous monkeys in MNP. C. apella and C. albifrons spend nearly 50% of their waking hours foraging for insects by searching through live foliage, stripping bark from dead limbs, tearing open decaying wood, and by rummaging through debris in vine tangles and in palm crowns (Terborgh 1983; Janson in prep.). Saimiri are also highly proficient insectivores, catching one prey item per minute for six hours daily; a total of 330 prey items each day (Terborgh 1983)(cf Fig. 18). Both species of sympatric tamarins (Saguinus fuscicollis and S. imperator), catch insects. S. fuscicollis spends only 16% of its time foraging for insects and catches a higher proportion of large insect prey than does Cebus and Saimiri. Most large insects are found where Callicebus does not forage, e.g., on tree trunks or in knotholes. The emperor tamarin forages for insects on leaves in a slow manner, much like the titi. However, these tamarins are better at catching orthopterans; 60% of their prey items are green grasshoppers and katydids (Terborgh 1983). Cebuella pygmaea is also an insectivorous primate in MNP. However the biomass of these animals is so small that they constitute little competition.

2. Competition from diurnal mammals at night

On three occasions during the full moon in the dry season, Cebus and Saimiri entered a large fig tree and displaced Aotus. They remained in the tree on each occasion from 23:00 to 03:00 hours. Aotus waited outside the fig tree, about 30-50m distant, until the other two species had left. At that time, the night monkeys re-entered the large-crowned fig tree and fed for 45 minutes.

3. Nocturnal competitors

a) Fruit and Nectar: Table 15 lists the nocturnal frugivores of MNP. The only species large enough to displace night monkeys from a fruit tree are *Didelphis*, *Potos flavus*, and perhaps *Bassaricyon*. However, I never observed any interspecific chasing in fruit trees at night. L. Forman (personal communication 1981) observed a kinkajou displacing *Aotus* in a fruit tree in central Peru. Based on my observations, this is not a common occurrence.

The bats of South America are all small microchiropterans that feed on insects, fruit, and nectar. The largest bat in the New World is *Vampirum spectrum* which weighs 145-190 grams (Walker 1975); it is carnivorous and 80% of its diet consists of birds (Vehrencamp *et al.* 1977). Therefore, no bat in South America is large enough to displace *Aotus* in trees. In fact, Bates (1863) states that night monkeys eat bats. Morrison (1975) described *Philander oppossum* preying on *Carollia* fruit bats (10-20 grams body weight) in fruit trees. This strengthens the suggestion that bats avoid other mammals in fruit trees. A comparison of fruit-eating between *Artibeus* and *Alouatta* (Estrada *et al.* 1984) suggests that competition for fruit between bats and primates may not be extensive, at least in the tropical forests of Mexico.

b) Leaves and Vegetation

Mammals: The arboreal herbivore that might be an important competitor is the bamboo rat (*Dactylomys dactilinus*). A pair of these large rats (500 grams body weight) live in each bamboo patch visited by *Callicebus*. Population densities at Cocha Cashu are approximately $20/km^2$ (Emmons 1981). Because bamboo rats eat the stalk and titis eat leaf bases, competition for specific plant parts is minimal although destruction of patches by the rats may ultimately effect the titis. If an entire bamboo patch is destroyed, a reliable year around resource is eliminated. Patches were searched at night; *Aotus* was never observed in bamboo patches.

c) Insects

At night, bats are the most common insectivore in MNP. Although there may be over 100 spoecies of bats at Cocha Cashu (L. Emmons, pers. comm.), only twenty bat species have been identified, and of these, 11 are insectivorous. It is difficult to determine how competition from bats affects *Aotus*. Six species of owls take insects as part of their diet. Many of the arboreal marsupials (Table 15) include insects in their diet also. Olingos (*Bassaricyon alleni*) include large orthopterans in their diet (P. Sherman personal communication). Frogs, snakes, and small rodents are also known to be insectivorous, and therefore may pose some competition. Calculating competition for these insect resources is difficult because the foraging behavior of the bats and other insectivorous animal species is unknown.

F. Summary and Discussion of Aotus and Callicebus Diets in MNP

1. Similarities in Diet - An overview

Aotus and *Callicebus* share many morphological and ecological similarities, such as small body size (1kg), small canine size, small group size (2-5 members), and small territories (4-12ha). These similarities are reflected in the similarities in diets of the two genera.

a) Both species eat a primarily frugivorous diet supplemented with a mix of leaves, flowers, and insects.

b) Due to small mandibles, short canines, and small teeth in general, both species are restricted to small, easy-to-open fruit. Neither has the equipment to break open palm nuts or thick-husked fruit.

c) A large caecum and broad, wide intestine may make digestion of unripe fruit, and bulky vegetation possible for both species. This factor may result in both species being able to subsist on a wide variety of food items unavailable to other primates with shorter digestive tracts.

d) Both species can feed economically in small-crowned trees because of their small group size.

2. Differences in Diet - An overview

The diets of the two species are not the same. The four main differences are as follows:

a) *Callicebus* uses more small-crowned fruit trees, whereas *Aotus* prefers bigger trees (cf. proportion available).

b) *Aotus* catches more insects than the less-successful *Callicebus*.

c) *Callicebus* ingests more leaves and vegetation than *Aotus*.

d) *Aotus* ingests nectar while *Callicebus* does not.

These four differences in feeding behavior may be a consequence of contrasts in day and night activity cycles. Diet of the two genera differ only slightly during most months of the year. However, there is one time, the dry season, when their diets are almost mutually exclusive. During the season of scarce resources, closely related species diverge most in their behavior (Charles-Dominique 1977; Gautier-Hion 1978a, 1978b; Emmons 1980; Terborgh 1983). The lack of dietary overlap in *Aotus* and *Callicebus* in this difficult season is especially important in defining the niche separation of the two species.

3. Leaves - Similarities

Both species eat leaves from vines or young leaves from trees. Neither eats mature leaves from freestanding trees. Leaf-eating distinguishes *Aotus* and *Callicebus* from some other New World monkeys like *Saimiri* (with similar body weight), and the Callithricids (smaller body size) which do not eat leaves. It also may contribute to the ability of

Aotus and Callicebus to subsist in small territories.

4. Leaves - Differences

The proportion of leaves in the diet of titis is higher than that of night monkeys at all times of the year. Titi territories are located on lake or river edges that provide a plentiful, year-round supply of ever-growing vine leaves and bamboo leaf bases. There are seasonal fluctuations in leaf eating. It occupies a quarter of the feeding minutes scored for Callicebus in the wet season, and increases to nearly half of the feeding minutes scored in the dry season. Of all the New World monkeys studied to date, only the howler monkey (Alouatta, Milton 1980) and the woolly spider monkey (Brachyteles, Milton 1984) are more folivorous. However, competition for leaves is minimal between Alouatta and Callicebus. Milton (1980) reports that over 90% of the leaves eaten by howlers are leaves from trees, while only 3% of the leaves ingested by titis are from trees. Almost all of the leaf-eating by titis is at a height of less than ten meters and on thin substrates that would not support the weight of larger monkeys.

At first, it may appear contradictory that Callicebus eat more leaves in the dry season, a time when many trees are defoliated and there is little leaf flush, than in the wet season, September-November, the beginning of the rainy season when trees and bamboo flush new leaves. Examining the diet as a whole, there is a inverse correlation between insect eating and leaf-eating. In the wet season, when insects are abundant, insect-foraging increases to nearly a quarter of all feeding minutes; this drops to 15% in the dry season when insects are dormant. In this difficult season, the titis are relying on ever-present vine leaves and bamboo patches. From this evidence, it appears that insects are a preferred source of protein. But, most of the year insects are not abundant and are difficult to catch. Instead, Callicebus gain its protein from leaves available throughout the year.

In contrast, Aotus does not rely on leaves for protein. This may be because insects calling and moving about at night are more readily available to night monkeys at all times of the year. In addition, leaf protein takes more time to digest; more leaves must be consumed to obtain comparable amounts of protein. Aotus may have difficulty discriminating between young and mature leaves at night. The only nocturnal folivorous primates are prosimians (Avahi and Lepilemur) (Tattersall 1982). Both have specialized caecums and colons which permit them to digest mature leaves. Lepilemur also practices caecophagy, which enhances the return from vegetation ingested initially. Many leaves are less nutritious after sundown (Franck and Loomis 1949), and thus, the same leaves may be less nutritious for Aotus than for Callicebus.

5. Fruit and Nectar - Similarities

Fruit is the mainstay of both the Aotus and

Callicebus diet. Both species fed on fruit about two and one half hours per 24-hour period. Throughout much of the year, the two species ate the same fruit. Their morphology constrains the type of fruit they may consume. Most fruit eaten is less than 2cm in diameter, and palm nuts, regardless of size, are rarely taken. Both eat fruit of all colors, ranging from orange, to purple, to green. Color cues are probably not as important to *Aotus* and *Callicebus* as they might be for species of monkey with large group size and large home range which may cue into yellow and orange fruit from a distance (Janson 1983). Both monitor their small home ranges constantly, often locating and eating a fruit resource in a unripe stage, when there are frequently no color cues. Both rely on one species of plant per month to provide 50% of their fruit intake. The remainder of their fruit-feeding time each month is spent on from 2-18 species, for *Aotus*, and 2-23 species for *Callicebus*. For *Aotus*, the predominant fruit species is often a large-crowned fruit tree located in the territory; *Callicebus* often traplines many small-crowned fruit trees of a single species.

Both *Aotus* and *Callicebus* can resort to scattered crops of fruit in small trees because small patches can be economically exploited by small monkeys in small groups. Most small-crowned vines or trees ripen a few fruits each day over 2-6 months. These predictable resources in small patches are a mainstay for the titis (82% of feeding minutes were spent on fruit species available for 2-6 months). If unripe, as well as ripe, fruit is used as a resource, then a single tree is a food resource for many months. Because the two species ingest spicy, acid, or bitter fruit (Table 9), that other monkeys do not eat, they have yet another method of circumventing competition within a small territory.

6. Fruit and Nectar - Differences

Callicebus feeds primarily in small-crowned fruit trees. Most feeding minutes spent in large-crowned trees were on unripe crops, before frugivores of other species had discovered the tree (Table 12). Titis avoid nectar resources found high in the canopy during the dry season. This avoidance may be a result of fear of raptors or a fear of interference by larger monkeys.

In contrast, Aotus prefers fruit found in medium- and large-crowned trees (Table 12). Only 15% of feeding minutes scored for night monkeys were spent in trees with crown diameters of <10 meters, while 85% of feeding minutes were in crowns of 10-40 meters in diameter. There may be several reasons for this preference:

1) Large-crowns are easier to locate. Fixed routes may limit search and night monkeys may have more difficulty locating a few inconspicuous fruits in the small trees at night;

2) Aotus is not displaced from any trees at night while titis are chased out of large fruit trees and nectar sites

during the day by larger monkeys (especially _C. apella_ and _C. albifrons_). This interference competition is especially critical in the dry season. At this time of resource scarcity, _Aotus_ feeds on figs and nectar unmolested, while _Callicebus_ feeds on leaves and small fruit unpalatable to other monkeys.

G. Predators

In the following section, the potential predators of small monkeys in South American rain forests are reviewed. Observed incidences of predation at Cocha Cashu are described. A night-active monkey may have adapted to different predator protection strategies than a day-active monkey. These possibilities are discussed at the end of the section.

1. Potential Predators

a) Snakes: Poisonous snakes in the rain forests of South America include several species of *Bothrops* (Fer de Lance) and *Lacustris* (bushmaster). The species of Fer de Lance large enough to eat a monkey are all terrestrial. The bushmaster is also terrestrial. Non-poisonous snakes include the aquatic anaconda and boas. Boas identified in MNP include the emerald and rainbow boa. Both are arboreal and grow to a maximum size of two meters in length, large enough to eat small monkeys.

b) Birds: There are seven species of hawks and eagles in MNP. Six have been observed to eat monkeys (Table 17). One species, the harpy eagle, is known to specialize in predation of arboreal mammals including monkeys (Table 16). There are six owl species in MNP. Although little is known about the ecology of tropical owls (Burton 1978), available evidence suggests that none takes mammals larger than rats and small marsupials. The largest is 800g, probably too small to take a monkey the size of *Aotus*.

c) Cats: Four species of cat have been sighted at Cocha Cashu. Cats hunt both day and night (Schaller and Crenshaw 1980; Emmons and Janson, personal communication). Ocelots have been observed to attack *Proechymys* rodents (spiny rats) and trumpeters (pheasant-sized terrestrial bird); their ability to catch an arboreal monkey successfully is doubtful. Schaller and Crenshaw (1980) describe an *Aotus* cadaver that they suggest was killed by a jaguar in the Mato Grosso of Brazil. Cats cannot be ruled out as potential predators, but probably pose only a minor threat to both diurnal and nocturnal primates.

d) Tayras: Tayras (Mustelidae) weigh 3-5 kilos as adults and are diurnal omnivores. In other areas they eat fruit, honey, mice, agoutis, rabbits, chickens, and small opossums (Walker 1975). In MNP, tayras have been seen eating fruit and termites.

e) Primates: *Cebus* monkeys are omnivorous and weigh 2-5 kilos when fully grown. They have been observed to attack and injure seven species of mammals, including squirrels, infant prehensile-tailed porcupines, marsupials, and the silky anteater (*Cyclopes*) (Janson personal communication). During the day, *Cebus* chased *Aotus* from its sleeping site, pursued it for 100m, and almost succeeded in overtaking a straggler male who was carrying a three month-old infant.

2. Predators observed in proximity to Callicebus

Table 18 summarizes the incidences of predators observed near enough to _Callicebus_ to cause flight or flight accompanied by an alarm call. From these observations, there is evidence that diurnal raptors, cats, and _Cebus_ are potential predators on titi monkeys. Tayras were seen in close proximity to an adult and six month-old _Callicebus_, but neither individual fled nor gave any signs of alarm.

3. Predators observed in proximity to Aotus:

No predators were ever observed in the proximity of _Aotus_. Diurnal raptors are potential predators, however, because of the strict nocturnality of _Aotus_ and the fact that the night monkeys sleep in protected trees during the day, no observations were made of raptors attacking them.

4. Summary and Discussion

It is generally accepted that predators are a strong selective agent for many animals (Pulliam 1973; Wilson 1975; Curio 1976; Pulliam _et al._ 1980; Tuttle and Ryan 1981). Being preyed upon is a once-in-a-lifetime event, and those who are successful in avoiding predators live longer and have greater reproductive success than those who are not.

Primates, especially arboreal rain forest primates, are apparently adept at avoiding predation, because observed incidences of predation on these primates is low. There are reports of unsuccessful attacks on monkeys by hawks and eagles (Struhsaker 1975; Oates 1977; Rudran 1978), and reports of raptors eating primates (Dittus 1975; Rettig 1978; Charles-Dominique et al. 1980; Terborgh 1983). Attacks on primates by other mammals are rare (Charles-Dominique 1977; Schaller and Crenshaw 1980), as are attacks on primates by snakes (Jones 1969) and crocodiles (Galdikas 1984).

More incidences of predation on New World monkeys have been observed than on Old World monkeys per hour of observation (Dittus 1975; Struhsaker 1975; Oates 1977; Rudran 1978; Terborgh 1983). The difference is attributable to differences in body size. Old World monkeys are larger than those in the New World. In fact, among Old World species only the talapoin (*Miopithecus*) weighs less than 2 kilograms; 65% of all New World species weigh less than 2 kilograms (Napier and Napier 1967). Hawks and eagles are the major predators on primates worldwide (Dittus 1975; Struhsaker 1975; Charles-Dominique 1977; Rettig 1978; Terborgh 1983). Raptors have approximately the same body size across the globe (Brown and Amadan 1968); it is possible that Old World monkeys avoid predation by body weight too great for the raptors to handle.

In South America, hawks and eagles are the major predator on monkeys, especially the smaller species. Small, diurnal monkeys can avoid predation by employing two different strategies. Detection of predators can be increased by banding together into large groups for 'more eyes and ears', for cooperative defense, to confuse predators, and/or to increase the probability of predator satiation (Hamilton 1971). Saimiri form large groups and use this method of predator protection. Alternatively, crypsis may be used to avoid predation. Small, quiet groups, dark coloration, and keeping in low shadows can result in predators overlooking hidden prey. Callicebus may avoid predators with this approach. They spend 50% of their time lower ten meters above ground and 50% of their time is spent resting.

Aotus avoids these raptors by sleeping in dense vegetation tangles during the day and by being active when raptors are normally inactive, i.e., by exiting their sleeping sites after sunset, and by entering their sleeping trees before sunrise. Group size is important only in reference to the number of individuals that may be hidden in a given tangle. Large groups of sleeping monkeys in a single huddle may be detected by predators.

Male parental care, in the form of infant carrying, may provide good protection for small, infant monkeys. A female, already stressed by the energetic requirements of lactation, may not be able to flee carrying an infant on her back, whereas a male can escape effectively (Wright 1984).

H. Sleeping Trees and Sleeping Patterns

In this section I present the data on sleeping sites, and use patterns of sleeping trees for both species, beginning with _Aotus_. Data are summarized and discussed for sleeping trees in general and for observed differences and similarities in use by titi and night monkeys.

1. Sleeping Trees: Aotus

Morphology: Fifteen trees were used by eight groups of _Aotus_ in the Cocha Cashu study site. These were covered by various species of vines, so densely packed that the parent tree was obscured almost beyond recognition. The crown diameters of these trees ranged from 5 to 15 meters. Tree height ranged from 20-26 meters (Table 19). _Aotus_ disappeared into the vines in the tree crown, about 18 meters above the ground. It is possible that in some trees the night monkeys were sleeping in trunk holes but I could not verify this.

Tree Number and Location: _Aotus_ repeatedly used certain trees to sleep in. Group I used five trees during the fifteen months I observed them. Each of these trees was located at least one hundred meters from any other sleeping tree used by that group, and 15m distant from territory shared with another _Aotus_ group. During the 12 consecutive months Group I was studied (1980-1981), it used Sleep Tree A

57% of the time, and Sleep Tree B 21% of the time. This group used one sleeping tree per sample for 6 samples (55%), and two sleeping trees per sample for 5 samples (45%). The group never used more than 2 sleeping trees per 5-day sample.

Yearly Tree Use: Sleeping trees may be used by the same group over a period of years. An *Aotus* group was observed to leave Sleep Tree A in 1976 (Janson and Terborgh personal communication); the same tree was slept in 57% of the nights during 1980-1981. It cannot be determined whether or not this group was the same as Group I observed in 1980-1981. In 1982, Sleeping Tree A was used on 64% of the nights Group I was sampled during a three-month period. In 1981, *Aotus* Group II used one sleeping tree for 6 consecutive days. This same tree was used for at least three days in 1982. Habitual use of certain sleeping sites is not a local phenomena. In Puerto Bermudez, an *Aotus* group was observed leaving a sleeping tree used consistently two years previously (Wright 1981).

Availability: To determine whether or not scarcity of sleeping sites was a factor in tree selection, trees throughout Group I's territory were rated for suitability. Thirty-one trees in the territory were 20-25 meters tall with dense vine tangles in the crown. Adequate sleeping sites did not appear to be a limited resource.

Proximity to food: Is the habitual use of sleeping sites related to dispersion of food? All fruit resources were ranked by the number of minutes night monkeys fed in them each night. Distances between the sleeping tree and fruit ranked number one were calculated. In 54 out of 58 nights, the group used the sleeping trees closest (usually within 50 meters) to fruit ranked number one or two (95%). In all samples when the group used two sleeping trees, both were within 50 meters of a major fruit tree. For example, in May a Ficus (fig) tree with a 25 meter crown diameter near sleeping tree II was at the end of fruit production. A Brosimum (breadnut) tree with a 30 meter crown diameter near sleeping tree I had fruit ripening on it. The Aotus group I alternated between the two trees in May, then used exclusively sleeping tree I in June when the breadnut tree was at its fruiting peak.

2. Sleeping Trees: Callicebus

Morphology: It is difficult to characterize a typical tree titis use for nightly sleeping. Only 30% of the sleeping sites were in dense vine tangles similar to those consistently used by Aotus. Callicebus never slept in holes in trees. The trees used ranged in height from 12 to 30 meters. In 30 of 43 sleeping trees used by two groups, the family could be seen from the ground, and presumably from the air as well. However, the group never slept totally exposed on a branch. Leaves offered protection from detection and rain.

Number: Callicebus study group II used 26 sleeping trees during the year 1980-1981. Consecutive use occurred only once for Group II. They never used fewer than 3 sleeping trees per 5-day sample (Table 19). In two sample periods, they used a different tree each night. The average number of trees used for a six-day sample was 5.4 (N=11). Of 26 sleeping trees, 16 (62%) were used once, 5 (19%) were used twice, two (8%) were used thrice, 2 were used five times, and one was used six times. Therefore, Callicebus had preferred sleeping sites, but these trees were not constantly used, and were too open to afford predator protection, and were variable in their morphology.

Yearly use: In 1982, Callicebus Group II used 2 sleeping trees used in 1980-1981 in addition to 12 new sleeping trees. To my knowledge, none of the sleeping trees used by Group I in 1982 had been used in 1980-1981.

Location: The criteria for use of sleeping trees by Callicebus were not discernably related to tree morphology. However, location of the trees was consistent in two respects for Group I:

1. all trees but one were within 5 meters of the lake;

2. all trees were at least 100 meters from the closest border with another Callicebus group.

In Group II the criteria were also consistent:

1. all trees were within 25 meters of the river, but at least 10 meters from the bank;

2. all trees were at least 100 meters from the closest border with another _Callicebus_ group.

Proximity to food: All fruit resources were ranked according to number of minutes used for each day and distances from sleeping trees to food was calculated. In Group I, 21.7% of the major fruit trees ranked number 1 and 2 were within 50 meters of the sleeping tree. In Group II, 28.5% of the top two ranked fruit trees were within 50 meters of the sleeping site.

If protection from predators and proximity to resources are not criteria for sleeping tree selection, why is there a consistency in the location of sleeping trees? Choice of sleeping tree is probably related most closely to location of other conspecific groups in the area.

3. Discussion of differences in Sleeping Trees Used by Aotus and Callicebus

The conclusions drawn from comparing the diets of _Aotus_ and _Callicebus_ suggest that most dietary differences are a consequence of temporal differences in interference competition for food. It might be expected then, that other behavioral contrasts could be attributed to diurnal versus nocturnal competitors for food. But, there is evidence that suggests other selective pressures also distinguish the nocturnal monkey niche.

One behavioral variable not inherently affected by competition for food is choice of sleeping sites. *Aotus* sleeps during the day, but *Callicebus* and all other monkey species sleep during the night. Since sleeping sites are not depleted by continuous use, it is theoretically possible that both night monkeys and titis will choose similar, or even the same, sleeping trees. But this is not the case. The *Aotus* and *Callicebus* groups that shared the same territory, were never observed to sleep in the same trees, nor to show similar patterns in choice of sleeping trees.

a) *Aotus* in Peru sleep in dense vine tangles, consistently using the same sleeping site, or sites, for years. In contrast, *Callicebus* sleeping trees vary in amounts of vine cover, and groups do not habitually use the same trees. It is possible that vine tangles offer *Aotus* more predator protection, particularly from diurnal raptors.

b) *Aotus* chooses sleeping trees near a large fruit tree with ripe fruit. Compared to *Aotus*, ripe fruit trees are of minor importance in sleeping tree selection by *Callicebus* (Chi square 57.46, df = 1, p =<0.001). *Aotus* travel quickly into a major fruit tree after awakening, while *Callicebus* do not. One possible explanation for this difference in behavior is the use of twilight for rapid travel by *Aotus*.

c) *Aotus* sleeps in the same 2-5 trees in its territory consistently over a period of years, while titis sleep in 26-50 trees, rarely in the same tree two nights in a row. Reasons for the constant use of certain trees by *Aotus* may include a combination of factors, including proximity to fruit trees, predator protection, and easy orientation in the dark. Sleeping areas of Callicebus may be chosen for good locations to hear other group's dawn calls.

4. Comparison of entrance and exit times for sleeping trees by Aotus and Callicebus

a) Aotus: Aotus exits from and entrances into sleeping trees were highly correlated with sunset and sunrise throughout the year (times obtained from metereological tables). Aotus Group I left its sleeping tree a mean of 15 minutes after sunset, and entered 13 minutes before sunrise (Fig. 20). Weather conditions did not affect these times. All family members exited and entered within one or two minutes of one another, usually in single file less than a meter or two apart. In Aotus, timing of entrance and exit to and from sleeping trees did not fluctuate with fruit availability.

b) Callicebus: Callicebus exits and entrances were not always correlated with sunrise and sunset. Although daily variations were greater than those found in Aotus, seasonal variations were more significant (Figure 21). For example, in March Callicebus exited an average of 6.5 minutes before sunrise, in April exited at sunrise; but in June, averaged 115 minutes after sunrise, in July and August at 42 minutes after sunrise. Weather conditions did affect this behavior. Rain and cold were correlated with delays in exit and early entrance times. Family members exited the tree five to ten minutes apart. Juveniles often entered the sleeping tree from five to fifteen minutes after parents and infant. Callicebus exited sleeping trees earlier than sunrise when fruit was abundant and later than sunrise when fruit was scarce.

Rising early gives Callicebus a competitive advantage in the wet season because the family can feed early in large fruit resources before larger monkey species diaplace them. Callicebus feeds on leaves just before entering sleeping trees; there is little competition for leaves at any time of the year. This may explain the constancy with which the titis enter their sleeping sites year round.

5. Discussion Summary

Raptors: Because raptors maintain territories year-round, seasonal variation in predation pressure is minimal. Raptors are active throughout the daylight hours and therefore, predation pressure from raptors is no greater at dawn and dusk than at any other time of day. Callicebus spends 50% of its time low and in the shadows. Time of exit and entrance would not alleviate the pressure. However, Aotus can avoid the dangers of raptors by exiting its sleeping tree after raptors have stopped hunting and by entering the sleeping tree before the raptors are awake. Predation pressure does not vary significantly during the year, and neither does the timing of Aotus entrance/exits.

In the 15 months of study at Cocha Cashu, *Aotus* never exited in daylight unless chased out by *Cebus*, and they always entered before dawn (except when chased by *Cebus*).

Restrictions on vision: Do the exit and entrance data simply reflect a difference in the capabilities of the two species to see at different light levels? *Callicebus* could see and travel 18 minutes before dawn in March. Theoretically, titis could have left the trees that early at all times of the year. *Aotus* run and jump through trees in daylight when chased by *Cebus*. In captivity, *Aotus* often reverts to diurnal activity with no apparent handicap. *Callicebus* and *Aotus* are capable of exiting earlier and entering later than they do.

Although fear of raptors may explain why *Aotus* consistently does not travel in daylight, it does not explain why they do not exit sleeping trees late, or why they enter sleeping trees early. Perhaps restrictions on vision are important here. Twilight light levels are higher than light levels of the full moon (Pariente 1980). It is to *Aotus*'advantage to use these high light levels to travel quickly into the nearest fruit tree. And indeed, *Aotus* travels farther in the first 30 minutes and during the last 30 minutes of the night than during any other hour-long period.

a) *Aotus* consistently exits sleeping trees 13 minutes after sunrise and 15 minutes before sunset year-round in the rain forest. This constancy may be a compromise between two selective pressures; by being active after daylight Aotus avoids raptors. But, Aotus uses the twilight hour to travel to fruit trees when light levels are most advantageous.

b) Callicebus exits and enters its sleeping trees with much seasonal variation. In the wet season, Callicebus exits before or near sunrise; in the dry season they exit up to four hours after sunrise. Exiting early gives Callicebus a competitive advantage over larger species of monkeys, other titis groups competing for border trees, and birds. But when fruit is scarce, Callicebus exits late to minimize energy expenditure. Fruit trees (figs) are monopolized by large monkeys, and Callicebus eats leaves for which there is little competition if any.

I. Ranging Patterns

1. Aotus

a) Nightly path length: Mean nightly path length of the focal *Aotus* group for the 11 months samples was 708 meters (range = 340-1025m; S.D. =243)(Table 20). There was considerable variation that can be partly attributed to resource availability. The months of February and July (1981) had the shortest mean path lengths (340 and 385m respectively); shortest path length was 240m, the longest 1,200m. In both months, there were only one or two resources ripe in the range, and these resources occurred in one or two large patches. In January, March, May, and September - the months with the longest average path lengths - resources were located throughout the range in discrete, small-crowned fruit trees.

The size of an *Aotus* home range at Cocha Cashu varied from 7-14 hectares. Because *Aotus* used the same sleeping trees, the nightly path was often circular. *Aotus* exited the sleeping tree, ranged in a loop throughout its range, and arrived at dawn at the same sleeping tree where the night's activity had begun (Fig. 22). *Aotus* seems to have fine-tuned its ranging to include factors like moonlight and large fruit trees or nectar resources. If the moon was new, or there were only one or two large fruit trees available in the range, *Aotus* did not range very far. The low, backwater areas and bamboo patches where titis ate leaves were rarely visited by night monkeys.

c) Habitual pathways: Aotus did not wander randomly throughout its range, but used habitual pathways. Because I tagged trees with the date every ten meters as I traveled underneath the night monkeys, I could document the continual use of certain pathways. These paths were used at all times of the year, regardless of resource availability. Range maps (Figs. 22, 24, and 25) illustrate how habitual these routes are. Ranging patterns suggest that monitoring forays occur every four to six nights to check resources that may be ripening. These forays occur in the full or bright moon when visual cues can be used. The remainder of nights are spent traplining trees known to have ripe fruit. These trees are located along habitual paths. Although the species of tree with ripe fruit varies each month, each path remains nearly constant throughout the year.

d) Effects of light levels on ranging: There was evidence that light levels do affect ranging patterns of Aotus. First of all, night monkeys range farther during the twilight of dawn and dusk than during any other hour of the night. Consistent use of twilight for traveling may explain why Aotus does not enter its sleeping tree early on some nights or leave it late on others, in the manner of Callicebus.

To obtain an overall view of moonlight effects, I compared path lengths of nights with no moon (+ 3 days; mean=436; S.D.=283; n=11) and path lengths of nights when the moon was brightest (+ 3 days; mean =780; S.D.=242.7; n=49). There is a significant difference between the two sets of path lengths (Mann-Whitney U; Z=2.69; n_1=11; n_2=23; p <0.01) suggesting that Aotus ranges farther on nights with bright moonlight than on nights that are within three nights of the new moon.

Next, I divided each night into time of darkness and time with moonlight and compared meters ranged for each category. According to the the Sign Test, Aotus ranges significantly farther during the portion of night with moonlight than the dark portion (Z=-4.57; n=43; p <0.01). For example, on January 13 (1981), the moon was bright until 23:00 hours. From 18:20 until 23:00, Aotus traveled 750 meters. When the moon set, the monkeys rested, ranging again only at twilight (50 meters into the sleeping tree). On January 31 (1981), the Aotus group traveled 175 meters, from 18:28 to 03:20 hours, when there was no moonlight. As the moon rose over the trees, the Aotus group began to travel and traveled 700 meters between 03:20 and 05:25 hours.

Because Aotus feeds an average of two to three hours per night, and travels on the average of one to two hours per night, they have the flexibility to fit these active hours into times when they can see best. There are from 10-12 hours per night. They regulate their ranging to fit moonlight patterns. For example, on January 13 (1981), when the moon was bright between 18:30 and 11:00 hours, Aotus ranged 750 meters. On January 23 (1981), they traveled exactly the same route, feeding on exactly the same trees, but with different timing. The group arrived at the last feeding tree at 02:00 hours, just as the moon was setting. It took 7.5 hours to travel the same 750 meters which took only four hours to cover when there were fewer hours of moonlight. Although a group averages about 150 meters per hour on most nights, it can travel up to 350 meters per hour. These high rates of travel have been recorded only on nights when bright moonlight is limited to 2-3 hours.

What happens when there is a new moon, or when it rains all night? On these nights ranging is slow and not extensive. Sleeping trees are located within 50 meters of a large fruit tree or nectar resource. Like diurnal Callicebus, Aotus does not forage or travel during heavy rain. Remarkably few nights have heavy rainfall for 12 hours (perhaps one night per month in the rainy season;none during the dry season). On very few nights is the cloud cover so dense that moonlight is totally obscured, unless it rains as well. Moonlight shines through all but the heaviest clouds.

2. Callicebus

a) Daily path length: Mean daily path length of Callicebus Group II during the 11 months sampled was 671 meters (S.D.=192.9)(Table 21). The longest recorded daily path length was 1450 meters in March (1981); the shortest daily path length was 150 meters,recorded on a cold, wet day in June (1981).

Mean daily path length of _Callicebus_ Group I for the 5 months sampled was 552 meters (S.D.=105.84). The longest recorded daily path length was 1050 meters in November (1982); the shortest daily path length was 330 meters in July (1981). Seasonal variations in path length were not significant for either group.

b) Use of space: The size of a family group of _Callicebus_ home range averaged 6.9 hectares (see Table 4). In general, each _Callicebus_ group visited most of its territory every 4 or 5 days (Figs. 23, 24, and 26). Some parts of the territory were used more often than others. For example, the lake edge was used every day by Group II and the river edge daily by Group I. In both groups, the 200-300 meters of edge nearest the center of the territory was used. The remainder of the territory was visited every 3-5 days, depending upon resources. In some samples, only the edge of the territory was visited in a series of nearly straight lines up and down the lake or river edge. Never did a _Callicebus_ group cover their whole range in a single day. They often covered the entire territory in four or five days.

Unlike night monkeys, _Callicebus_ never remained in one fruit tree for long periods of time, regardless of the size of the resource. Ranging involved slow, methodical journeys from one small fruit resource to another, with occasional hour-long visits to a bamboo patch or viney area where leaves are abundant. Ranging within these leafy areas was in a lawn mower pattern. The back and forth pattern is efficient for avoiding recently harvested areas. Time is allowed for renewal of leaf resources by not revisiting a 'leaf patch' for 3-5 days.

c) Dawn and dusk ranging: Does the *Callicebus* family travel farther when exiting or entering a sleeping tree? To test this question, I calculated the distance moved in the first half hour plus the last half hour of the activity cycle per day sampled (mean meters traveled at twilight = 61.75; S=20.61; n=53). I then compared the distance moved during that hour to the average hourly distance moved during the remainder of the day (mean =59.91; S=47.93; n= 53). The difference is not significant (Sign test Z=1.10; $p < 0.05$; n=53).

d) Habitual pathways: *Callicebus* pathways were also tagged so that I might compare exact trees traveled through for a period of years. Titis do follow traditional pathways. Many used in 1982 were also used in 1980 and 1981. This was not entirely unexpected because mammals, especially those with small territories, tend to use habitual routes.

e) Weather conditions: *Callicebus* did not feed or travel in heavy rain. Daily path length was shorter on days with light rain than it is for days when there is no rain.

3. Summary and Discussion of Ranging in Aotus and Callicebus

a) Aotus and Callicebus groups range in small territories of about 10 hectares.

b) Both Aotus and Callicebus use habitual pathways. This may be a consequence of small territory size. However, Aotus path use is especially advantageous for an animal whose ability to see may be hindered by darkness. Monitoring of fruit trees is another advantage of traveling along habitual pathways and covering the entire territory in 1-5 days.

c) Aotus territories are found in all types of habitat; Callicebus territories are restricted to the edges of swamps, lakes, or rivers. This difference can be attributed to titis relying on vine leaves and bamboo leaf bases, both of which are found in abundance in water edge habitats.

d) Path lengths of each species averaged about 700 meters for each activity cycle when calculated over the year. Variance in nightly path length was greater between months for Aotus. Variability in night monkey path length may be attributed to differences in intensity of moonlight and differences in resource use. Aotus traveled farther when moonlight levels were high. They traveled less when a large fruit or nectar tree was available within the territory.

e) Aotus often ranged in a large circle around the perimeters of its territory in one night. Callicebus often covered all its territory in small loops over a 4-5 day period. They never circled their entire range in a single day. This slow but steady ranging allowed for renewal of resources, especially vine leaves and bamboo.

f) There is evidence that light levels affect ranging patterns of Aotus. Night monkeys range farther during twilight of dawn and dusk than they do at any other hour of the night. Aotus ranges significantly farther in the portion of the night with bright moonlight than the dark portion of the night. In general, Aotus' nightly path lengths are longer on nights of the full moon (+3) than on nights of a new moon (+3), and more at dawn and dusk than at other times of night.

This is not true of all nocturnal mammals. Some nocturnal rodents range farther on nights with no moon, and remain in their dens on full moon nights (Blair 1943, 1951; Kavanau 1967; O'Farrell 1974; Getz 1968). Small bats may also avoid flying during high moonlight levels (Morrison 1978b).

g) The fact that Aotus uses high light levels for traveling indicates that predation pressure does not affect ranging patterns for the species in this habitat. Nocturnal predators like larger bats (Fenton et al. 1977), and especially cats (Emmons, personal communication), and a few owls hunt more effectively in moonlight (Clarke 1983). If predation pressure is an important selective pressure on *Aotus*, then night monkeys would be expected to travel shorter distances on full moon nights. Since light levels and predation pressures remain more or less constant throughout the day, and across the daylight hours of the month, it would be predicted that *Callicebus* will not show significant differences in ranging patterns at different times of the month.

h) Day or night, ranging is primarily a result of locating and traveling to food and interacting socially with groups of conspecifics. Light levels and predation pressure vary each month with the moon cycle for *Aotus*, but remain more or less constant for *Callicebus*. Monthly variations in traveling to fruit trees, fighting, and calling may indicate some costs of nocturnality to *Aotus*.

Color vision depends on light intensity; color cues announcing resource availability may be denied nocturnal animals. Janson (1983) has evidence that yellow and orange colors on fruit attract monkeys like *Cebus* and *Ateles* across long distances in neotropical rain forests. Pollock (1979) suggests that *Indri* in Madagascar locate new leaves by their red and orange coloration, visible at 300 meters. If locating ripe fruit is a problem for nocturnal *Aotus*, two observations may be expected: 1) location of ripe fruit trees will occur only on nights with high light levels, and 2) *Aotus* will constantly monitor of all potential fruit trees in the range.

i) It is possible that low light levels handicap Aotus locomotion. Running and jumping through trees require precise judgements and adept movement even during the optimal light levels. There is some evidence that Galago demidovii, a quick-moving nocturnal, runner and jumper, travels farther on moonlit nights than on nights with no moon light (Bearder and Martin 1980). Because there is a positive correlation between nightly path length and nights of the full moon, it is possible that low light levels restrict movement of night monkeys. Because social interactions like intergroup calling and fighting, occur only at time when light levels are high, there is additional impetus for assuming that visibility is an important factor.

J. Intergroup Interactions and Territoriality of *Aotus* and *Callicebus* (See Methods, Chapter II, for definition of territory.)

1. *Aotus* Territorial Patterns

Size: The size of an *Aotus* territory at Cocha Cashu ranged from 7-14 hectares, with a mean of 9.2 ha (n=7). *Aotus* Group I's territory was 7 hectares (Table 4).

Location: *Aotus* groups can be found in all types of habitats throughout the Cocha Cashu study site, including well-drained upland forest, fig swamp, river edge, and lake edge habitats. Although the low bamboo thickets and viny backwater areas where *Callicebus* eat leaves is included in the *Aotus* territory the night monkeys spend little time in these areas. They bypass these areas by traveling over them.

Long-term Stability: The territory of *Aotus* Group I had almost identical boundaries during the 1980 and 1981-1982 observations. In 1982, a major portion of Group I's area was eroded by a flood which felled an eighth of all fruit trees used by *Aotus* during the year 1980-1981. Group I did not range further beyond its former boundaries to compensate for this loss. However, since the group was followed for only three months after the flooding, this evidence is inconclusive.

Although ranging data on other groups at Cocha Cashu are not as extensive (Group II = 12 nights; Group III = 1 night;

Group IV = 6 nights; Group VI = 18 nights), there is some evidence that groups remain in the same territory over a period of years. Marked groups are necessary for conclusive evidence, and none were marked in this area.

2. Aotus Interactions (Intergroup fighting and loud calls:

a) Agonistic encounters (Intergroup fighting): From September, 1980, through August, 1981, *Aotus* Group I had at least 16 encounters with other groups. These encounters involved attacks, chases, noisy branch shaking, and resonant whooping by both groups. The sex of the fighters could not be distinguished, but at least two monkeys from each side chased and gave resonant whoops (whoops are produced by both sexes).

Duration: Battles lasted about 10-15 minutes. One group which had participated in an agonistic encounter, remained in the tree where the fight occurred for at least 15 minutes after the episode ceased. The other group involved traveled quickly into the center of its territory.

Location: Fourteen out of 16 fights occurred on boundaries between groups. In at least 15 of 16 encounters, an invading group was fighting for access to a large-crowned fruit tree filled with unripe or ripe fruit.

Hour: These fights occurred only when the moon was full or nearly full and directly overhead and bright. In 8 of 16 battles (50%), the moon was between two nights before full to two nights after being full. This is the time when maximum illumination can be gained from moonlight. Thirteen of 16 battles occurred between 18:17 and 22:10 hours. Figure 29 shows that timing of a battle can be correlated with time of night when the moon is directly overhead. No battles occurred in the dark of the moon or when the moon was obscured by clouds. One battle occurred at twilight.

Seasonality: Fights occurred in all months of the year and seemed to depend on the ripening of a large-crowned fruit tree on a boundary between groups, but not on availability of resources in the forest as a whole (Fig. 28). Fighting is not correlated with estrous cycles. Group I fought most battles in February, when the infant was less than one month old; there is no postpartum estrus in *Aotus* (Hunter *et al.* 1979). It should be noted that the cycle of *Aotus* females is every 16-17 days, not every 28 (Bonney *et al.* 1979), and therefore, any correlation with monthly fighting in the full moon seems unlikely.

b) Calling: Although *Aotus* has eight discrete calls (Moynihan 1964; Wright 1981), only one is used to convey information over long distances. This call is termed the hoot.

Call Structure: The hoot is composed of a sequence of from 2-6 pulses, each lasting an average of 165 milliseconds, with interpulse durations of about 440 milliseconds. Hoots have no harmonic structure and little frequency variation. Hoots were recorded as high as 380 Hz and as low as 230 Hz. (Figure 29a).

Sexual dimorphism in calls: Hoots separate into two patterns (Figure 29a). Analysis and recordings from *Aotus* of known sex revealed that the pure tone hoots are produced by females, while the hoots with extensive spectral splatter are produced by males. Only one individual night monkey hoots from each territory, however, that animal may be either male or female.

Audibility: *Aotus* hooting can be heard by humans 500 meters away.

Duration: Although the hoot itself lasts only a few seconds, the duration of a hooting session is from one to two hours (Table 22).

Frequency: In each territory an individual animal hoots an average of once per month (Table 22). There are some months when there is no calling, and others when an individual in a territory will hoot for two or three nights. More hoot nights were recorded in the months of the wet season when fruit was abundant. No hoots were heard on rainy nights.

Hours: More hoots were given in the early evening; 20 of the hoot sessions occurred between 18:00 and 22:00 hours (Fig. 29b). However, correlation with moonlight levels maybe more relevant in each case than the time of night (n=22). Hooting occurs when the moon is between a half moon and full moon, when the moon is directly overhead (Fig. 29b).

Duetting: Aotus does not call in duets. One individual from the group calls and there is some indication that the same individual calls each month. Individuals hoot at different frequencies and with distinctive spacing between hoots.

Location of caller: Usually, the animal hooting traveled during hoot sessions. The mean distance traveled was 220m (range =50-600m). One solitary calling individual traveled over 3km in a hooting session which lasted at least eight hours (these data were not included in analyses). Group I hooted along boundaries on six out of nine calling sessions. It appears that the other five groups followed were also hooting along territorial boundaries, but this question is still not resolved. Calling routes remained quite constant over a period of years (cf. Robinson 1979).

Response: There is often counter-calling by other Aotus from neighboring territories. As many as six groups may hoot in a square kilometer area in one evening. Often, two Aotus from bordering territories will progress toward each other and their common border while hooting. As the callers approach one another, they hoot faster and louder. However, when 25 meters apart, each retreats back towards the center of its respective territory.

Aggressive interactions: Only two out of 24 hoot sessions observed in the 12-month period were associated with intergroup encounters. In both of these cases one of the animals hooted while at least four others (two groups) attacked and made resonant whoops. The resonant whoop calls are very distinctive and are always associated with these encounters. Both males and females give a resonating call from the throat pouch which consists of an ascending series of 10-17 slurred notes. These calls are given after attacks and after agonistic intergroup encounters. The number of resonating calls per battle ranged from 2-15, with a mean of 17. It was difficult to distinguish exactly how many night monkeys were calling, but there were at least two involved in each battle.

Mate attraction: It is possible that hoots are given to attract mates. In captivity, night monkeys of both sexes hoot when separated from their mates. In the full moon of April (1981), a solitary monkey traveled over three kilometers, stopping only for two 10 minute intervals to feed during the course of an eight hour journey. This adult-sized monkey hooted constantly through at least six established *Aotus* territories. No other night monkeys hooted or attacked. According to sonographic analysis, the caller was male.

3. Callicebus Territorial Patterns

Territory size: The *Callicebus* territories ranged from 6-8 hectares (n=6), with a mean size of 6.9 hectares (Table 4). All fights were also plotted on a map containing all daily path lengths for the year (see Methods, Chapter II). As described for other *Callicebus* groups (Mason 1966, 1968; Kinzey *et al.* 1977; Robinson 1979; Easley 1982; Kinzey and Beckman 1983), *Callicebus* at Cocha Cashu maintained virtually exclusive territories which were defended at borders. A 50 meter 'neutral zone' separated borders where fruit trees were abundant. Fights occurred here and trees on this border were used by two or three neighboring groups. Solitary titis occasionally wandered through the study group's territory. These animals were chased by the subadult from the focal group and therefore did not remain long within the territory.

Long-term stability: The territories of *Callicebus* Group II had almost identical boundaries during the 1980, 1981, and 1982 observation periods. *Callicebus* Group I, studied in 1980-1981, expanded territory use one half hectare into the upland area during 1982. No *Callicebus* group had been observed in this area before. It is possible that this change resulted from territory lost during the flood of 1982.

Census of groups of *Callicebus* conducted from 1975-1982 reveal that most territories are maintained over a period of years with little change in location of boundaries. Kinzey (1979) and Terborgh (1983) followed Group II during 1975 and 1976 respectively. I found that paths, and even fruit trees fed in, were the same as those used in the same months of 1980-1981-1982. Territories may be more permanent than the individuals who hold them. Group IV (an mature adult pair and their two offspring) was replaced by Group VII (a young adult pair) in 1982, but boundaries remained the same. Displaced individuals were observed to wander from territory to territory. Areas devoid of titis may suddenly contain a group. From 1975-1982 there were no titis from for a distance of 800 meters along the lake between markers 6.2 - 6.10. In 1983, a group had moved into this area (Terborgh personal communication).

4. Callicebus Interactions (Intergroup fighting and loud calls:

a) Agonistic encounters: In 11 months of observing the *Callicebus* Group II and five months of observing Group I, I witnessed only seven encounters with other groups or individuals. Calling and chasing in these contexts were performed by the adult male of each group, or in the case of Group II, by the subadult male and/or the adult male. Females did not participate in these encounters.

Duration: Fights ranged from 5-30 minutes. An intergroup encounter ended when the loser retreated with the winner chasing him at least 30 meters. Often the winner called after the final chase.

Location: Six out of seven fights occurred on the territory borders containing a large tree with ripe fruit. Both groups attempted to enter this border tree. The seventh fight occurred at dawn when a solitary adult approached the established group's sleeping tree in the middle of their territory. The subadult male from Group II attacked and chased the intruder for 100 meters. The adult male and female of the group huddled near the sleeping tree with their two month-old infant and one and one half year-old juvenile during the episode.

Hour and seasonality: Fights did not occur at any particular time of the month. However, all the battles occurred in the wet season when resources were plentiful. In the dry season, when the situation was reversed, Callicebus ranged less and relied more on leaves located at least 100 meters from territorial borders. Because there were few fruits available, there were also few fruits to fight over.

I observed little correlation between female estrus and fights. The adult female in Group II was in estrus April 7 and 8, 1981. A male with half of his tail missing arrived at the border late in the afternoon of April 9; he was a mated territory holder from 1975-1980 in a neighboring territory (Group IV), but was replaced by another male. The adult male and adult female of Group II retreated with the seven month-old juvenile close behind. The one and a half year-old juvenile repeatedly chased the aged, solitary intruder to the edge of the territory, while other family members observed from 75 meters away. Finally, the juvenile abandoned the chase, joined his family, and they then traveled together to a sleeping tree 100 meters into the center of their territory. The lone male then fed in the large fruit tree on the border until dark. All other battles occurred when the adult female was either lactating or pregnant and not sexually receptive.

b) Calling: The intergroup call of *C. moloch* has been described by Moynihan (1966) and Robinson (1979a, 1979b, 1981). I shall therefore restrict comparisons to differences between loud calls of *Callicebus* and *Aotus*.

Structure: The dawn call of the titi has elaborate harmonics and varied structure (Fig. 31).

Audibility: *Callicebus* calls can be heard by humans up to 500 meters away.

Duration: *C. moloch* calls usually last from 2-5 minutes. On occasion calls are given repeatedly within a 15 minute period. The repetition is usually stimulated by counter-calling from other groups.

Frequency: *Callicebus* Group II called on the average of once every other day. There was seasonal variation and all groups called much less frequently in the dry season when resources were scarce. Groups rarely called on rainy mornings, but they did call on cloudy and/or sunny mornings.

Hour: Ninety percent of the intergroup calls of *Callicebus* were given before 09:00 hours, and calling was most frequent between 06:00 and 07:00 hours. Kinzey and Robinson (1983) found similar results in their study of C. torquatus; 90% of the calls were before 09:00, with modal frequency between 06:00 and 06:30 hours.

Duetting: In Group II, 39% of the intergroup calls given were duets between the adult male and adult female. Thirty-one percent of the intergroup calls were a trio given by the adult male, adult female, and the one and one half year-old subadult male. Twenty-seven percent of the calls were given by the adult male alone. Unlike Robinson (1981), I found that the duets and trios were usually given first thing in the morning, at least 100 meters from a territorial border. Thirty percent of the male calls were given at a border, usually during or after a battle with a neighbor group. Only 30% of the duets were given at a border. Duets were not given at a border when there was another group within 100 meters. The subadult male called alone during two battles in which he was involved. In 1982, the adult male and adult female duetted once while the two and one half year-old subadult male chased a solitary male from the center of Group II's territory. After a successful chase, the subadult male called alone.

Location: Only 22% of the calls produced by Group II (Lake Group) were within 50 meters of a territorial border (Fig. 30). Seventy-eight percent of the calls were emitted along the lake edge in the center of the territory.

Perhaps the lake edge area was preferable for both broadcasting and hearing the calls of other groups. If other groups began to call, and Group II was away from the lake edge, they never replied to other calls. Group I (River Group) both slept and called most often at the river edge. However, all the calls given by Group I during my observations (n=10) were emitted at least 100 meters from the border with Callicebus Group III. Likewise, Group III called about 80% of the time from the center of their territory.

Response: There is a strong penchant for counter-calling. In 86% of cases when Group II called, at least one, but more likely three to five, groups answered. Groups, however, do not move towards each other unless callers are within 50-75 meters of one another.

Aggressive interactions: In addition to dawn calls, Callicebus often call during intergroup encounters. In eight encounters, I did not observe the females to call. Either the adult male called alone before and after the fight, the subadult male called alone before or after the battle, or the adult and subadult males duetted.

Solitary travelers: I have heard solitary males call during battle, but in contrast to Robinson (1981) I have never observed them to give territorial dawn calls or to vocalize while traveling through established group's territories.

K. Summary and Discussion of Range Type and Intergroup Interactions for Aotus and Callicebus.

In the previous section, I discussed the ranging behavior of Aotus and Callicebus, implying that both species were territorial (see definition of territory on p. 21). Family groups of Aotus and Callicebus remain in fixed territories and use of these areas are exclusive for over 90% of the time. In addition, there is slight overlap in each group's ranging behavior since two or three groups occasionally feed in the same tree located 25-45m on either side of a border. However, these groups do not feed there simultaneously. Solitary individuals roam throughout various territories and are chased by resident family members if seen.

In this section, defense by proclamation (loud calls) and actual battles with other groups of the same species are discussed. It is established that territories of Aotus and Callicebus are approximately the same size; group size and social systems are more or less equivalent in the two species. Thus, differences in calling and fighting may be interpreted as adaptations to the night niche as contrasted with the day niche. The nocturnal environment has different acoustic properties, predators, and fluctuating light levels. The calling and fighting behavior of Aotus have evolved to surmount these problems.

1) The structure of the Callicebus intergroup call is ornate and incorporates a series of chirrups, pants, whoo gobbles (Fig. 31), etc., whereas the Aotus loud call is monotonous and repetitive (Fig. 29a). The difference in structure between the calls of the two species may have evolved to compete in different acoustic environments. During the day, there is more convection and turbulence in the air. Competition for air space is acute because 500 species of birds and nine species of monkeys also may be calling. During the day, a more complex call may be necessary to insure that other groups can distinguish the loud call from background noise, as well as pinpoint the calls' locations.

During the night, Aotus calls compete with the high frequency (2-7 Hz) of insect and amphibian calls. The low frequency hoots avoid most of this interference. Convection and turbulence in the air are minimal at night. Therefore, the main obstacles to sound transmission are objects in the path of sound waves. Low frequencies are optimal for long distance communications because long wave lengths can travel around obstacles such as trees (Marler 1967; Waser and Waser 1977). The low frequency hoot (200-400 Hz) broadcasts well at night (many owls also vocalize at these frequencies).

2) The loud calls of both *Callicebus* and *Aotus* can be heard by humans for about 500 meters. The audibility function of *Aotus* is similar in shape and overall sensitivity to the curve for humans (Beecher *et al.* 1978). Therefore, it may be realistic to assume that *Aotus* (and perhaps *Callicebus*) can hear and distinguish hoots at about 500 meters. Due to the small size of *Aotus* and *C. moloch* territories, it is possible for each group to hear its neighbors call from most locations in the territory. Both genera emit loud calls structured to carry approximately the distance of the diameter of their territory so that the message may be heard by all neighbors.

3) *Callicebus* calls at 5-15 minute intervals about once every other morning throughout the month in different areas of its territory. *Aotus* calls continually for one to two hours about once a month when the moon is rising. Night monkeys tend to travel to boundaries (100-300 meters distance) while calling. A possible explanation for the *Aotus* requirement of high light levels is that the vocalizer can see and be seen by other hooting conspecifics. Another possibility is that night monkeys call when there is enough light to see potential attackers of the same species and potential predators. *Callicebus* gives a loud call from a fixed point, but each morning from a different fixed site, and very often calls throughout the month. Potential

trespassers are reminded almost daily that the territory is occupied, and by a mated pair because the pair duets. From the evidence on ranging, it appears that Aotus do not range far during nights when moon light levels are not high. If there is little possibility that other night monkeys will invade, then there is no reason to emit territorial calls on dark nights. In addition, if all intergroup calls are given just in one or two moonlit nights, perhaps it is best to call for longer periods of time to assure that all neighbors may hear the call. Traveling while calling may also insure that more neighboring night monkeys will hear the hoot.

4) Callicebus give territorial duets, while Aotus hoot alone. This poses some questions. In siamangs, and some species of gibbon, the mated pair may call at different times during the morning; both males and females from the same territory call. In Aotus, it appears that one sex calls each month in the same territory. It may be either male or female; however, this individual calls consistently from the same area for at least a year. Because the monkey calls alone, there is some question as to whether or not the caller is a member of a mated pair, a subadult member of the mated pair's family group still in the territory, or an adult who has left the group the year before but who still remains in the immediate vicinity. Until there are data from marked animals, these questions will remain unanswered.

5) A solitary Aotus may call continually while it is traveling through territories of family groups. There is a possibility that the Aotus hoots are used in mate attraction, in addition to or instead of their use territorial calls. A solitary or sexually maturing nocturnal monkey may have greater need to advertise its availability to potential mates than do mated animals. It may well be that a subadult begins calling months before it is prepared to migrate from its natal group. When ecological factors are favorable, it emigrates long distances, making its presence known along the travel route.

6) Callicebus loud calls may be given during and after agonistic encounters. In most instances, this is not the case with the Aotus hoot. The night monkey has evolved a very different call (resonant whoop) which is given before and after agonistic episodes. This evidence further suggests that the hoot is not a 'territorial call' in the usual sense, but may be used in mate attraction.

7) Both Callicebus and Aotus fight at boundaries of their territories. Fights usually occur in or near large trees filled with ripe fruit found at the border between two or three groups. Fights are more prevalent in the wet season, when there is a greater chance of a tree bearing ripe fruit along the border.

8) There is no correlation between the timing of fights and female estrus in either species. Males will engage in fights even with infants on their backs.

9) In _Aotus_, all fights occurred within three days of the full moon, or in a single instance, at twilight. This may be a consequence of wider ranging during high light levels (see ranging patterns for _Aotus_). _Callicebus_ fights were not correlated with any particular time of the month.

L. Summary and Conclusions for Results in Peru

Contrasts in behavior between Callicebus and Aotus are interpreted as indicating that during the day, interspecific competition and predator avoidance are strong selective forces which influence the diurnal behavior of the former and sleeping sites of the latter. Compared with diurnal Callicebus, Aotus is exposed to less interspecific competition for food resources and less raptor predation at night.

Ranging, habitat use, and feeding data suggest that Callicebus and Aotus partition resources only in the dry season when fruit is scarce. Food habits of many coexisting species diverge during the most difficult season (Charles-Dominique 1977; Gautier-Hion 1978a, 1978b; Emmons 1980; Terborgh 1983). During June, July, and August, the large diurnal monkeys with overlapping ranges dominate the large-crowned, superabundant and widely-dispersed fig and nectar resources; Callicebus is chased out. Denied access to the only ripe fruit available, titi monkeys feed in the low edge areas on bamboo shoots and vine leaves. In contrast, Aotus feeds extensively on these fig and nectar resources at night, unhindered by other monkeys or birds. The travel of Aotus is goal oriented from one fruit tree to another. Moving as directly as possible to preferred food sources is the best foraging strategy if foods are patchily distributed in space and time (Schoener 1971; Milton 1980).

Like the howling monkey, Callicebus minimizes energy expenditures by moving slowly, quietly, and resting often (Milton 1980). This behavior serves a dual function: allowing time for leaf digestion and giving protection from raptor predation. Aotus, active after raptors are asleep, moves quickly and noisily from fruit tree to fruit tree, opportunistically catching insects along the way. Evidence is mounting that nocturnal predators hunt using auditory cues (Konishi 1973; Tuttle and Ryan 1981; Tuttle et al. 1981). Not only does Aotus travel noisily, but its loud calls, (heard for 500 meters) are emitted for over an hour at the top of the forest canopy in bright moonlight. It seems unlikely that these behaviors would have evolved if nocturnal avian predators posed a serious threat. Aotus chooses dense vine tangles in trees for sleeping and enters and exits these trees before sunrise and after sunset, suggesting that diurnal raptors are indeed a strong selective force.

In sum, Aotus has two distinct adaptive advantages in being nocturnal: (1) Aotus avoids interspecific competitors by feeding at night when mammalian and avian competition is reduced, and (2) Aotus avoids raptorial predators by choosing cryptic sleeping sites when predators are active, and by being active when predation is minimal. Many of the behavioral differences between Callicebus and Aotus follow from these adaptations.

CHAPTER IV

RESULTS IN PARAGUAY

A. Introduction

My research in Peru established several facts about *Aotus* in the rain forest: (1) The activity cycle is consistently nocturnal. Unless disturbed by diurnal monkey species, *Aotus* leaves its sleeping tree after sunset and returns to it just before sunrise. This constancy does not vary seasonally. (2) *Aotus* uses two to four well-protected sleeping trees consistently over several years, even though other seemingly suitable trees are available as sleeping sites. (3) *Aotus* in the rain forest feeds predominantly on nectar and fruit from large-crowned trees rather than leaves at the time of year when fruit resources are scarce.

As discussed in the first chapter, the evolution of this consistent nocturnality is, at first glance, puzzling. Nighttime activity makes fruit location and efficient arboreal travel difficult. *Aotus* can maneuver well through the trees in broad daylight and travels farther and feeds more at high nighttime light levels. What advantages are there in a nocturnal activity cycle for this primate? Two hypotheses were suggested by my research in Peru:

1. In the rain forest, interference competition for high quality food items is less at night than during the day. During the months of resource scarcity, *Callicebus* was consistently chased from large-crowned fruit trees by *Cebus* and *Ateles*, while *Aotus* fed unmolested at night in the same trees.

However, if interference competition were the only selective pressure for nocturnality, we would expect seasonal variation in nighttime activity. This was not the case in the Peruvian rain forest. *Aotus* was consistently nocturnal during the entire year.

2. Predation pressure from hawks and eagles is nonexistent at night in the Peruvian habitat. In the rain forest, there are six species of hawks and eagles which eat monkeys. None of the owls are large enough to prey on monkeys. Predation pressure is not a seasonal phenomenon and perhaps could account for the constancy of exit and entrance time from sleeping trees.

To test the two hypotheses above, I studied *Aotus* in a habitat which contrasts markedly with the Amazonian rain forest. In the southernmost part of the *Aotus* range is a population that lives in drier subtropical savannah of western Paraguay and northern Argentina, the Grand Chaco. Small forest islands located in the savannah contain two monkey species: *Aotus trivirgatus* [*A. azarae*] and *Alouatta* *caraya*. *Cebus* and *Ateles*, the two species who chased *Callicebus* from feeding sites, are absent from the Chaco. The complement of predators in the Chaco is also different from the rain forest. Harpy eagles and crested eagles, the main predators on monkeys on the rain forest (Fowler and Cope 1964; Rettig 1978; Terborgh 1983), are rarely seen. However, the great horned owl (*Bubo virgineanus*) is common in the area. This nocturnal predator eats rabbits in North America, and could easily dispatch a monkey weighing one kilogram.

I hypothesized that under these ecological circumstances, the selection pressure to remain nocturnal would be released. *Aotus*, secondarily adapted to a nocturnal life style, would be more active during the day in the Chaco habitat than it was in the rain forest. In addition, Kreig (1930) suggested that *Aotus* in the Chaco was more diurnal because of low ambient temperatures during the winter months.

With these ideas in mind, an assistant and I studied one group of *Aotus* in the Chaco for five months. I chose this period because resources are scarce and competition for those remaining would be strongest. We followed intermittently a group of *A. caraya* (the black howler monkey) which lived in the same forest. To understand further nocturnal competitors for food, we trapped and marked the two species of opossum. Predation pressure from the pair of great horned owls that nested in the forest was estimated by: 1) examining daily boluses of both owls to tabulate prey items; 2) locating when possible, the owls in the forest during the night, and; 3) documenting the ranging and sleeping patterns of Aotus in relationship to the owl locations.

B. Population Densities and Life History Parameters of Aotus

1. Distributionof Aotus in Paraguay:

The Paraguay River divides Paraguay into two major vegetation and faunal zones. Rich volcanic soil and ample rainfall produce rain forest to the east of the river. In this rain forest, *Cebus apella* (brown capuchin) and *Alouatta caraya* (black howler monkey) are abundant. Smaller species are usually absent, *e.g.*, night monkeys, titis, and squirrel monkeys. Fauna is specific to each side of the river. Several explanations have been offered for this dichotomous situation:

1) vicariance (Myers 1982)

2) differential soil type and precipitation on each side resulting in differential fruit resources on each side (Myers 1982).

On the west side of the river, ancient infertile soils are not enriched by lava; rainfall is sparse. There is a precipitation gradient with the lower Chaco region closest to the river receiving 1300mm of rain per year. The most western sections, on the other hand, receive only 300mm of precipitation per year (Stallings 1984). Population densitites of *Aotus* increase across the gradient, with greater densities in the wetter areas to the East. In the northernmost area of the Chaco, there are five sympatric primates whose ranges are extended from adjacent parts of Bolivia and central-western Brazil. These species are *Aotus* sp., Alouatta caraya, Cebus apella, Callicebus moloch, and Callithrix argentata (Stallings and Mittermeier 1983). As the Chaco becomes drier, all species but Aotus and Alouatta are no longer present. In the lower Chaco area the only two primate species present are these two forms.

2. Population Density: Rathbun and Gache (1977) and Rathbun (1980) censused Aotus populations in the Formosa province, Argentina, and found the population density to be 18 night monkeys/square kilometer. The habitat in Formosa province and the habitat between Pilcomayo and the Rio Confuso are virtually identical (Espinoza personal communication). I assume that the population densities are not significantly different in the two locales.

Four adult Aotus trivirgatus lived in the 5 ha La Golondrina forest study site (Fig. 32). One pair of Aotus ranged throughout the forest, at the same time as two solitary adults. An adjacent forest of about 6 hectares contained one pair of night monkeys. Another forest of approximately 10 hectares contained at least one pair of Aotus, but these animals were only heard and never seen for an accurate census.

3. Life history parameters: Rathbun (1980) in his October, 1977, census found that mean group size was 2.9 animals (n=25; S.D.=.88). All groups contained an adult pair and all evidence suggested a monogamous social system. Three groups (12%) had infants on the father's back (infant = age

1-3 months). Twelve groups (48%) had 4 to 9 month-old offspring; ten groups (40%) had juveniles aged 1 to 2 years. Because visibility in the Paraguayan habitat is excellent, I doubt that any family member was overlooked in the census. No groups had more than one offspring. Because the ages of the offspring ranged from a few months to subadult, there is no indication that juveniles in this harsh environment emigrated from their natal groups at a younger age than rain forest night monkeys. There is some suggestion that offspring were killed more often than those elsewhere. This mortality might have resulted from predation or from malnutrition and disease.

4. Discussion: In my census of Peruvian *Aotus* I found mean group size to be 4.1 monkeys (n=9). A census of *Aotus* in Puerto Bermudez, Peru, found a mean group size of 4.2 animals (n=5). Although the sample size in Paraguay is small (n=2), group sizes at the study site were well within the range of variation for Paraguayan night monkeys observed by Rathbun (1980). It remains an assumption that group size of *Aotus* in the Chaco is nearly half that found in the tropical rain forest, and total population densities are about half those in the tropical rain forest. At Cocha Cashu, population density was 36-40 per square kilometer; Rathbun (1980) estimated 18 animals per square kilometer in the Chaco.

C. Environment in Paraguay

1. History and geology: The Chaco of Paraguay consists of a vast alluvial plain formed by soils eroded from the Andes (Eckle 1959). The climate becomes increasingly arid from the Paraguay river northwest to the foothills of the Andes. The terrain is relatively flat, and the altitude is slightly above sea level, rising to the west one meter per two kilometers. Along the Paraguay river the lower or wet section of the Gran Chaco (where the La Golondrina study site is located at 24° 25' S and 58° 40' W) marshes and palm savannas or pantanals (Short 1975) are interspersed with gallery forest and shrub woodland. Forest soil surfaces are often a few centimeters higher than the savannah. Principal carriers of Andean sediments are the slow, meandering rivers (Myers 1982), such as the Rio Confuso which flows through the study site. The soil is extremely dense gray clay. This soil is impermeable to water; rainwater stands in pools on the surface of the soil. This causes seasonal flooding. During the dry season, the clayey soil is baked by the sun until it has a consistency like concrete. In the area of La Golondrina, salts, particularly magnesium compounds, create salt pans on the surface and render standing water unpotable (Eckle 1959). Even rivers are extremely saline and potable water is difficult to find even in the rainy season. The extremes of wet and dry conditions, the nutrient-poor soils,

and unpredictable onset and intensity of precipitation (Gorham 1973) all contribute to the creation of a stressful environment which may account for low species diversity of flora and fauna.

2. Vegetation mosaic: The lower Chaco, as defined above, consists of open, subtropical savannah, covered with one species of grass which grows to about one meter or less in height. *Atta* ant hills dot the landscape; each may reach one meter or more in height. Fan-shaped palm trees (*Copernicia alba*) occur throughout the grassland, but not inside forested regions. Small island forests of three to ten hectares are located about 500 meters apart in the savannah. These forests grow up from the fertile soils created by abandoned ant hills. Forests are short (the tallest trees are approximately 25 meters tall), and open forests have botanical composition similar to that of the gallery forests that line the rivers. *Aotus* and *Alouatta* are found in both habitats: forest islands and gallery forests throughout the grassland.

3. Climate: The subtropical Chaco is located between 19° South and 25° South; seasonal differences in temperature are extreme (Fig. 33). During the cold winter months of June and July, temperatures may reach -5°C at the study site (A. Espinoza, personal communication). Frost is commonly seen for about five days each year. During the five-month period from May to September (1982), the lowest

temperature was 5°C in July, the highest was 42°C in August (Fig. 34). According to long term averages, the hottest months in the Chaco are December through March when the daily maximum temperature equals 41°C (Fig. 33). The two coldest months are July or June with long-term average daily temperatures of 18.4 and 18.7 °C respectively. In general, temperature extremes are very pronounced. The highs of the year are higher than in the rain forests of Peru, and the lows are both lower and longer lasting than the lowest temperatures in MNP.

4. Rainfall: Rainfall is more uniform throughout the year than the temperature. Approximately 1,340 mm of rain falls each year in the so-called wet Chaco (along the river as defined above), just north of Asuncion. The months of highest rainfall are January through April; the driest months are June through October (Figs. 35, 36). Although this mirrors trends in the Peruvian rain forest, the wettest months in the Chaco receive about one-half the rainfall recorded during the same months in MNP. The dry months in the Chaco are not as dry as the same months in the rain forest.

5. Botany/Species diversity: Results obtained from botanical surveys of the five hectare forest and the savannah outskirts confirm that there is not a high diversity of plant species (Table 23). Although there are approximately 300 plant species at the study site (including epiphytes,

grasses, trees, and shrubs), within the forest only 25 species of tree are common. Most of these trees are in the families Bignoniaceae, Euphorbiaceae, Leguminosae, Meliaceae, Myrtaceae, Palmae, and Sapindaceae. There were two palm species: *Copernicia alba* in the savannah and forest edge; *Arecastrum romanzoffianum* within the forest at a density of 56/hectare. The forest was rather open, with a density of 3760 trees of two or more meters in height per hectare. Eighty percent of the trees were under ten meters in height, and only 46 trees per hectare (4%) grew in excess of 20 meters tall. Small trees and shrubs from the families Celestraceae, Rubiaceae, and Ulmaceae were common at the forest edge. Arboreal bromeliads (*Tillandsia duratii*), Spanish moss (*T. usneoides*), and orchids were scattered throughout the forest, the former two most concentrated at the forest edge. Cactus, particularly *Cereus sp.* (28/hectare; mean trunk diameter = 8-10 cm; height=2 m) and climbing cactus (88/ha) were found in open areas within the forest. Vines with diameters of 2-4 cm were found at densities of 1104/hectare. Two species of terrestrial bromeliads (*Aechmea polystachya* and *Bromelia serra*) with pineapple-like fruit and spiny hooked leaves formed a thick ground cover at 13,100/hectare. During the winter months, many of the trees are defoliated (*e.g.*, *Caesalpinia paraguayensis*, *Tabebuia ipe*, *Terminalia argentea*).

6. Fruit trap results: Fruit availability was

determined by two different methods. Fruit trap data were collected biweekly from June to September. The results are summarized in Figure 37. June, July , and the beginning of August are times of fruit scarcity. The end of August and September are times of flowering peaks and new leaf flush.

7. Census of trees with fruit, flowers, and new leaves: Fifty trees over 15 meters in height were censused every two weeks between May and September 1982, and were scored on a scale of one to five according to the amount of fruit, flowers, and/or new leaves they contained; one is barren, five indicates full, and two through four are gradations on the scale. Twenty percent of the trees in the forest were leafless during June, July, and the first half of August. At the end of August, and during September, flush new leaves appeared on these trees. Sixty percent of the trees flowered during August and the early part of September. Eighty-two percent of the trees censused had fruit during the last count in September.

8. Fruit and flower production: Only about five percent of the tree species were dependent on wind for seed dispersal. Nearly every tree is a potential producer of fruit edible by mammals and birds. Low species diversity, particularly in a seasonal climate, can greatly restrict food availability. There were only two tree species that produced ripe fruit during the months of June and July. The density and fruit production of these two species are critical for

Aotus in the Chaco. In contrast to the Peruvian rain forest, trees did not flower during the dry season winter months. Instead, most trees produced flowers at the end of August or the end of September. In other words, one of the primary foods that sustained animals in the dry season of the Peruvian rain forest, nectar, was not available in this area of Paraguay. However, flowers were a major food item in early spring.

9. Crown diameter: Eighty- six percent of the trees in the forest had a crown diameter of five meters or less (Table 24). Twelve percent of the trees had a crown diameter between five and ten meters, only 2% had large crown diameters of 11-20 meters. These large trees were Caesalpinia trees which produced fruit with a tough ectocarp that Aotus could not open. There were no trees with crown diameters over 20 meters; the large-crowned fig and Brosimum trees which fed most of the monkey species in Peru throughout the dry season, are absent from these savannah forests. Many of the small-crowned fruit trees resemble their rain forest counterparts because they ripen only a few fruits at a time across a period of several months.

10. Insect availability: Tape recording results from June and July showed that neither amphibians nor Orthopterans called during the night. However, in late August and throughout September, there was a burst of insect and amphibian calling (Fig. 38). This evidence, coupled with

observations of availability, suggest that there are very few insects available in June and July. Cold temperatures probably render both insects and amphibians inactive. However, in the spring months of August and September, larval forms of Lepidopterans were particularly abundant, feeding on new leaves. Katydids, grasshoppers and moths were also abundant at this time. Time constraints prevented us from doing a more quantitative analysis of insect availability.

11. Discussion of climate and botany in Peru and Paraguay

Similar trends in seasonality are seen in both sites. The period of intense rains in Peru occurs at the same time as the period of lighter rainfall in western Paraguay (*i.e.*, the Chaco region). The dry season, with minimal rainfall, occurs in both Peruvian rain forest and Paraguayan Chaco in June through early August. Fruit is scarce in the dry season in both habitats. A few asynchronous species (*e.g.*, *Ficus sp*. in Peru and *Arecastrum* in Paraguay) provide the only fruit at this time of year. The *Ficus* trees which have fruit in the dry season of Peru, have crown diameters of 20-30 meters, while the *Arecastrum* of the savannah forests have a few clusters of ripe fruit located in a crown which measures less then five meters in diameter.

In both environments, leaf flush occurs at the beginning of the rains in August or September. However, because nearly one quarter of the trees in the lower Chaco are deciduous, there is a greater percentage of new leaves in August and September. Although the Peruvian rain forest dry season is a time when nectar is abundant, there is no corresponding abundance of nectar in Paraguay. Flowers appear in late August and September here and few species produce abundant nectar.

Although rains are more uniformly distributed throughout the year in this region of Paraguay, temperature range is extreme by comparison with the rain forest. Low temperatures and frost may restrict tree flowering in June and July. Insect and amphibian populations also seem inhibited by low temperatures during these months.

In both the dry forest and the rain forest of South America below the equator, the period of resource scarcity occurs in the cold, dry months of June through early August. However, the Peruvian rain forest has at least two major resources that can sustain many species of bird, bat, and nonhuman primate during this lean time of year: the large-crowned fig and *Brosimum* trees, and the abundant nectar sources. In the dry forest of the Chaco, there is no nectar and no figs. The one tree with ripe fruit during these winter months, *Arecastrum*, has only a few clusters of fruit in its small crown. Since insects and new leaves are also in short supply in the Chaco at this time, these months offer considerable food-finding difficulty for an animal like *Aotus*. The data in the following sections illustrate how *Aotus* dealt with these problems.

D. Diet

Introduction

Aotus study group I (an adult pair) spent 30% of its time feeding, 13% traveling, 53% resting, and 4% in other activities such as hooting, grooming, etc. The monkeys spent about three-five hours per 24 hour day actually feeding. During the study period, Aotus spent 16% of feeding minutes on fruit, 40% on leaves, 33% on flowers, and 11% on insects (Fig. 39). Insect-feeding scores include foraging time, while fruit-, leaf-, and flower-feeding scores did not include the time necessary to travel to these resources. It should be noted that the data are from 430 hours of observations during only the winter and spring months.

During the study, the monkeys used 204 individual plants. Of these, 145 were trees (nine of the trees were palms), 20 were bromeliads, 31 were vines, and eight were trailing cacti. Plants eaten represented 13 families and 19 species (Table 25). Food items were ranked according to number of feeding minutes spent on them. Acacia praecox flowers ranked number one, with Randia armata leaves second, Sapium sp. flowers third, Celtis spinosa leaves fourth, Tabebuia ipe flowers fifth, and Arecastrum romanzoffianum palm fruits sixth (Table 25).

There was seasonal variation in availability of resources, and the feeding patterns of the night monkeys correlated with these changes. At times of the year when fruit and flowers were scarce, night monkeys ate leaves. When palm fruits ripened, the night monkeys ate them. When flowers became abundant in late August and September, the monkeys ate flowers. When new leaves became abundant, new leaves replaced mature leaves of *R. armata* and *C. spinosa* as a preferred food. When insects became abundant, the amount of time devoted to foraging for them also increased.

1. Fruit: Fruit trap data indicated that few fruits were available during the winter and spring months in the Chaco. This would account for the low percentage of feeding minutes spent on fruit (16%). In July, 27% of the feeding minutes were spent eating three species of fruit: 1) nuts of the pindo palm (*A. romanzoffianum*), 2) berries of the palm *Copernicia alba*, and 3) the small fruits of *Sebastiana brasiliensis*.

a) Arecastrum nuts: These nuts are found in clusters of 100-200, each tree typically bears 2-4 clusters. The 2.5cm nuts ripen within a two week period on each tree, although some trees have fruit for a 2-3 month period. *Aotus* ate the pindo palm nuts in two stages of development. The monkeys mouthed off the orange, sweet, squash-like fibrous outer flesh, and dropped the seed of ripe nuts. *Aotus* also ate the 'milk seeds' or seed embryos of the immature palm nuts and then discarded the green inedible husk. Pindo palms also occur in taller, moist forests on the east side of the

Paraguay River and are preferred food of *C. apella* in the dry season.

b) *Copernicia berries:* The berries of *C. alba* do not seem to be the preferred food of any animal. These abundant palms, scattered throughout the savannah, are often laden with long strings of berries (over 300 to a string, 4-10 strings per tree, each berry is 2cm long). I never observed animals other than *Aotus* eating the fruit. (Ranch owner, A. Espinoza, in 30 years of careful observation had not observed any animals eating these berries either, and he hypothesized that they might be a water-dispersed species.) The night monkeys did crack open the outer husk with their teeth, and ate the gelatinous, white, bitter material inside. *C. alba* does not occur inside the forest, and night monkeys had to leap three meters out of the forest into the trees which stood in the savannah.

c) *Sebastiana fruit:* *S. brasiliensis* is a six-part, dehiscent fruit measuring 1 cm in diameter enclosed by a hard, nutlike husk. *Aotus* ate the fruit by crunching the husk and eating the seeds inside. The 4-10 meter high trees occur in the forest edges, particularly on the southern and eastern borders. By August, palm nuts are no longer available and fruit feeding dropped to 12%. In September, fruit feeding dropped farther to only 4% of total feeding minutes. At this time, *Aotus* fed on two other species of fruit, *Trichilia catigua* (Meliaceae) and *Rhipsalis schaferi*

(Cactaceae).

d) Trichilia fruit: The dehiscent fruit of T. catigua is encased in a soft husk measuring 1.5 cm, which opens to reveal a bright red, sweet aril when ripe. This fruit occurs on small trees (6-10 m tall) that ripen a few fruits at a time. Because bird populations are high in the area, and other fruit rare, most trees entered by night monkeys had already been emptied of fruit.

e) Rhipsalis berries: The tiny (0.6cm), green-white fruit of the Rhipsalis cactus were eaten whole by Aotus. This green, spaghetti-like, trailing cactus grows abundantly on large canopy trees, and bear fruit in late August and September.

2. Leaves: Leaves are an important item in the diet of Aotus in the Chaco. Forty percent of all feeding minutes were spent eating leaves. There was significant seasonal variation in leaf eating. In June through early August, when insects, fruit, and flowers were scarce, leaves were a major part of the diet, 47% of the total feeding minutes. As flowers and fruit became more abundant, at the end of August through September, leaf-eating dropped to 11% of the total feeding minutes (Fig. 39).

a) Location: The small shrub-trees, R. armata and C. spinosa, were located in stands at the southern and eastern edges of the forest. In July and August, the monkeys traveled to these stands in late afternoon and ate leaves constantly until dark. This location of leaf resources agrees with evidence found at Cocha Cashu and elsewhere by Cates and Orians (1975), Foster (1980), and Coley (1983), *i.e.*, that edges and successional areas provide a year-round source of palatable leaves. The arboreal bromeliad, *T. duratii*, is also most often encountered on the forest edge.

b) Timing of consumption: Although leaves were eaten at all times of the day and night, there was a tendency for major leaf-eating bouts to occur in the late afternoon and at dusk (16:00-18:30 hours). The least likely time for leaf-eating was at dawn. This was contrary to expectations because *Alouatta* and *Callicebus* tend to concentrate on leaf feeding before entering the tree in which they spent the night. It has been suggested that late afternoon leaf-eating allows for nocturnal digestion of the leaves (Milton 1980). But, the ingestion of leaves by *Aotus* in late afternoon, at the *beginning* of the activity cycle, tends to support the argument that leaves are most nutritous in late afternoon. Photosynthesis and carbohydrate production occur at greater rates during daylight hours (*e.g.*, photosynthesis and carbohydrate production at midday is eight times higher than during hours of darkness [Franck and Loomis 1949]).

c) Type: Forty-seven percent of all leaf-eating minutes were spent on young and mature leaves of small trees (*R. armata* and *C. spinosa*), 26% on vine leaves, 16% on flush leaves of trees,, and 11% on bromeliads (Fig. 39). During

June through early August, *Aotus* ate the mature and young leaves of small-crowned (1-3 m in diameter), short (2-10 m tall) trees listed above. Although the monkeys ate the entire *Celtis* leaf, they consumed only the distal two thirds of each *Randia* leaf. Another preferred food item during the dry season was the leaf of an arboreal bromeliad, *T. duratii*. The monkeys tore the leaves from the rosette and munched on the proximal ends. *Aotus* also fed on the leaves of the common vine *Aristolochia esperanzae* (Aristolochiaceae). In September, *Aotus* no longer visited the stands of *Celtis* and *Randia*, and rarely ate a bromeliad. Instead, the monkeys preferred the flush leaves of several deciduous trees. I never observed a night monkey eating mature leaves of a tree over ten meters tall. In fact, eating mature leaves was restricted to *Randia*, *Celtis*, and *Aristolochia*. This may be due to either to chemical composition of the leaves or their fiber content.

3. Flowers and nectar: Flower feeding was an important part of the *Aotus* diet, 33% of all feeding minutes. In July, 21% of the feeding minutes were spent on flower feeding. In August, 21% of feeding was also spent on flowers. In September, however, when flowers became abundant, flower feeding increased to 81% of all feeding minutes (Fig. 39).

Night monkeys did not feed on all flowers available in the forest, but specialized on the flowers of certain species. The families Bignoniaceae and Leguminosae were especially important. *Aotus* also ate the tiny flowers of *Terminalia argentea* (Combretaceae), the tiny, fleshy flowers of *Sapium sp.* (Euphorbiaceae), and the small flowers of the vine *A. esperenza* (Menispermaceae). These flowers, in addition to *Acacia* and the other legume flowers, were eaten whole and abundant pollen was thus ingested also. In the Chaco, there are no plentiful nectar resources except *Tabebouia*. Although hummingbirds relished the nectar of these flower-filled trees, the night monkeys ate the petals rather than the nectar. Petals of *Tabebouia guayacan* in Panama are high in protein (25%) (Milton 1980), and petals of *T. ipe* may also be protein-rich.

4. Insects: Few insects were active in the cold months of June and July. Virtually no insect nor amphibian noise was heard at night. Insect feeding by *Aotus* was minimal, only 4% of all feeding minutes scored for July.

In August, the monkeys began to catch flying insects out of the air, pick ants off branches, and catch spiders and a few large Orthoptera. In fact, insect eating increased to 22% of feeding minutes. Rains and warm temperatures increased insect populations, and tape recordings of their sounds reflected the increase. Also, there seemed to be an outbreak of insects feeding on *Piptadenia rigida* trees. *Aotus*, especially on bright moonlit nights, would carefully survey each branch, moving quickly from branch to branch, searching. When an insect was encountered, it was grabbed with one hand and popped into the mouth. The search was then resumed. When one *P. rigida* tree had been covered, the monkeys traveled to the next and resumed systematic searching.

In September, insect foraging time returned to a low of 4%. Insects did not decrease in number, but the Varo image intensifier broke down, limiting my capacity for nocturnal observation. Insect-eating was probably more frequent by *Aotus* during September than I was able to detect.

5. Summary and Discussion of Aotus diet in Peru and Paraguay

a) Overview of similarities: *Aotus* in rain forests of Peru and *Aotus* in dry forest patches in Paraguay both ate a mix of small fruit, flowers, leaves, and insects.

b) Overview of differences: However, the proportions of each of the above items in the diet varied from habitat to habitat. Fluctuations in proportions of each depended on availability. Food availability is determined by a wide range of factors including extremes in seasonality and competition from other animals.

c) Similarities in leaf-eating: Both populations of *Aotus* (and *C. moloch* in Peru) ate leaves.

d) Differences in leaf-eating: In July and August, *Aotus* in the subtropical dry forests of the Chaco consumed more leaves than *Aotus* in the tropical rain forest of Peru during the same months. In fact, the leaf portion of the

Aotus diet in the Chaco was as high, or higher, than the proportion of leaf consumption by Callicebus in the rain forest during the same months. Obtaining protein from leaves seems to be least preferred by Callicebus and Aotus. However, when insects are not available (as is the case both night and day in the cold winter months of July and early August in the Chaco), leaves are eaten in large quantities. Unlike C. moloch in Peru, who has never observed to eat mature leaves from trees, Aotus in the Chaco did eat mature leaves from a few a selected species of trees. This difference could be attributed to differences in availability of immature leaves. When leaves flushed in the Chaocoan spring, Aotus preferred the young flush and was not observed to eat mature leaves at this time.

e) Similarities in flower-eating: Both populations of Aotus (and C. moloch in Peru) ate flowers, especially those from the families Bignoniaceae and Leguminosae. A nutritional analysis of Tabebuia guayacan flowers by Milton (1980) found them to contain 25% crude protein, 14% nonstructural carbohydrates, and 3.7% crude fat. It is also possible that legume flowers are high in protein; both leaves and fruit are high in nitrogen (Windsor 1978).

f) Differences in flower- and nectar-feeding: Aotus eats more flowers and less nectar in the Chaco forests than in the continuous rain forests. The vines and trees that produce copious amounts of nectar are absent from the

Chaco. However, synchronous flowering of common species offers an abundant food resource in the months of late August and early September, before fruiting begins. In the rain forest, flowering is less synchronous, perhaps due in part to greater species diversity.

g) Similarities in insect-feeding: In both habitats, Aotus searches foliage and branches for insects, locating them by sound or movement, and snatching them quickly with one or both hands. The same type of insects are eaten in both habitats, including caterpillar adult and pupae of Orthopterans, and ants.

h) Differences in insect-feeding: In Paraguay, insect feeding is minimal in July and part of August, while in Peru, insect foraging continues through the dry season. However, proportions of the diet comprised by insects in different seasons varies between habitats. Severe cold inhibits insect activity in the Chaco during June and July, and therefore, availability limits the amount of insect foraging done by Aotus at this time. However, in August after the first rains, insect foraging increases to 22% of all feeding minutes. This figure is higher than any recorded for C. moloch in Peru at any time of the year. It should be noted that catch rate of Aotus in Piptadenia trees in Paraguay was 30 insects per hour, six times the best rate of C. moloch.

i) Similarities in fruit-feeding: Small fruit with thin ectocarps were eaten in both habitats. Constraints on fruit size were imposed by the morphology of a small monkey.

j) Differences in fruit-feeding : Figs were not eaten in the Chaco of Paraguay and yet, comprised a quarter of the diet in Peru. Fig trees are rare in the dry forests and therefore, availability limits fig-feeding by *Aotus* in the Chaco. Palm fruits were eaten by *Aotus* in the Chaco more than in the rain forest. The only palm fruits eaten in MNP were *Iriartea ventricosa*, a small, 1cm long fruit with an edible outer meat. However, this common palm fruit was also eaten by other primates, birds, and a few available to either *Callicebus* or *Aotus* because of intense competition for them from other larger consumers. Most other palm species were unavailable to *Callicebus* and *Aotus* in Peru because of the difficulties of opening the tightly-packed fruit clusters. *C. apella* specializes in these species during the dry season (Clarke personal communication).

Aotus in the dry Chaco forest, ate a palm species similar to *Iriartea*, *Arecastrum romazoffianim*. Like its rain forest counterpart, *Arecastrum* palms were common in the forest. However, competition for these palms was minimal and ripe fruit was available for *Aotus*. It is interesting that in the western forests of Paraguay, *C. apella* subsists on *Arecastrum* palm fruit in July and August (Clarke, personal communication; Wright personal observation). Neither *Aotus* nor *Callicebus* are present in these forests. In a week-long study in these forests, I observed *Cebus* monkeys, with their large groups, depleting palms of fruit by traplining them. There is circumstantial evidence that enough palm fruit to sustain a night or titi monkey group would not be available in the western forests due to competition from *Cebus* monkeys and frugivorous birds.

During the dry season in Peru, *Aotus* did feed in fruit, primarily fig and *Brosimum* trees. In the Chaco large-crowned fruit trees are nonexistent. Few fruits are available from June through September, and fruit feeding by *Aotus* is according low during these months in the Chaco. Variation in proportion of the diet comprised of fruit between the two habitats is due to a combination of severe seasonality and reduced species diversity.

Aotus fed in trees with crown diameters of less then ten meters in Paraguay, and in trees with crown diameters exceeding ten meters in Peru. The crown diameters of trees used in Paraguay are restricted by availability because 99% of the trees are small-crowned. *Aotus* in Peru can feed in trees with a wide variety of crown diameter due to lack of competition for fruit during the night.

E. Competitors for Food

1. Primates: *Alouatta caraya*, the black howler monkey, is the only sympatric primate (Table 26). A group of seven black howler monkeys, including one large adult male, an adult female, and an infant male age 4-6 months, a smaller adult male, two subadult males, and a one year-old juvenile female, lived in the forest with *Aotus* Group I. Observations were made on the howler monkeys on censuses conducted four times per week in the early morning, at noon, and again at 16:00 hours. These observations indicate that the diet of the howler monkeys may be less diverse than the diet of *Aotus*. In June through early August, *Alouatta* remained high in the tallest trees, feeding on the fruit of *Caesalpinia paraguayensis*, the thin seeds inside old pods of *Piptadenia rigida*, the leaves of *P. rigida*, *Tabebouia ipe* and several unidentified canopy trees. In contrast, *Aotus* fed on leaves and fruits found on small shrubs in the forest at this time of year. However, in August and September both *Aotus* and *Callicebus* fed on flowers and fruits, but their diet was temporally partitioned by the two species with *Aotus* feeding in the night and *Alouatta* in the day. There were several instances of *Aotus* and *Alouatta* feeding in the same small trees (*Acacia* and *Sapium*) during the day at different times. One day at 15:50 hours, the male *Aotus* fed in a *Sapium* tree at the same time as a juvenile male *Alouatta* with no

aggressive exchange between them. Because of the abundance of flowers at that time of year, perhaps competition was not a problem for either species. Neither species was ever seen chasing or displacing the other. During June through early August, when resources were scarce, there was little overlap in diet between Alouatta and Aotus. Aotus did not feed on the above foods listed for Alouatta. In addition, Alouatta did not eat the leaves found on the low bushes of Randia and Celtis which Aotus ate in June and July.

2. Marsupials: Although both Didelphis albiventris and Philander opossum are omnivores (Table 26), fruit and flower consumption is not high in winter and spring months. My observations of the foraging of both species (n=12 nights, 36 contact hours) revealed that their winter and spring diet consisted of 75% vertebrate and invertebrate prey (e.g., snails, insects, frogs, carrion). Because population densities of the opossums are low, less than one per hectare, and these subadult opossums are small animals (150-850 grams body weight) competition for food between opossums and Aotus in this forest was not great. Opossums were never observed to displace Aotus from any tree.

3. Birds: Birds are competitors for both fruit and flowers. Night monkeys often entered fruit trees already emptied by frugivorous birds. Trichilia catigua is a small tree which ripens a few fruits each day over a two-month period. Birds ate these fruits early in the day, and trees

were often barren when *Aotus* entered them in the late morning (after 10:00 hours). Chachalacas (*Ortalis canicollis*) fed on *C. paraguayensis* fruit, *Tabebouia ipe* flowers, and *Celtis* leaves. Several flocks of these large birds inhabited the study site. Monkeys chased them from fruit trees. Because of the abundance of flowers in spring, competition for flowers from birds was probably negligible.

4. Bats: Phyllostomatid bats are rare in the Chaco (Myers 1977; 1982; Myers and Wetzel 1983). Bat species that are frugivorous and nectivorous all but disappear in the crossing of the Paraguay River. Perhaps they can not survive the long winter when no fruit or nectar is available. The few bat species that do exist in the Chaco eat insects. My nightly observation confirmed that bat populations were very sparse in the area.

F. Predators

1. Feeding and activity of *Bubo virgineanus*.

A pair of great horned owls (*Bubo virgineanus*) maintained a nest at the southern corner of the forest. Mating occurred in June, two chicks were born at the end of July, and reached fledgling size by the second week of September. Roost sites were noted daily for the owls and their pellets collected and examined each morning.

2. Weight of Bubo: The weight of male great horned owls in North America is approximately 1650 grams, while the female in the same range weighs an average of 1876 grams (Burton 1978). Since the largest owl in the rain forest of Peru weighs 800 grams, the difference in size and number of prey items taken is probably considerable.

3. Prey items of Bubo at La Golondrina study site: Examination of the data in Table 27 shows that great horned owls are eclectic feeders in the savannah of Paraguay. Most of their prey items were captured from a swampy pond area 50 meters from their nest. However, 40% of their prey were captured in the dry forest. Because owls are capable of traveling long distances, it is possible that prey items could have been captured in an adjacent forest patch also. It should be noted here that there is an increase in size and number of prey items as the two chicks increased in size. Many of the mammalian prey items had been trapped and collared early in the study. Weights of items given in Table

27 are from known weights of previously trapped animals. Bones of primates were not found in the regurgitated owl pellets (boluses). It should be noted that no offspring were seen in any group of _Aotus_ in this or adjacent forests. This may be attributed to: 1) chance, 2) infant mortality due to scarcity of food (malnutrition) coupled with temperature extremes, and 3) juvenile _Aotus_ may have been preyed upon previously by great horned owls.

4. Discussion of nocturnal raptors: Horned owls in North America are known to capture prey on the ground, rarely taking arboreal animals. Data from owl pellets gathered during my study do not present conflicting information. Opossums and small mice are often seen on the ground, as are marsh rats and rattle snakes, and therefore, are assumed to constitute the bulk of their diet in the study site. Remains in the pellets also include wading birds. Unlike the harpy and crested eagles, the large horned owl does not specialize in arboreal prey.

5. Discussion of diurnal raptors: Hawks and eagles are the major predators on South American monkeys, especially on the smaller species. Small, diurnal monkeys can avoid predation by employing two different strategies. Detection of predators can be increased by banding together into large groups for 'more-eyes-and-ears', for cooperative defense, to confuse predators, and/or to increase the probability of predator satiation (Hamilton 1971; Pulliam 1973; Curio 1976;

Bertram 1978; Pulliam *et al.* 1980). *Saimiri* and *Miopithecus* (in Africa) form large groups and use this method of predator protection. Alternatively, crypsis may be used to avoid predation. Small, quiet groups, dark coloration, and keeping in low shadows can result in predators overlooking hidden prey. *Callicebus* may avoid predators with this approach. They spend 50% of their time lower than ten meters above ground and 50% of their time is spent resting.

Aotus avoids these raptors by sleeping in dense vegetation tangles and by being active when raptors are normally inactive, *i.e.*, by exiting their sleeping sites after sunset, and by entering their sleeping trees before sunrise. Group size is important only in reference to the number of individuals that may be hidden in a given tangle. Large groups of sleeping monkeys in a single huddle may be detected by predators.

Male parental care, in the form of infant carrying, may provide good protection for small, infant monkeys. A female, already stressed by the energetic requirements of lactation, may not be able to flee carrying an infant on her back, whereas a male can escape effectively (Wright 1984). Male parental care may be partially an adaptation for predator protection of infants.

G. Sleeping trees and use patterns:

1. Sleeping trees

Morphology: The 47 sleeping trees used by the two pair and two solitary *Aotus* in Paraguay varied in their morphology. Out of the 42 used by Study Group I, the mean height was 13 meters (range =5-22 meters). Six of the trees had open crowns (one palm, one leafless unidentified tree, flowering *Acacia*). Twenty-eight sleeping trees were shaded, but open. Five were located in vine tangles; the monkeys were visible but slightly obscured. Three trees had large hollow trunks (diameter at breast height=25 cm) (Fig. 40). The solitary monkeys preferred less open trees, and three of five trees they used were in vine tangles.

Number: The Study Group I used 42 different sleeping trees in the five months of observations. Twelve of these were slept in more than once. The *Aotus* pair slept in two to four trees each day, feeding and traveling about an hour between each sleeping site. The pair slept 3-17 meters above the ground (mean=8m above the forest floor), in open branches (n=34), vine tangles (n=5), or hollow trees (n=3). Seven sites used by this pair were slept in four to six times; one on an open branch the sun, three on open, shaded branches, one in a vine tangle partially obscured from sight, and one in a hollow tree trunk (Fig. 40)

Location: The sleeping trees were located in all parts of the forest, but were concentrated in the northern section of the study site (Fig. 41). It may be more than a coincidence that Bubo sleeping trees are in the southern sector of the study site. Is the location of Aotus sleeping trees correlated with distribution of food trees? There is no difference in distribution of food trees between southern and northern half of the forest (Chi square = 1.27; $p < 0.05$; df=1). Therefore, sleeping trees were not distributed in relation to the 206 food resources (Figs. 41 and 42).

Temperature and tree choice: Selection of sleeping tree type depended upon ambient temperatures. During the cold winter days of June and July, many of the sleeping trees were located in sunny spots. On the coldest winter mornings, the pair would switch to a sunny branch as the sun rose over the trees. Later in the afternoon, the monkeys would change to a more sheltered sleeping tree. In the extreme heat of late August and September, a different pattern emerged. As the sun rose in the sky, the monkeys changed to a more shaded sleeping tree, and during the afternoon the monkeys changed to a hollow cavity in a tree. Most of the monkey's body was inside the cool tree cavity, with head and arms extended from the hole.

2 Timing of sleeping tree entrance: The Aotus pair slept in at least two sleeping trees each day (mean = 2.4; range 2-4). The timing of sleeping tree change was unpredictable. Although 40% of the entrances occurred early in the morning (from 05:00 to 08:00 hours), sleeping trees

changes occurred any where from 08:00 until 16:00 hours (Fig. 43). The monkeys traveled and fed on fruit, flowers, or leaves between sleeping sites. Distances between sleeping trees used in one day ranged form 5 to 200 meters. There was no pattern in either the number of sleeping trees used per day or in the time that the change occurred from one site to another. Perhaps the very unpredictable nature of the change is important. Nocturnal predators would have difficulty predicting the whereabouts of the monkeys at dusk, assuming the predators knew the monkeys' location at dawn. This explanation is strengthened by the fact that sleeping trees near the great horned owls' nest were used only in the middle of the day. In other words, they were used between the hours of 10:00 and 14:00, the hours when the owls are least active. However, protection against predator pressure may be only a partial explanation for: 1) use of multiple sleeping sites each day; 2) random patterns in time of changing sleeping sites; or 3) the random pattern in distance traveled between each sleeping tree.

H. Ranging Patterns:

1. Location of territories: Aotus groups in the Chaco are found in gallery forests along rivers and in forest patches (habitat islands) in the savannah grasslands. Aotus groups have rarely been seen on the ground, although Rathbun and Gache (1977) describe a family group traveling from one forest patch to a neighboring patch through a 200 meter gap of grassland.

2. Size of territories: The island habitat forests containing Aotus were 5-10 hectares. Groups of Aotus, or single animals, were never seen in forests smaller than 4 hectares (n=5 small forests censused), nor were night monkeys ever heard to hoot from these small forests. The size of the study group's territory was 5 hectares.

3. Daily path length (24 hours inclusive): Mean path length for each 24 hour period was 550 (n=20; range = 400-730m) for the months of July and August (1982). Although Group I was followed in June and September (1982), complete path lengths were not obtained in these months. The general impression was that path length decreased in September when food became abundant.

4. Influence of high moonlight levels: Aotus tended to be more active when the moon was bright, and sleep when the moon was new or during the section of night when the moon was not bright (Table 28).

5. Use of space: The Chaco group of Aotus did not cover its entire territory in one 24 hour period. During most 24 hour periods half the forest was covered, and the other half monitored the next 24 hour period. Although certain routes were frequently used, this group seemed less rigid about following these routes than their rain forest counterparts. Because habitual sleeping trees were not used, circular routes were not used and the monkeys would sleep in any part of the forest.

6. Time of day: Aotus was active and traveled in daylight, as well as during the night (Fig. 44). They fed and traveled more during the night than during the day, regardless of season. The night monkeys could be active at all hours of the day and were not limited by bright sunlight. Traveling and feeding on fruit, flowers, leaves, and insects were observed even at noon on a bright, sunny day. However, the average time spent traveling was 52 minutes during the day, compared to 2-3 hours each night, depending on the amount of moonlight. The mean distance ranged during the day was 199 meters (n=10; range = 100-400m; S.D.=80.75), while the mean distance during the night was 309.5m (n=10; range = 200-500m; S.D. =157.4) (Table 29).

7. Influence of temperature and climate: Cold weather did not inhibit ranging (Table 45). The longest nightly path length of 500 meters was recorded on August 2 (1982)

when the low was 11°C. The shortest nightly path length was 200 meters, recorded on July 25 and 25 (1982) when the low was 5 °C and 10 °C respectively. In fact, when temperatures were high, ranging both day and night was less (250-400m). However, temperatures did influence timing of daily activity. When night time temperatures were low (5°C-10°C) in June through early August, *Aotus* fed late in the afternoon or at dusk. When daytime temperatures were high (35°C-42°C), *Aotus* did more feeding and traveling early in the morning before 10:00 hours. The night monkeys in Paraguay did not range far if it was raining heavily.

8. Proximity to resources: The night monkeys monitored about half of their territory during each night in June through early August (1982). During this cold season, resources were scarce and widely scattered throughout the forest. However, flowers became an abundant resource in late August and September, and the focal group ranged less widely during this time of year. About one quarter of the forest (1 1/2 hectares) was covered each 24 hour period.

9. Discussion and Summary of Ranging in Paraguay

In the rain forest of Peru, *Aotus* ranged farther during bright moonlight than during the dark phase of the moon. Was this same trend also true of the *Aotus* in Paraguay? Although the sample size of nights in Paraguay was less than in the rain forest, and restricted to a single season (cold months of July and August), the available data show that ranging was curtailed by low light levels (Fig. 46). Comparing two equally cold nights (to eliminate temperature effects) with contrasting moonlight levels, shows that traveling in the dark of the new moon was limited to three widely spaced intervals of 15 minutes each (19:00, 23:00, and 04:00 hours), while the traveling under the full moon occured at all hours of the night except 02:00 and after 04:00 when the moon had set and dawn was an hour away. It appears that low light levels do affect Aotus ranging whether the groups are in the rain forest or in subtropical dry forests.

It should be noted that there are some differences in amounts of light available in the two types of forests. The short trees and openness of the subtropical forests allow light to reach more areas easily. Sunrise is perceived sooner and the light from the setting sun lingers longer. The same is true of moonlight. This fact, coupled with the tendency of Aotus to feed at some interval during the day, suggests that there would be less pressure for Aotus to feed at less optimal light levels (darkness). However, this does not take into account predation pressure. Theoretically, if Aotus feared horned owls, the night monkeys would tend to travel and feed less at high light levels when the owls hunt (Effects of horned owls on ranging). My data show no evidence of this.

10. Summary:

a) Territories in the subtropical dry forest are small, 5-10 ha. (Table 4)

2. *Aotus* remains arboreal in the Chaco and ranges within the confines of isolated forests greater than 4 hectares in size, or in strips of gallery forests along rivers. Groups or single individuals may cross open grassland on rare occasions; however, this was never observed during my study. Food is not obtained from the grassland areas.

b) Path lengths are short, 200-750 m per 24 hour period. (Table 28)

c) The night monkeys travel during the day as well as during the night, regardless of high or low ambient temperatures (Figs. 44 and 45). In most samples, nighttime path lengths were longer than daytime path lengths.

d) There is a tendency for the monkeys to range farther when resources are scarce and scattered than when resources are abundant and clumped.

e) The monkeys travel more during bright moonlight than when the moon is new and light levels are very low. (Fig. 46)

f) There is a difference in timing of ranging during temperature extremes. In cold weather, activity began in the afternoon (16:00 hours) whereas when daytime temperatures are high, there is more activity in early morning hours (before 10:00 hours) and little activity in the late afternoon.

I. Intergroup Interactions, Calling, and Fighting

1. Fighting: No fighting was observed between groups at La Golondrina. Pairs were located in forests separated by 500 meters or more of grassland and had no opportunity to encounter one another during nightly ranging. Solitary individuals in the same forest avoided each other and the mated pair.

2. Intergroup calling: During periods when the moon was bright, overhead, long distance hooting was heard both from the study group's forest and two adjacent forests. The focal study group did not hoot, but two solitary night monkeys who lived in the same forest hooted. Neither Solitary A nor Solitary B hooted on the same night, but each would hoot during the same month. Neither solitary individual answered the calls of others, yet callers from other forests would answer the same night. Both solitaries moved while hooting. Calling sessions lasted from 1-3 hours each, but bouts were often interspersed with 15 minutes periods of silence (Table 22).

3. Similarities between Paraguayan and Peruvian long distance calling: In both sites, calls were structurally similar with frequencies of about 200 Hz. In both sites, calling sessions lasted from 1-3 hours, and the individuals called while solitary and moved from 100-350 meters while calling. In both sites, hoots were given when the moon was bright and overhead. Two types of callers were heard in

Paraguay and Peru - gruff and pure tone callers. (In Paraguay, the gruff caller was identified as male.)

4. Differences between long distance calling in Peruvian and Paraguayan Aotus groups: In Peru, the mean number of notes in each hoot was 3, while in Paraguay the mean number of notes was 2. Sample size of individuals heard in Paraguay was small (n=4), while more individuals were heard in Peru (n=12), and it is possible that the difference in number of notes per hoot was only a consequence of sample size.

5. Behavior of solitary callers: In this short forest, the individual calling could be seen in the bright moonlight. Solitary Caller A was observed insect foraging between calls. At dawn, he was identified as a lone male. He slept 200 meters from the focal study pair. On a different date, Solitary Caller B was followed to her sleeping tree. At dawn, she was identified as a lone female. Both lone adults were in the forest at the same time, yet did not fight nor form a pair. Neither called on the same night as the other. Both callers were not habituated to humans and were difficult to follow on nights when they did not call. I have no idea how long these two solitary adults had lived in this forest. Each carefully remained apart from the other, and to my knowledge, never met.

6. Reaction of focal study group to callers: When calling commenced, the pair stopped eating, became very active (jumping from branch to branch), peered intently toward the direction of the call, but did not answer. As the call continued, the pair headed very slowly in the direction of the call, some 450 meters distant. In four hours, the group was 200 meters from the caller, and he had stopped calling after three hours. it is unknown if the pair and the Solitary Caller A met that night.

CHAPTER V

Summary and Conclusions

A Introduction

This comprehensive study of *Aotus trivirgatus nigriceps* in the Peruvian rain forest with *Callicebus moloch brunneus* in the same forest, and to *Aotus trivirgatus azarae* in the Paraguayan subtropical dry forest provides insights into some of the parameters of niche separation between closely-related nocturnal and diurnal monkeys. Ecological variables may influence the costs and benefits of nocturnality and may result in behavioral changes. In this concluding discussion I will first compare the diet, territoriality, sleeping behavior,, fighting and calling, and ranging behavior of *Aotus* in both sites. These results will then be discussed in relation to the same behaviors in *Callicebus*.

In the concluding synthesis, possible selection pressures for nocturnality in monkeys will be discussed, including temporal partitioning of resources, competition with the diurnal frugivore/nectivore community, and avoidance of diurnal predators.

B. Diet

1. Similarities of Aotus diet in the two study sites:

a) In both habitats *Aotus* ate a combination of fruit, flowers, leaves, and insects.

b) At both sites insect eating increased as insect populations increased. Conversely, leaf eating decreased when new leaves flushed. Because insects are plentiful when new leaves appear after the beginning of the rains, this negative correlation suggests that insects are a preferred source of protein. Leaf protein requires more digestion time and is bulkier than insect protein, and has potentially less complete amino acid composition.

c) In the dry forest, Aotus ate 19 species from 13 plant families during the months of June through September. In the rain forest during the same months, Aotus ate 20 species from 11 plant families. In both sites, a variety of fruit, flowers, and nectar sources were eaten, from 4-10 species per day.

2. Differences between Aotus in the rain forest and those in the dry forest:

a) Size of fruit tree crowns: In the rain forest, Aotus fed in trees with crown diameters of 5-40 meters. In the dry forest, Aotus fed on leaves, flowers, and fruit in small trees with crown diameters of less than 10 meters.

b) Proportion of leaves in the diet: During the dry season in the rain forest, Aotus derived the bulk of its diet from figs and nectar. In the dry forest, where these items are not available in the dry season, leaves constituted more than 50% of the Aotus diet.

c) Dietary diversity: Although there is no significant difference in number of species of plant families used over the four month dry season in both habitats, the proportions of time spent on favored fruit differs. Fifty percent of feeding time in the dry forest included five different plant species. In contrast, one or two species constituted at least 50% of the diet each month for the rain forest night monkeys.

3. Adaptive Significance of Dietary Differences

The diet of a species and the process of harvesting it efficiently are of utmost importance in the definition of a species' niche. Differences in the diet of night monkeys in Peru and Paraguay could be attributed to 1) differences in availability of food, and/or 2) differences in competition for food.

a) Differences in food availability: In the Chaco of Paraguay Aotus feeds in small-crowned trees because those trees were the only ones producing palatable fruit. In both Paraguay and Peru, the night monkeys ate fruit in all sizes of tree crowns. This was not true with Callicebus. The titis prefer small-crowned trees (Tables 12, 13). Two covariant explanations for the consistent use of small-crowned trees by titis are avoidance of competition from larger monkey species and exposure in large tree crowns may make them vulnerable to raptor attack.

The Chaco has a severe winter when insects are dormant, fruit is rare, nectar is unavailable, and there are no new leaves being produced. In order for the monkeys to survive in this harsh climate, they eat mature leaves from shrubs and small trees. At this time, *Aotus* spends 50% of its fruit feeding minutes on five or six species, in contrast to dependence on only one or two in the rain forest habitat. The difference may be attributed to the small amount of fruit available for each species during the dry season in the Chaco. There was a trend in the spring months for less diversity in diet, with larger portions of time devoted to one or two species. Food scarcity does not reach severe status in the rain forest of Peru. Although most fruit and new tree leaves are rare in the dry season, nectar from certain species abounds, some large-crowned fig and *Brosimum* trees have ripe fruit, and insects are present, although in decreased number when compared to the rest of the year. At night, *Aotus* feeds primarily on figs, nectar, and insects throughout the dry season. However, these foods are not eaten by *Callicebus*. During the dry season in Peru, the two species have almost mutually exclusive diets; *Callicebus* spends 40% of its feeding minutes on leaves, few on fruit, and none on nectar. The diet of *Callicebus* approximates that of *Aotus* in the Chaco during the leanest time of the year. Fruit and nectar may be present in the dry season at Cocha Cashu but direct interference competition from other species make them unavailable to the titi monkeys.

2) *Differences in competition for food:* In both sites,

Aotus rarely is displaced from fruit trees. Kinkajous (Potos flavus) may occasionally be aggressive to night monkeys, but the monkeys move to a different part of the tree rather than leave it. In Paraguay, Alouatta and Aotus partition resources in the winter and share the abundant resources of other seasons. This is not the case with Callicebus, however. During all months of the year, titis are displaced from fruit trees by other diurnal monkeys; chasing results in their being excluded an entire day at some times of year. Interference competition accounts for low fruit consumption in June through August. Large fig trees were fruiting, but large monkeys monopolized them.

C. Territoriality, territory size, and group size of Aotus in two habitats

1. Similarities:

a) Aotus lived in family groups in both habitats.

b) Family groups maintained exclusive territories, excluding all other conspecific groups (there was some overlap in Peru at border trees).

c) Solitary adult Aotus used parts of a family's territory without joining the group as it fed and/or slept. It is unknown whether or not these solitary animals were older offspring of the resident mated pair that have remained in their natal territory; the length of time solitary animals remain in another group's territory is also unknown. In Peru, a solitary animal ranged in Aotus group

II's territory for over six months. In Paraguay, an adult solitary male remained in the study site forest for at least four months; a solitary female remained for two months. All solitary monkeys avoided contact with resident groups and apparently, one another.

2. Differences:

a) Group size in Peru ranged from two-six, with a mean of 4.1 animals per group. In Paraguay, two groups at La Golondrina consisted of only pairs; Rathbun (1980) censused 25 groups in Argentina and reports a mean group size of 2. There are fewer infants and subadults in these Chaco groups.

b) Territory size in Peru averaged 9.2 hectares. In Paraguay territory size averaged 4.9 hectares.

c) Population density of Aotus in Peru was $40/km^2$. In the Chaco population density was calculated at only $18/km^2$ (Rathbun 1980) - nearly half the density of rain forest populations.

3. Discussion: Differences in these parameters might be explained by the possible selective forces: 1) availability of resources; 2) competition for food, and; 3) predation pressure.

Paraguay is a seasonally harsh climate; overall productivity is not as high as the rain forest. Low population density of Aotus in the dry forest may be a direct reflection of lowered habitat productivity. However, the population density of Callicebus in the rain forest is also half that of Aotus in the same habitat. The same resources are potentially available to both species. Therefore, it is unclear whether or not gross productivity of a given forest is a major determinant of monkey population density. Other factors, such as numbers of competitors, may also be major limiting parameters of monkey populations (Table 29).

The data suggest that group size is smaller in the Chaco because fewer offspring survive. Perhaps resource scarcity and very low ambient temperatures caused by the severe winters are strong selective pressures; few offspring may survive infancy. Further, predation pressure is more intense in the Chaco; horned owls may take infants and subadults. Because none of the groups censused had offspring before the onset of winter, the latter explanation is plausible.

D. Sleeping behavior of Aotus in both study sites

1. Similarities: The sleeping behavior of Aotus at the two study sites did not exhibit any similarities.

2. Differences: 1) Aotus in Peru used well-protected vine tangles to sleep in, while night monkeys in Paraguay slept on open branches, in loose vine tangles, and in hollow trees. 2) In the rain forest, certain sleeping trees were used habitually for several consecutive years. In the Chaco, choice of sleeping tree appeared to be random. 3) Aotus in the rain forest punctually exited sleeping trees

within ten minutes of sunset and entered within ten minutes of nightfall; no seasonal variation was observed. No predictable pattern for entering and leaving their sleeping sites was detected in the Paraguayan night monkeys.

3. Adaptive significance of sleeping tree use: Why would the sleeping habits of *Aotus* in two habitats be so different? Possible explanations include: 1) difference in the morphology of available sleeping sites; 2) climatic differences; 3) differences in predation pressure; 4) differences in competition for sleeping sites; or 5) differences in competition for resources. To understand some of the selection pressures that might enforce sleeping patterns in *Aotus*, I will review the sleeping habits of *Callicebus*. *Callicebus moloch* in Cocha Cashu used over 40 sleeping trees in a 15-month period. Most were protected from rain, but the monkeys were visible from the ground. In contrast, *Aotus* in Cocha Cashu used only five sleeping trees during the same time period and each was located in a dense tangle of vines which partially hid the night monkeys from view.

4. Differences in morphology of sleeping sites: At first, I assumed that the night monkeys used these few protected sites because they preferred to sleep in darkness, and few vine-tangled trees were available. However, two sets of data contradict this possibility. First, I censused the territory for trees similar to those chosen as sleeping

sites. I found 31 such trees. Second, the data from Paraguay confirm that Aotus can sleep quite well in bright daylight. The pair at La Golondrina used 42 sleeping trees in a four month period, 34 of which were on open branches, 5 were in vine tangles which did not hide the monkeys from view, and three were inside hollow trees. Differences in vegetation between the two sites is not an adequate explanation for choice of sleeping site because both habitats offer similar sites with varying degrees of protection.

5. Effect of climate on sleeping sites: Temperatures are more extreme in the Chaco than in the tropical rain forest of Cocha Cashu. The dry forest itself offers less protection from the elements. Can the differences between Aotus sleeping sites in the rain forest and the Chaco be attributed to adaptations to climatic extremes? The data indicate that to a small extent, climate does influence sleeping tree choice in the Chaco. In cold weather, i.e., 5-15°C, the night monkeys select open branches to sleep on which catch the first warming rays of the sun. During hot afternoons when temperatures rise to over 40°C, the monkeys retreat to the cool hollows that occur in legume tree trunks. However, these climatic extremes do not account for all the differences observed. Even on the hottest day at Cocha Cashu (32°C), Aotus did not change its sleeping tree choice to favor a hollow trunk. When

nighttime temperatures reached a low of 11°C, Cocha Cashu night monkeys did not choose an exposed sleeping site that received the first sun's rays. Contrasts in climate between the two sites do not explain adequately behavioral differences in sleeping site choice.

6. Competition for sleeping sites: In the rain forest, it is possible that Aotus could sleep through the day in any of the nighttime Callicebus sleeping sites; yet, the two species never chose the same tree. If Aotus preferred to sleep in a protected, dark area in the Chaco, these areas were available to them. Competition for space in hollow trees appeared to be minimal because only one animal, Otus, the tropical screech owl, was discovered sleeping in tree trunk hollows when we conducted a systematic search of these sites. The tropical screech owl is not a potential predator of Aotus.

7. Effect ofpredation pressure: Can differences in predation pressure between the two forest types account for the difference in morphology and number of sleeping trees used by Aotus in each study site? In the rain forest, birds that prey on monkeys are diurnal. In Paraguay, the predatory birds are nocturnal; diurnal raptors are rare.

a) By using protected sleeping sites in the rain forest, Aotus would be hidden from the keen eyesight of raptorial birds. Callicebus, and other diurnal monkeys, are not subject to being hunted as they sleep, and can therefore choose a less protected sleeping site. Likewise, *Aotus* in the Chaco chooses a less protected site for a daytime roost because there are no avian predators active in the daytime. These data suggest that protection from predators strongly influences sleeping site choice.

b) Additional supportive evidence for the above hypothesis lies in the negative correlation between location of *Aotus* sleeping trees in the Chaco and the location of the sleeping/nesting sites of the great horned owl in the same habitat. Except for trees used for brief noontime rests, *Aotus* chose sites far from those of the owls.

c) Is the use of large number of sleeping sites a result of predation pressure? In the rain forest, *Aotus* groups are easy to find, once the location of their sleeping tree is known. Each dawn and dusk they can be seen entering and leaving the same tree. Habitual use of a sleeping site has specific advantages in addition to the distinct disadvantage of the possibility of easy location by predators. *Callicebus* groups are not easy to find in the morning unless they begin calling. The random use of sleeping sites located throughout the territory discourages predators from learning where the monkeys are and effectively prohibits them from attacking sleeping monkeys in the first light of day. In fact, if a predator discovered a sleeping location one morning, it is almost certain that the diurnal monkeys will not sleep there again the following night. *Aotus* in the rain forest avoids diurnal predators by regulating its activity peak to correspond to the time when predators are no longer hunting, rather than by randomizing sleeping site choice.

In the Chaco, the major predator is nocturnal, not diurnal. Exiting a sleeping tree after dark will not discourage the horned owl. The strategy to thwart nocturnal raptors is exiting the sleeping tree prior to night fall, before the owl begins hunting. An active, alert monkey is a difficult prey item to catch. Entering a sleeping tree after dawn, choosing various sites, using sites in an apparently random manner, and using more than one site per day, are all effective ways to discourage would-be predators. The owl may have some general knowledge of where the monkey group was at dawn. However, because *Aotus* travel hundreds of meters each day, the monkeys could be in an entirely different section of the forest by the time the owls begin hunting at dusk.

8. Timing of sleeping tree entrances and exits: *Aotus* in the rain forest promptly entered and exited its sleeping tree during twilight hours. The precise correlation with light levels did not vary seasonally. *Callicebus* at Cocha Cashu was much less exacting about the timing of entering and leaving sleeping trees, and there was considerable seasonal variation in this behavior. *Aotus* in the Chaco resembled *Callicebus* in the unpredictable nature of entrance and exit timing. The Paraguayan night monkeys also used from 2-4 sleeping sites during the day; timing of sleeping site change during the day was also apparently random. What selective pressure can account for these dramatic differences in behavior?

1) There is no evidence that differences in the morphology of sleeping trees would make more than a few minutes difference in timing of exits.

2) Climate is not a major factor because Aotus in the rain forest uses the same sites habitually, without regard for seasonal or weather changes. In the same site, Callicebus does not exhibit similar patterned behavior. The Aotus in the Chaco also fail to show predictable patterns of leaving and entering sleeping sites.

3) Differences in competition for resources may be a factor in the timing. There are fewer competitors for fruit during the night than during the day. It would not be to Aotus' advantage to reach fruit trees early; in fact, it may be a disadvantage because diurnal monkeys may chase them away then. However, when large-crowned fruit trees bear ripe fruit, it would be an advantage for Callicebus to exit the sleeping tree early enough to arrive at the feeding site before Saimiri, Cebus, and Ateles. Indeed, at times of year when fruit is more abundant, Callicebus exits early. When no fruit is ripe in the territory, Callicebus remains in the sleeping tree until late in the morning.

4) There is some indication that *Aotus* in Peru uses the high light levels of twilight to expedite travel. *Callicebus* often exits late or enters the sleeping tree hours early. *Aotus* does neither of these things. After the sun has set and before the sun actually rises, light levels are as high as they are in the full moon (Pariente 1974). *Aotus* travels farther during these twilight hours than at any other time. The use of twilight may explain *Aotus*' punctual behavior concerning sleeping sites. In the Chaco, traveling at dawn and dusk is not essential because the monkeys can travel during the bright daylight.

5) Differences in predation pressure between the two sites may influence timing of sleeping tree exit and entrance. In the rain forest, daytime activity exposes monkeys to the possibility of attack by large hawks and eagles. However, by leaving the sleeping tree after sunset, and entering it again before dawn, *Aotus* is safely hidden in its sleeping site before hawks and eagles begin to hunt. *Callicebus* is vulnerable to predation by these raptors, and avoids them by traveling low in the canopy and silently, and by resting in vine tangles. It would not be to *Aotus*' advantage in the dry Chaco to travel during twilight because the owls are already hunting. Data from Paraguay show that *Aotus* begins foraging as early as 16:00 and often continues traveling well after sunrise. Diurnal raptors do not dictate an early bedtime for *Aotus*, in fact, nocturnal raptors may make *Aotus* more diurnal.

E. Fighting and calling by Aotus in the two habitats

1. Similarities:

a) During the week before, or the week after, the full moon, when the moon is located overhead, a solitary night monkey calls for a period of one-three hours, traveling from 50-300 meters as it calls.

b) The call is contagious and may be answered by other night monkeys from different territories.

c) The call consists of from two-six notes, repeated monotonously. Each note is low in frequency, 200-400 Hz, with little variation and no harmonics.

d) The call is never given by mated pairs.

e) Two types of calls are given in each habitat, suggesting that males can be distinguished vocally from females.

f) There was no evidence of seasonal variation in calling frequency. Calls were given in the bright moon when resources were both scarce and plentiful.

2. Differences:

a) Calling was more continuous in Peru than in Paraguay. In the Chaco, pauses sometimes lasting as much as 15 minutes occurred between calling bouts. Peruvian night monkeys continued to call without pausing.

b) The number of notes contained in each call varied from one site to the other. The mean number of notes in Paraguay was two, while in Peru it was three.

c) No intergroup encounters were observed in Paraguay, perhaps due to isolation of groups in forest 'islands'. However, in Peru where night monkey territories were adjoining, battles between groups occurred on the average of once a month when the moon was bright and located overhead.

Calling behavior showed only minor variation between the two sites; intergroup aggressive encounters were observed only in Peru. Callicebus calls are discussed to provide insights into the differences in the two populations of Aotus. The differences seen in the two habitats may be attributed to differences in: 1) climate, 2) population density, and 3) predation pressure.

3. Effect of Climate: Aotus in both habitats called during both cold and hot ambient temperatures, but not during rainy or dark nights. Even the winds of the savannah did not discourage Aotus on moonlit nights. The frequency of Callicebus dawn calling decreased during months when resources were scarce. No seasonal fluctuations in the calling behavior of Aotus was observed at either site.

4. Effect of Population density: Intergroup encounters were not observed in Paraguay because groups were isolated from one another by 500 meters or more of savannah. There is some evidence from Peru that the frequency of intergroup encounters decreases as population density decreases. Aotus at 40 animals per square kilometer had 15 encounters in 15 months; Callicebus at 20 monkeys per square kilometer had

seven encounters with groups of conspecifics in 15 months. Based on these data, it is predicted that *Aotus* in the Chaco would have few fights because of their low population density. Calling behavior may not follow this pattern because a lower population density may mean a more difficult search for mates. In fact, the number of groups divided by the number of monthly calls gives Paraguay a slightly higher score than in Peru for calls divided by group number.

5. Effect of Predation pressure: The presence of the great horned owl may have influenced two differences in the calling behavior of *Aotus* in the Chaco. Pauses between series of calls followed by the monkey traveling quickly between bouts could discourage location by the owl. The great horned owl's hoot consists of four-five notes at the same frequency as the night monkey's hoot. In Peru, each monkey call consisted of two-six notes with a mean of three. However, in Paraguay, calls consisted of only *two* notes. Discrimination between owl and night monkey hoots over long distances was facilitated by the difference in the number of notes contained in each. Note number may have decreased by chance. In Peru, there were no animals who gave calls in the same temporal pattern as *Aotus*, although they may be emitted at the same frequency.

F. Ranging behavior of Aotus in two habitats

1. Similarities:

a) *Aotus* ranged farther when resources were scarce and scattered throughout the territory. Path lengths decreased when only a few clumped or large resources were available in the territory.

b) Aotus traveled less on dark, moonless nights than on nights with bright moonlight.

c) Aotus traveled less on nights with heavy rain.

2. Differences:

a) Path lengths were longer in Peru than in Paraguay (708 meters annual mean distance traveled in Cocha Cashu versus 550 meters annual mean distance traveled in Paraguay). Reduced path length may be due to reduced group sizes of the Chacoan Aotus populations.

b) Habitual pathways were used in Peru, while in Paraguay strict adherence to certain routes was less obvious.

c) In Cocha Cashu, nightly paths were most often circular with the group returning to the same sleeping tree they used the day before. In Paraguay, paths were never circular and the group never returned to the sleeping tree used the previous day.

d) Paths included daytime travel in Paraguay, whereas in Cocha Cashu they were strictly nocturnal.

e) Aotus in the rain forest rarely ranged in bamboo patches or lake/river edge areas where vine leaves were abundant. Aotus in the dry forest used only forest edge areas where palatable leaves were abundant during June and

July. They rarely ranged into these areas when flowers and fruit were abundant.

3. Adaptive Significance of Ranging patterns: Although some aspects of ranging behavior do not change with habitat, the differences in ranging at the two sites are striking. These differences can be attributed to differences in 1) forest structure and abundance of resources, 2) climate, 3) predation pressure, and 4) competition for food. These possibilities will be discussed in light of the ranging data on *Callicebus*.

a) Effect of resources and forest structure: Differences in mean *Aotus* path length in the two sites may result from the differences in abundance of resources and consequent carrying capacity of the two forests. It is difficult to compare productivity in these two forests because factors such as consumption and consequent competition from other consumers (birds, bars, etc.) are difficult to measure. Because both territory size, group size, and path length are similar for both *Callicebus* and *Aotus* in Peru (Table 29), and because territory size, group size, and path length are about one third to one half the size in Paraguayan *Aotus*, there is some evidence that the parameters may be correlated. Smaller groups may range less in the same habitat, based on data gathered by Waser (1977) and Kinzey (1983), but such comparisons between diverse habitats are unwise. Further, group size samples in my study (Peru=4.5; Paraguay n=2) may be too small for accurate statistical comparisons.

Differences in forest structure between the two forests may explain why Aotus adheres to strict routes in the rain forest, but behaves more like Callicebus in its routes in the dry forest. In the short, open forests of the Chaco, light levels are higher than in the rain forest. Better visibility may replace memorization of routes necessary for accurate travel in the dark at Cocha Cashu.

b) Effect of Climate may result in some ranging differences. Ranging during daylight increased slightly during the cold winter months in Paraguay.

c) Effect of competition for food: There were no large monkeys at the Paraguayan study site except for A. caraya; black howling monkeys did not chase Aotus from feeding sites. This may have contributed to Aotus daytime feeding and daytime travel.

4) Effect of Predation pressure : Nightly path lengths and monitoring of all parts of the territory were less consistent for Aotus in the rain forest than for either Callicebus at Cocha Cashu or Aotus in the dry forest. Callicebus path lengths exhibited less variation between consecutive days and less deviation from the mean over the entire annual cycle. Paraguayan data tended to follow this trend. Variation in the nocturnal Aotus path length can be attributed to chances in lunar cycle. Aotus ranged farther

on bright nights and rested more on moonless nights. In Paraguay, night monkeys also traveled farther on moonlit nights, resting more on moonless nights. However, these monkeys also traveled during the day, making the total path length for any 24-hour period more consistent. Consequently it is possible that the threat of hawk and eagle predation during the daylight hours in the rain forest combined with the use of high moonlight levels for foraging account for the variation in path length.

There was a difference in ranging patterns within each territory. *Aotus* in the rain forest rarely visited leaf eating areas; *Callicebus* spent over an hour each day in these areas regardless of season. *Aotus* in the Chaco fed in leaf eating areas only during the season when resources were most scarce. Because *Callicebus* was chased from fruit trees all year, interference competition for fruit partially may explain this behavior. At night when insects are active and vocal, *Aotus* may be able to rely on insects for protein.

G. General Discussion

In this study, I have attempted to gain insights into some of the costs and benefits of nocturnality for the only nocturnal monkey, *Aotus*. it is not possible to discover clearly the earliest origins of behavior or to know absolutely its causes. We cannot know the reasons why a small ceboid monkey some millions of years ago began to travel and feed during the night. But, by studying the life of the night monkey in diverse habitats, we can understand more clearly the forces that stabilize and shape night monkey behavior today, and therefore, gain insight into behavioral ecology.

1. Effect of light levels:

The structure of the environment does not alter from day to night, and yet perception of the environment is very different. In limited light, vision becomes difficult, odors, on the other hand, are amplified at night by the increased humidity. What are the effects of these nighttime differences on the behavior of *Aotus*?

Foraging techniques that result in feeding success in the daytime are different from those that are successful at night. *Callicebus* sits and scans leaves and branches for insects, capturing the immobile insect after discriminating it from its similarly-colored background. *Aotus* may find this style of insect predation impossible in dim light, relying instead on detecting movements of insect prey. *Callicebus* relied on visual cues, like shape and color, to locate fruit; *Aotus* may fall back on olfactory cues or may rely on constant monitoring of ripening fruit.

Social behavior may also be influenced by nocturnality. The grooming behavior involves parting the fur with the hands, detecting detritus or ectoparasites, and removing these with a combination of hands and mouth. *Aotus* rarely grooms. This behavior occurs frequently in *Callicebus* groups. Perhaps the cleaning function of grooming cannot be achieved in darkness. Scent marking is a form of communication which relies on enhanced messages at night. Aotus communicates with two types of scent: urine and an oily exudate from a gland at the base of the tail. Callicebus rarely scent marks, perhaps because scents are not as powerful during the day or because visual signals communicate more effectively.

Ranging and active periods of Aotus are synchronized with high moonlight levels or with twilight. In fact, playing, long distance calling, and intergroup fighting occur only in bright moonlight or twilight. These data suggest that although night monkeys can see at much lower light levels than we humans, maneuvering through the trees in the dark is not easy for them. The advantages of accurate visual perception would produce a constant selective pressure to feed and travel during high light levels, daylight. The selective pressures for Aotus to remain nocturnal in the rain forest, those pressure that oppose a diurnal life style, must be strong.

2. Temporal partitioning:

Temporal partitioning of resources has been described in nonprimates by Schoener (1968) and suggested as an adaptation of nocturnal prosimians by Charles-Dominique (1975). Is there evidence that Aotus has altered its activity rhythm to ensure ecological separation from the frequently sympatric Callicebus (a monkey with similar body weight, group size, and morphology)?

The night monkey niche, as opposed to the day monkey niche, appears to be more complex than simply using the same resources at different times of the 24-hour cycle. Many of the same foods (e.g., fruit, nectar, leaves, and insects) are available to both species. However, these foods are not consumed year-round in the same proportions by the two rain forest species. Differences in behavior including size of fruit trees used, suggest that additional factors influence diet and behavior. These differences cannot be explained by simple temporal partitioning of resources.

Geographical distribution of these two species suggests that competition from Callicebus does not inhibitAotus from adopting a diurnal life style in the rain forest. In most forests where Callicebus is absent and Aotus is plentiful (e.g., Panama), the latter is still strictly nocturnal (Moynihan 1964; Thorington et al. 1976; Wright 1978).

3. Competition and Predation

Avoidance of competition for food may account for differences in feeding and foraging behavior between closely-related species (Gartlan and Struhsaker 1972;Sussman 1974; Clutton-Brock 1977; MacKinnon and MacKinnon 1980; Mittermeier and van Roosmalen 1981; Fleagle et al. 1981). Charles-Dominique (1977) suggests that nocturnal prosimian primates avoid competition with diurnal monkeys by being active at night and by specializing in food items unpalatable to other primate species. Is it possible that Aotus avoids competition for fruit from birds and diurnal, frugivorous primates by a nocturnal life-style? This hypothesis is difficult to test. However, it seems unlikely that the limitations of trying to see well in low light levels would outweigh the benefits of this means of reducing competition. Unlike nocturnal prosimians, Aotus has neither a naked rhinarium for increased olfactory sensitivity nor a tapetum lucidum for more efficient vision in low light levels.

There is some evidence from my study, however, that a certain type of direct interference competition does affect the behavior of small monkey species in South America. Waser (Waser and Case 1981) found that in African rain forests this type of interference affects timing in fruit tree use by different monkey species. Small monkey species tend to have small territories and they constantly monitor the fruiting condition of the few trees within their territory. Larger species do not monitor all the trees in their larger core areas and as a result, may not arrive at a tree with ripe fruit as soon as the smaller monkeys. The small monkeys are thus able to feed on fruit before the larger monkeys locate the food and displace them from the tree. In South America, the outcome of competition between large and small monkey species for a common food resource is more marked than among Old World species. During the season of resource scarcity, _Callicebus_ are excluded from fruit trees by other monkeys to the extent that they do not gain access to any large-crowned fruit trees and nectar resources. As a result, titis reduce their overall activity, range less, and increase their consumption of leaves to almost one half their entire diet. _Aotus_, on the other hand, gains access to the preferred food items by foraging at night when the large monkey species are away from feeding sites in their nighttime resting trees.

Terborgh (1983) and von Schaik _et al._ (1983a, 1983b) suggest that predator pressure may exert a more pervasive influence on primate behavior patterns than previously supposed. Diurnal raptors pose the greatest threat to arboreal mammals in the South American rain forest (Fowler and Cope 1964; Rettig 1978; Terborgh 1983). There are no nocturnal rain forest avian predators which regularly take prey which exceeds 500 grams in weight. In Peru, there is little indication that _Aotus_ accomodates its foraging behavior to predation pressure. Diurnal behavior, however, does reflect consistent predator avoidance, _i.e._, the night monkeys sleep in tree trunk holes, or in trees covered with dense vine tangles which hide them. _Aotus_ enter and exit sleeping sites before diurnal raptors hunt. In the Chaco, where there is a major nocturnal raptor, the erratic entrance/exit of night monkeys into sleeping sites, use of multiple sleeping sites in an irregular pattern for a single 24-hour period, and the positive correlation of movement patterns with owl resting/nesting sites, all strengthen the hypothesis that avoidance of avian predators, rather than avoidance of fruit resource competition, has the greatest effect on *Aotus*' nocturnal adaptation.

However, if daytime predation pressure is such a problem is South American rain forests, why aren't all small monkeys nocturnal? Other small monkey species seem to have evolved different means to avoid these predation pressures. Squirrel monkeys may forage in large groups for protection, whereas titis and tamarins may hide from predators.

In Asia and Africa, diurnal monkeys all have large body size (a form of predator protection), except the talapoin which occurs in very large groups. There are no nocturnal monkeys in the Old World, however there are many species of nocturnal prosimian primates, *e.g.*, galagos, lorises, and pottos. These prosimians avoid predators by being small, cryptic, and nocturnal foragers.

All prosimians have a *tapetum lucidum* for keen vision even in low light levels. Therefore, prosimians can forage during the dark of the moon to avoid being exposed to hunters who are active during moonlit hours. Tarsiers, on the other hand, do not have this light gathering layer in the eye. But, like *Aotus*, they have evolved larger eyes to aid nocturnal visual perception.

A study, parallel to that presented in this dissertation, would be possible on tarsiers because they are reported to be active exclusively at night. However, this prosimian, which lives on different islands (Napier and Napier 1967), has yet to be studied systematically in all habitats. The effects of interference competition and predation pressure as they relate to nocturnality in this genus have yet to be calculated for the species in contrasting island environments.

When did the first nocturnal monkey evolve in South America? There is some evidence from the fossil record that _Tremacebus harringtoni_ from the late Oligocene of Argentina, was a ceboid of the same body weight as the extant _Callicebus_ and _Aotus_ (Hershkivitz 1974; Szalay and Delsen 1979; Rose and Fleagle 1981). The orbit size of is intermediate between that of _Aotus_ and _Callicebus_, suggesting a transitional form. it is possible that this fossil form was crepuscular. However, we can only speculate on the behavior and ecology of _Tremacebus_ based on the few fossil remains recovered to date (Rose and Fleagle 1981). It is possible that a rain forest ancestor of _Aotus_ adopted a nocturnal life-style to avoid avian diurnal predators and large sympatric monkeys, but information on the sympatric fossil fauna is unavailable.

In this dissertation, I have presented data and analyses on the behavior and ecology of two South American primates, Aotus trivirgatus and Callicebus moloch which describe the costs and benefits of a nocturnal life style for Aotus. The costs incurred are difficulties in traveling, friendly and agonistic social interaction in low light levels, whereas the benefits derived are avoidance of predation pressures and interference competition from large-bodied diurnal monkeys.

TABLE 1

Sympatric Primate Species at Cocha Cashu, MNP

Species	Group Size	Range Size/ Range type*	Body Weight (in kilograms)	Biomass (kg/km^2)
Alouatta seniculus (red howler)	5-7	25ha/O	5.0-8.0	180
Ateles paniscus (black spider monkey)	2-35	200ha/O	5.4-7.0	175
Cebus apella (brown capuchin)	8-15	80ha/O	1.5-3.5	104
Cebus albifrons (white capuchin)	10-18	150ha/O	1.5-3.5	84
Saimiri sciureus (squirrel monkey)	20-35+	250ha/O	1	48
Aotus trivirgatus (night monkey)	2-5	10ha/T	1	28
Callicebus moloch (dusky titi)	2-5	6ha/T	1	17
Saguinus imperator (emperor tamarin)	2-8	80ha/T	0.35-0.50	5
Saguinus fuscicollis (saddle-back tamarin)	2-8	80ha/T	0.25-0.40	5
Cebuella pygmaea (pygmy marmoset)	2-8	1ha/T	0.10	1
Lagothrix lagotricha**				
Pithecia monachus**				
Callimico goeldii**				

*Range type: O=overlapping ranges
T=exclusive ranges, territorial

** These monkeys were observed very rarely and no data on group size, ranging patterns, and biomass are available.

These data taken, in part, from Janson (1975) and Terborgh (1983).

TABLE 2

Aotus Group Composition at Cocha Cashu, 1980-1981, 1982

Group/Year	Adult Ma	Adult Fe	2-year old	Yearling	<1 Year	Total
River I						
1980-81	+	+	+	+	+	5
1982	+	+	+	+	+	5
House II						
1980-81	+	+	+	+	+	5
1982	+	+	+	+	+	5
East III						
1980-81	+	+	?	?	?	2-5
South IV						
1980-81	+	+	+	+	?	4-5
S. Lake V						
1980-81	+	+	+	+	+	5
North VI						
1980-81	+	+	+	+	+	5
1982	+	+	+	+	+	5
Swamp VII						
1980-81	+	+	+	?	?	3-5
N.E. VIII						
1980-81	+	+	+	+	?	4-5
S. River IX						
1982	+	+	-	-	-	2

TABLE 3

Callicebus Group Composition at Cocha Cashu, 1980-1982

Group/Year	Adult Ma	Adult Fe	2-year old	Yearling	<1 Year	Total
River I						
1980-81	+	+	+	+	+	5
1982	+	+	+	-	+	4
House II						
1980-82	+	+	+	+	+	5
North III						
1980-82	+	+	+	+	+	5
South IV						
1981-82	+	+	-	-	+	3
S. Lake V						
1980	+	+	-	-	+	3
1981	+	+	+	-	?	3-4
N. Central VI						
1980	+	+	+	+	+	5
1981	+	+	+	+	?	4-5

TABLE 4

Home Range and Group Composition for *Aotus* and *Callicebus*
Peru and Paraguay, 1980-1982

Genus/Site Group	Mean Number of Animals per Group	Home Range in Hectares^2
Aotus/Cocha Cashu		
River I	4.5	7
North II	4.5	14
House III	4.8	8
South IV	4.0	7.5 (est)
East VI	4.0 (est)	10 (est)
Swamp VII	4.0 (est)	8 (est)
South Lake VIII	4.5	10 (est)
North East IX	4.5 (est)	?
New South River (1982 only)	2.0	?
Overall mean:	4.1	9.2
C. moloch/Cocha Cashu		
River I	4.2	6
House II	4.8	7
North III	4.8	8
South IV	2.7	7
South Lake VI	3.0	6
North Central VI	4.5	6.5
Overall mean:	4.0	6.9
Aotus/Paraguay		
Focal I	2	5
Solitary A	1	5
Solitary B	1	5
Group II	2.0	4
Overall mean:	1.5	4.8

*Group size in Peru for September and March, 1980-1982, averaged to obtain this number. Data for Paraguay includes only May-September, 1982.

(est) = estimated

TABLE 5

Dates of Subadult Emigration and Infant Births in MNP

Genus Group	Year	Emigration date	Date of births
Aotus			
I	1980	Before September	February
	1981	September	February
	1982	Before October	September
II	1980	Before September	February
	1981	April	January
	1982	after November	August
III	1980	December	September
	1982	after December, 7	September
IV	1980	after December	November
Callicebus			
I	1980	September	July
	1981	after August	none
	1982	after December	August
II	1980	December	September
	1981	December	September
	1982	after December	September
III	1980	after November	November
	1981	after October	October
	1982	after October	October
IV	1981	none	July
	1982	none	September
V	1980	none	July
	(?) 1982 or 1981	none	?
VI	1980	after November	September

TABLE 6

Summary of Climatic Data for Cocha Cashu, MNP
for 1976-1977* and 1980-1981

	Rainfall in mm		Mean Temperatures C°					
			Mean Maximum		Mean Minimum		Monthly Mean	
Month\Year	76-77	80-81	76-77	80-81	76-77	80-81	76-77	80-81
September	50	95	27.7	27.7	20.4	19.9	24.1	23.8
October	270	135	28.9	28.0	21.9	22.3	25.5	25.2
November	220	220	28.6	27.4	22.1	20.6	24.0	24.0
December	190	227	27.0	27.0	22.3	22.0	24.7	24.5
January	290	235	27.2	27.0	22.6	22.4	24.9	24.7
February	180	256	27.5	26.9	22.4	22.3	25.1	24.6
March	390	157	27.0	27.8	21.7	22.7	23.9	25.3
April	270	179	25.1	25.4	21.7	22.1	23.5	23.8
May	90	245	24.3	25.4	20.4	22.1	22.6	23.8
June	50	212	24.5	23.9	20.0	19.9	22.2	21.9
July	20	25	26.4	24.0	21.2	18.1	24.1	21.1
August	80	30	28.0	26.3	20.9	19.7	24.4	23.0
Annual mm Total	2080	2016						

*From Terborgh 1983.

TABLE 7

Ranks of Fruit and Nectar Eaten by *Aotus* by Number of Feeding Minutes at Cocha Cashu

		Feeding	Months fed on Fruit											
Rank	Species	Minutes	J	F	M	A	M	J	J	A	S	O	N	D
1	*Guatteria* cf. *acutissima*	1540	–	–	–	–	–	–	–	–	+	+	+	–
2	*Combretum assimile**	1300	–	–	–	–	–	–	+	–	–	–	–	–
3	*Sloanea* cf. *obtusifolia*	1165	+	+	+	–	–	–	–	–	–	–	–	–
4	*Ficus kilipii*	1010	–	–	–	–	–	–	+	+	+	–	–	–
5	*Sloanea guianensis*	935	–	–	+	+	–	–	–	–	–	–	–	–
6	*Spondias mombin*	645	+	+	+	–	–	–	–	–	–	–	–	–
7	*Brosimum lactescens*	635	–	–	–	–	+	+	–	–	–	–	–	–
8	*Coussapoa obovalis*	620	–	–	–	–	–	–	–	–	+	+	–	–
9	*Celtis iguanea*	570	–	–	+	+	+	+	+	+	+	–	–	–
10	(Lauraceae) *sp.* 1	565	–	–	–	–	–	–	–	–	–	+	–	–
11	*Sorocea* cf. *briquetii*	510	+	–	–	–	–	–	–	–	–	–	–	+
12	*Quararibea cordata**	490	–	–	–	–	–	–	–	+	–	–	–	–
13	*Inga marginata*	460	+	–	–	–	–	–	–	–	–	+	–	–
14	*Cecropia sp.*	425	+	–	+	+	+	+	–	–	–	–	–	–
15	*Ficus mathewsii*	385	–	–	–	–	+	–	–	–	–	–	–	–
16	*Myrcia splendens*	325	+	–	–	–	–	–	–	–	–	–	–	–
17	*Ficus sp.*	215	–	–	–	–	–	+	–	–	–	–	–	–
18	*Trichostigma octandra*	215	–	–	–	–	–	–	–	–	–	+	+	–
19	*Ficus erythrosticta*	210	–	–	–	–	–	–	–	–	–	+	–	–
20	*Xylopia cuspidata*	135	–	+	+	–	–	–	–	–	–	–	–	–

Total feeding minutes 12,355

* = Nectar feeding.

TABLE 8

Percentage of Feeding Time Spent on Top Ranked Food Items, Cocha Cashu

Month	Aotus Group I #1	Aotus Group I #1 & #2	Callicebus Group II #1	Callicebus Group II #1 & #2
January	27%	54%	40%	65%
February	65%	91%	80%	90%
March	26%	45%	42%	67%
April	81%	92%	33%	58%
May	28%	52%	41%	59%
June	42%	66%	44%	69%
July	95%	100%	59%	78%
August	57%	94%	43%	63%
September	30%	48%	-	-
October	-	-	45%	71%
November	-	-	27%	54%
December	-	-	36%	59%
Annual Mean	50%	71%	45%	67%

Each species of food item (*i. e.*, fruit, nectar, flowers) is ranked by comparing feeding minutes of each species to total number of feeding minutes scored that month.

TABLE 9

Characteristics of Fruit Eaten by *Aotus* and *Callicebus*, at Cocha Cashu
By Percentage of Total Species Eaten

Characteristic	*Aotus* Group I % of Total	*Callicebus* Group II % of Total
Size		
0-2cm	75%	84%
2-10cm	22%	15%
10-20cm	3%	1%
Color		
orange or yellow	33%	33%
red or purple	33%	33%
green or brown	33%	33%
Taste		
sweet	39%	44%
bland and mealy	47%	43%
spicey, acid, or bitter	14%	13%

TABLE 10

Ranks of Fruit Eaten by *Callicebus* Group II by Number of Feeding Minutes

		Feeding	Months in Fruit											
Rank	Species	Minutes	J	F	M	A	M	J	J	A	S	O	N	D
1	*Celtis iguanea*	805	-	-	+	+	+	+	+	-	-	-	-	-
2	*Ficus erythrosticta*	790	-	-	-	+	+	-	+	+	-	-	+	-
3	*Inga mathewsii*	675	-	+	+	+	+	-	-	+	-	+	+	-
4	(Violaceae) *sp.*	525	-	-	-	+	+	-	-	-	-	-	-	+
5	*Calatola venezuelensis*	510	-	-	-	+	+	+	+	+	-	-	-	-
6	*Inga marginata*	495	-	+	-	-	-	-	-	-	-	-	-	-
7	*Brosimum alicastrum*	480	-	-	+	+	+	-	-	-	-	-	-	-
8	*Xylopia cuspidata*	405	+	-	+	-	-	-	-	-	-	-	-	-
9	*Sloanea quianensis*	305	-	-	-	+	-	-	-	-	-	-	-	-
10	(Lauraceae) *sp.*1	290	+	+	-	-	-	-	-	-	-	+	+	-
11	*Protium neglectum*	210	+	+	+	+	+	-	-	-	-	-	-	-
12	*Myrcia spendens*	205	+	+	-	-	-	-	-	-	-	-	-	-
13	*Lunania parviflora*	185	-	+	-	+	-	-	-	-	-	-	+	-
14	*Virola peruviana*	145	-	-	-	-	-	-	-	-	-	+	+	-
15	(Lauraceae) *sp.*2	140	-	-	-	-	-	-	+	+	-	+	-	-
16	(Bignoniaceae) *sp.*	130	-	-	-	-	-	+	-	-	-	-	-	-
17	*Eugenia punicifolia*	125	-	-	-	-	-	-	-	-	-	+	+	-
18	*Annona neglecta*	125	-	-	-	+	+	+	-	-	-	-	-	-
19	*Inga edulis*	115	+	+	+	-	-	-	-	-	-	-	-	-
20	*Trichilia peopigii*	110	+	-	-	-	-	+	+	+	-	-	-	-
	Total Feeding Minutes	6,770												

TABLE 11

Diet of *Aotus* and *Callicebus*: Fruit, Nectar and Flower Species Used per Sample

Month	*Aotus* Group I sp#/night	*Aotus* Group I sp#/month	*Callicebus* Group II sp#/day	*Callicebus* Group II sp#/month
January	5	12	4	8
February	3	6	4.5	13
March	8	18	8.5	23
April	2	6	8	10
May	5	8	7	21
June	5	9	5	14
July	1	2	4.8	11
August	2	4	7	10
September	6	7	-	-
October	7	13	5.5	12
November	5	12	8.3	17
December	-	-	-	12
Annual Mean	4.5	8.8	6.3	13.7

TABLE 12

Crown Diameter of Individual Trees Fed in by
Aotus Group I and _Callicebus_ Group I and II, Cocha Cashu
1980-1982

Crown Diameter	_Aotus_ I #	_Aotus_ I %	_Callicebus_ I #	_Callicebus_ I %	_Callicebus_ II #	_Callicebus_ II %
0-10 meters	81	61%	32	82%	134	93%
11-20 meters	46	34%	6	15%	7	5%
21-30 meters	7	5%	1	3%	3	2%
TOTAL	134	100%	39	100%	144	100%

TABLE 13

Percentage of Feeding Time in Trees by Size Class, Cocha Cashu

Crown Diameter	*Aotus* I	*Callicebus* II
0-10 meters	15%	79%
11-20 meters	52%	18%
21-30 meters	33%	3%
	100%	100%

Data represent 177 hours of fruit feeding time for *Aotus* and 118 hours of fruit feeding time for *Callicebus.*

TABLE 14

Size Comparison of Extant and Feeding Trees, Cocha Cashu

Crown Diameter	Aotus		Callicebus II	
	FT*	TT*	FT*	TT*
0-10 meters	5.0	1500	17.0	1500
11-20 meters	4.0	30	1.0	52
21-30 meters	1.3	14	.4	10
TOTAL	10.3	1544	18.4	1562

*FT = Feeding trees per size class per hectare
*TT = Total number of trees per size class per hectare (.5 ha surveyed)

TABLE 15

Nocturnal Arboreal and Volant Frugivores, MNP

Frugivore	Body Weight (in grams)	Group Size	Biomass (Kg/Km^2)
MARSUPIALS[a]			
Didelphis marsupialis (common opossum)	2000	1	45
Philander andersoni (four-eyed opossum)	270	1	7
Metachirus nudicaudata (bare-tailed opossum)	280	1	3
Caluromysiops irrupta (black-shouldered opossum)	250	1	3
Caluromys lanata (woolly opossum)	200	1	3
Marmosa cinerea (cinnamon opossum)	150	1	1
Marmosa noctivaga (mouse opossum)	60	1	1
BATS[a]			
Well over 20 species			
PRIMATES[b]			
Aotus triviragatus (night monkey)	1000	2-5	40
PROCYONIDS[c]			
Potos flavus (kinkajou)	2000	1-4	40
Bassaricyon alleni (olingo)	1000	1-2	5

a. Data from L. E. Emmons in Terborgh, 1983.
b. Data from P. C. Wright, complete count.
c. Data from P. T. Sherman census and trapping, personal communication.

TABLE 16

Prey Species of the Harpy Eagle in Guyana*

Genus species	Common Name	Estimated Weight (in kilograms)
Alouatta seniculus	red howler monkey	8.0
Cholepus didactylus	two-toed sloth	5.0
Mazama americana	brocket deer	5.0
Nasua nasua	coati	4.5
Tamandua tetradactlya	tamandua	4.0
Bradypus tridactylus	three-toed sloth	3.5
Didelphis marsupialis	opossum	3.5
Dasyprocta agouti	agouti	3.0
*Cebus sp.***	capuchin monkey	2.5
Coendou prehensilis	porcupine	2.5
Potos flavus	kinkajou	2.0
Eira barbara	tayra	1.8
Pithecia pithecia	white-faced saki monkey	1.3
Bassaricyon beddarti	olingo	1.0
Chiropotes satanus	bearded saki monkey	1.0

*Data from identification of 85 prey items brought to three nests (Fowler and Cope 1964; Rettig 1978; Terborgh in press).

**Capuchins constituted 28 out of the 85 individual prey items (33%) presented in the table above.

TABLE 17

Raptor Predation on the Primate Community at Cocha Cashu

Raptor Species Common name	Body Weight in grams	Primate Species of Predation Episodes Observed
Harpia harpyja Harpy eagle	4000-6000	*Cebus*, *Alouatta*, *Saimiri*
Morphnus guaanensis Crested eagle	2000-3000	*Saimiri*
Spizaetus tyrannus Black hawk eagle	1750	*Cebus*, *Saimiri*, *Callicebus*
S. ornatus Ornate hawk eagle	835-1607	*Saimiri*, *Saguinus*, *Callicebus*
Leucopternis shistaceae Slate-colored hawk	1000	*Saimiri*
Accipiter bicolor Bicolored hawk	204-454	*Saguinus*

TABLE 18

Observed Attacks on _Callicebus_ at Cocha Cashu

Date/Time	Predator	Reaction of _Callicebus_
6.9.81/08:30	A grey hawk _Accipiter_ (?)	Predator alarm call until 09:00 from vine tangle
7.6.81/08:28	Ornate hawk eagle _Spizaetus_ _ornatus_	Exit fig tree; predator alarm call until 08:43
5.22.81/07:25	Crested eagle _Morphnus_ _guianensis_	Exit fig tree and give predator alarm call
10.14.82/07:25	Bicolored hawk _Accipiter_ _bicolor_	Exit fig tree and go into vine tangle
4.26.81/07:00	Ocelot _Felis_ _pardalis_	Predator alarm call for 30 minutes after initial sighting

TABLE 19

Characteristics of Sleeping Trees, Cocha Cashu

Physical Characteristic	Aotus	Callicebus
Tree height (range)	20-26 meters	12-30 meters
Mean tree height	18 meters	21 meters
Mean number of different trees used per 6-day sample	1.4	5.4
Number of trees used per year	5	26
% trees with dense vine tangles	100%	30%
% trees in which monkeys were visible from the ground	0%	70%
% trees in which monkeys were visible from above	0%	10%
% trees with holes	0%	0%
% use of preferred tree per year	57%	3%
% trees within 50 meters of major fruit feeding tree	95%	26.%
% trees used per 6-day sample		
one tree used	55%	0%
two trees used	45%	0%
more than two used	0%	100%

TABLE 20

Mean Nightly Path Length of *Aotus* Group I at Cocha Cashu

Month	N	Mean Daily Path Length (in meters)	Standard Deviation
September, 1980	3	1025m	
October, 1980	5	633m	332.49
November, 1980	5	575m	225.00
December, 1980	4	437m	183.3
January, 1981	8	1025m	108.97
February, 1981	5	340m	156.20
March, 1981	5	980m	224.94
April, 1981	5	804m	338.26
May, 1981	5	949m	202.49
June, 1981	5	788m	114.80
August, 1981	5	560m	94.33
July, 1981	5	385m	113.57
Site Total	N= 60	Overall Mean 708m	242.74

TABLE 21

Mean Daily Path Length of *Callicebus* Group II at Cocha Cashu

Month	N	Mean Daily Path Length (in meters)	Standard Deviation
January, 1981	5	720m	67.82
February, 1981	4	706m	216.78
March, 1981	6	1108m	214.90
April, 1981	10	850m	160.08
May, 1981	5	647m	129.80
June, 1981	6	349m	143.63
July, 1981	10	545m	176.66
August, 1981	5	574m	120.22
October, 1982	5	599m	97.93
November, 1982	4	791m	68.22
December, 1982	3	488m	62.50
Total N	63	Overall means 671m	192.88

TABLE 22

Aotus Loud Calling Behavior in Paraguay, 1982

Date	Moon Phase	Bout Length	Distance Traveled During Bout
2 June	full-4	3 hours	235 meters
3 July	full-3	1.5 hours	125 meters
4 July	full-2	2 hours	250 meters
31 July	full-4	3 hours	100 meters
4 Aug.	full	0.5 hour	100 meters
11 Aug.	full+7	2.5 hours	250 meters
25 Aug.	full-8	1.5 hours	200 meters
2 Sept.	full-1	1.0 hours	100 meters
3 Sept	full	3.5 hours	350 meters
	Average	2.1 hours	190 meters

TABLE 23

Flora La Golondrina Study Site, 1982

Species	Type	Mean DBH*	#/ha
Aechmea polystachya *Bromelia serra*	terrestrial bromeliads		13,100
Cereus sp.	tree cactus	8 cm	28
Opuntia sp.	cactus		
sp.	climbing cactus	2 cm	88
spp. all	vines	2-6 cm	1,104
sp. above 2m	trees		1,878
Acacia praecox	trees		12
Arecastrum romanzoffianum	palm tree		56
Caesalpinia paraguayensis	tree		14
Eugenia ssp.	tree		124
Piptadenia rigida	tree		154
Sapium sp.	tree		8
Tabebuia ipe	tree		22
Terminalia argentea	tree		18
Trichilia catigua	tree		30

* DBH = diameter at breast height

TABLE 24

Tree and Vine Census at La Golondrina Study Site, Paraguay

Vines Stem Diameter	#/Hectare	Trees Crown Diameter	Height
<2.3 cm	1008		
4.4 cm	90		
6.5 cm	6		
	1608	0-5 m	
	236	6-10 m	
	34	11-20 m	
	1374		1-10 m
	446		11-20 m
	58		21-30 m

Total Vines = 1104 Total Trees = 1878

TABLE 25

Ranks of Plants Eaten by Aotus by Number of Feeding Minutes at La Golondrina Ranch

Rank	Species	Family	Part Eaten	Feeding Minutes
1	*Acacia praecox*	Leguminosae	flower	430
2	*Randia armata*	Rubiaceae	leaf	370
3	*Sapium sp.* (?)	Euphorbiaceae	flower	330
4	*Celtis spinosa*	Ulmaceae	leaf	275
5	*Forsteronia brasiliensis*	Apocynaceae	leaf	255
6	*Tabebuia ipe*	Bignoniaceae	flower	230
7	unidentified sp.	---	leaf	215
8	*Arecastrum romanzoffianum*	Palmae	fruit	205
9	*Sebastiana brasiliensis*	Euphorbiaceae	fruit	180
10	*Tillandsia duratii*	Bromeliaceae	leaf, center	150
11	*Terminalia argentea*	Combretaceae	flower	115
12	*Piptadenia rigida*	Leguminosae	leaf, seed	90
13	*Aristolochia esperanzae*	Aristolochiaceae	leaf, flower	80
14	*Rhipsalis schaferi*	Cactaceae	fruit	70
15	*Trichilia catagua*	Meliaceae	fruit	60
16	*Copernicia alba*	Palmae	fruit	50
17	*Eugenia sp.*	Myrtaceae	fruit, leaf	20
18	*Acanthosyris falcata*	Santalaceae	fruit	10
			Total	3135

Total Feeding Minutes in the Study 3570

TABLE 26

Mammals Observed at La Golondrina Ranch, 1982

Species	Common name	Order	Diet
Didelphis albiventris	white-bellied opossum	Marsupial	omnivorous
Philander opossum	four-eyed possum	Marsupial	omnivorous
Dasypus novencinctus	9-banded armadillo	Edentates	insectivorous
Tamandua	anteater	Edentates	insectivorous
Cerdocyon thous	crabeating fox	Carnivora	carnivorous
Nasua nasua	coatimundi	Carnivora	omnivorous
Procyon cancrivorous	crabeating raccoon	Carnivora	omnivorous
Oryzymys chacoensis	arboreal rodent	Rodentia	omnivorous
Alouatta caraya	howler monkey	Primates	frugivorous/ folivorous
Aotus trivirgatus	night monkey	Primates	frugivorous

TABLE 27

Prey Species in Great Horned Owl Pellets, La Golondrina, Paraguay, 1982

Prey species	Common Name	Body Weight
Rodents		
Holochilus brasiliensis	Chaco marsh rat	800 grams
Orizymyz sp.	Forest mouse	200 grams
Marsupials		
Philander opossum	Four-eyed opossum	200 grams
Didelphis albiventris	White-bellied opossum	600 grams
Birds		
Jacana americana	Lily trotter	
Egretta sp.	Egret	
Aramides sp.	Grey-necked wood rail	
unidentified sp.		
Reptiles		
Crotalus durrissus	Rattlesnake	
Bothrops alternatus	Fer-de-lance	
Amphibians		
unidentified spp.	frogs	
Fish		
unidentified spp.	fish	
Invertebrates		
unidentified spp.	land snails	

Weight data are based on trapped and marked specimens.

TABLE 28

Ranging Patterns of *Aotus* at La Golondrina, Paraguay, 1982

Date	Moon Phase	Daily Range in meters	Nightly Range in meters	Total Range in meters
22 July	dark	100	300	400
23 July	dark	200	455	655
24 July	dark	180	550	730
25 July	full-10	250	450	700
29 July	full-6	80	350	430
30 July	full-5	250	425	675
31 July	full-5	300	450	750
1 August	full-3	280	120	400 (rain)
2 August	full-2	250	500	750
4 August	full	100	600	700
Average		199m	420m	619m

TABLE 29

Seasonal Feeding and Ranging Behavior of Four Monkey Species at Cocha Cashu

	*Cebus** *apella*	*Cebus** *albifrons*	*Callicebus* *moloch*	*Aotus* *trivirgatus*
Dry Season (June - August)				
Range (ha)	73	75	6	4
# trees fed in	50	19	11	6
Feeding min/day	45	111	118	187
Wet Season (October - December)				
Range (ha)	34	52	7	10
# trees fed in	225	190	27	22
Feeding min/day	115	86	168	178

*Data from Terborgh 1983.

TABLE 30

Comparisons Among *Callicebus moloch* and *Aotus trivirgatus* in Peru and *Aotus* in Paraguay

Variable		*C. moloch* Rain forest	*Aotus* Rain forest	*Aotus* Dry Forest
Diet in dry season or winter	Fruit	43%	52%	20%
	Leaves	40%	5%*	47%
	Nectar (Flowers)	2%	33%	21%
Size of Fruit Tree (Crown Diameter) Used (May-September)	0-10m	93%**	61%	99%
	11-20m	5%	34%	1%
	21-30m	2%	5%	0%
Group Size		2-5	2-5	2-4***
Territory size/ Group Range		6-10 ha	8-12 ha	5-8 ha
Activity Cycle		Strictly Diurnal	Strictly Nocturnal	Mainly Nocturnal With Daily Diurnality (1-3 hours/day activity)

*Estimates derived form scatological samples; all other data are percent of feeding minutes.

**Difference between *C. moloch* and *A. trivirgatus* in utlization of fruit trees: X= 59.61, p= 0.001, df= 2 (X^2 test performed on original frequency data rather than on percentage summaries.

***Rathbun (1980) observed groups of 3 and 4, however I observed only groups of 2.

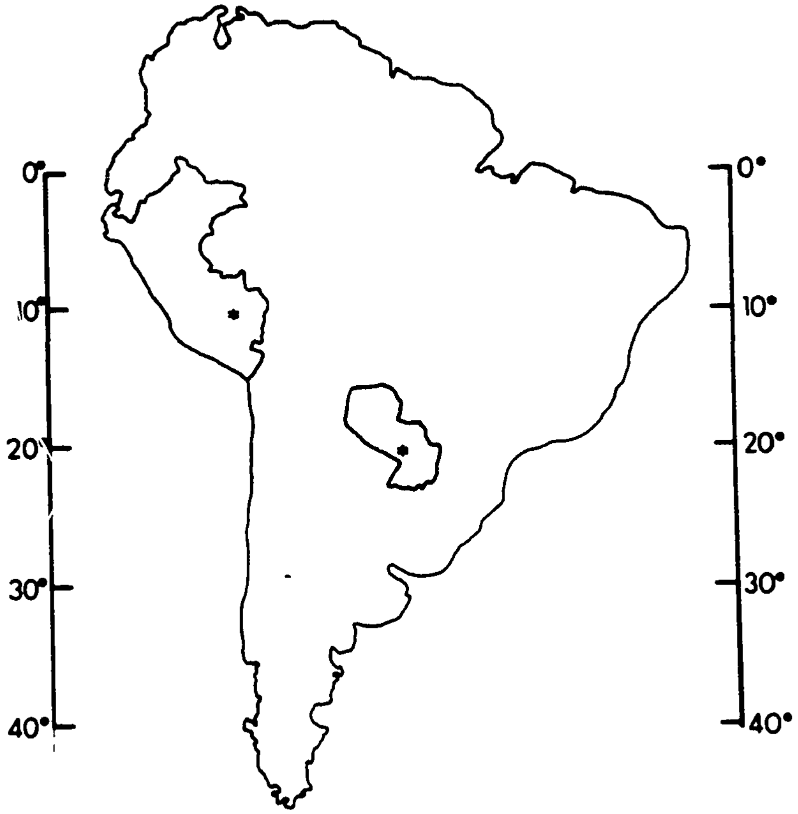


Fig. 1 Map of South America with the study sites marked by stars. Cocha Cashu Biological Research Station, Manu National Park, Madre de Dios, Peru and La Golondrina Ranch, Villa Hayes, Paraguay.

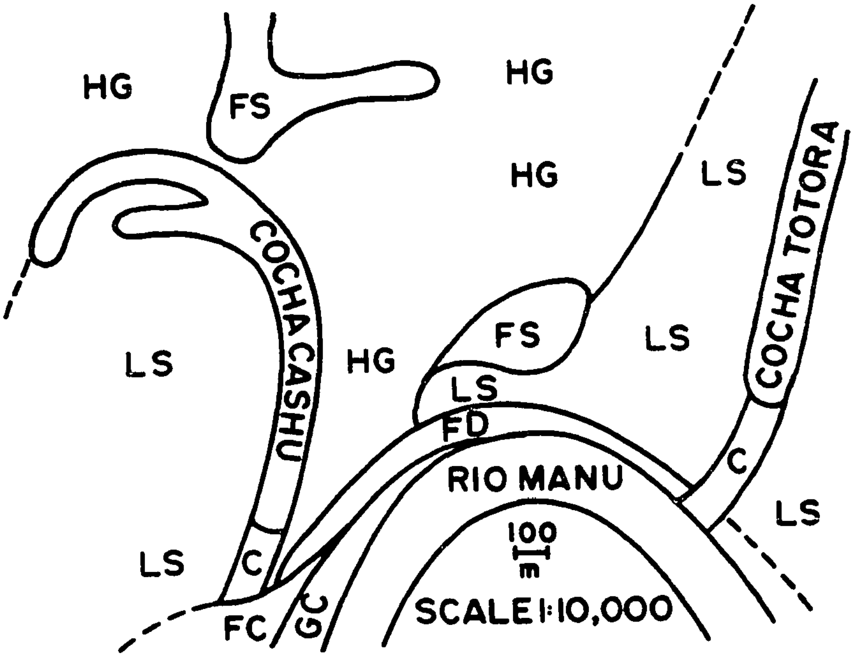
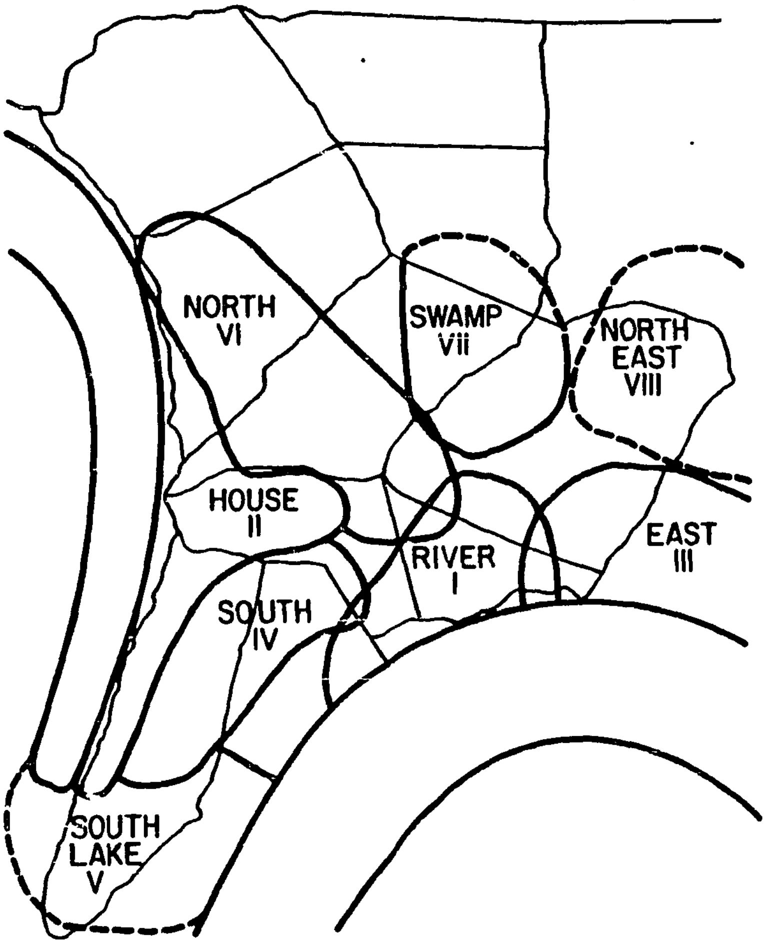


Fig. 2 Habitats at Cocha Cashu (MNP)
GC= riparian canebreaks of *Gynerium sagittum* ;with *Cecropia sp.*, C= late successional forests dominated by *Ficus insipida* and *Cedrela odorata*, FD= flooded forest, LS+ late successional forest subject to seasonal flooding, FS= fig swamp (*Ficus trigona*), HG= mature high ground forest.

(From: Terborgh 1983)



TERRITORIES OF AOTUS 1980-1981

Fig. 3 Map of Aotus territories at Cocha Cashu, Peru (MNP) 1980-1981. Perimeters of territories of Groups I - VI are outlined in black. There is 25-40 meters overlap between some groups (Groups I and III, IV and I, I and VI).

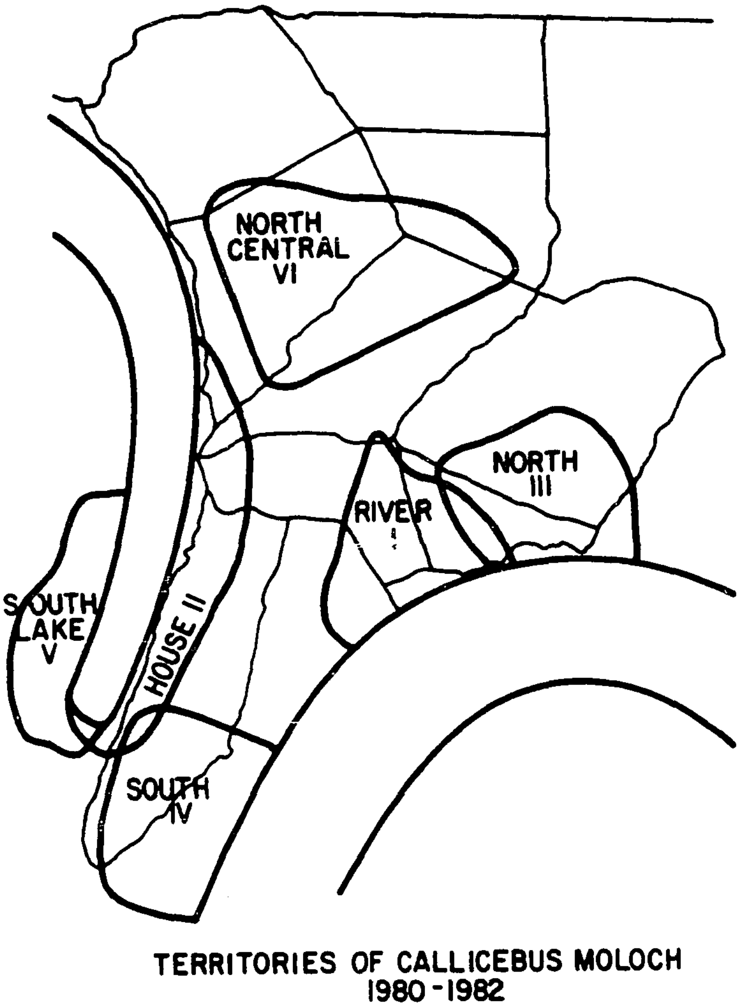


Fig. 4 Map of <u>Callicebus moloch</u> territories at Cocha Cashu, Peru (MNP) 1980-1982. Perimeters of territories of Groups I - VI are outlined in black. Notice that the only overlap of about 20-40 meters is between Groups II and V, I and III, and II and IV.

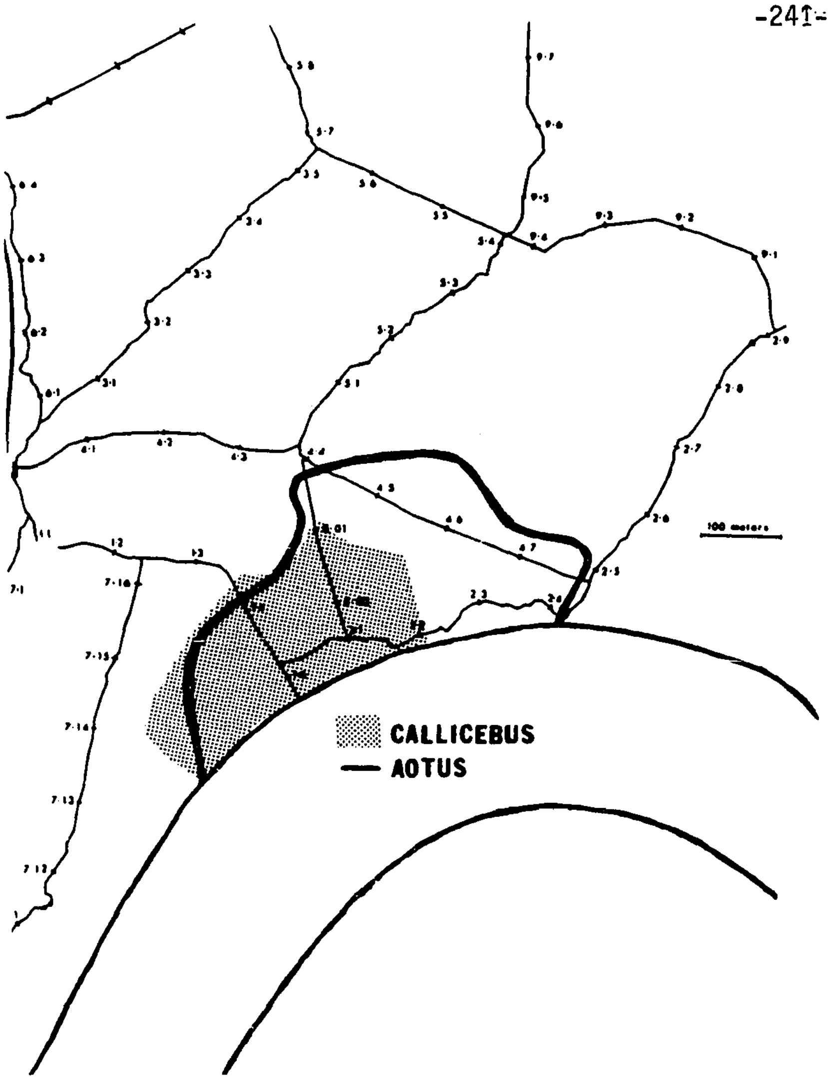


Fig. 5 Location of C. moloch and Aotus "River" groups at Cocha Cashu. C. moloch Group I's territory was smaller than that of Aotus Group I. Ranges determined from path lengths taken over a one-year period from September 1980-August 1981.

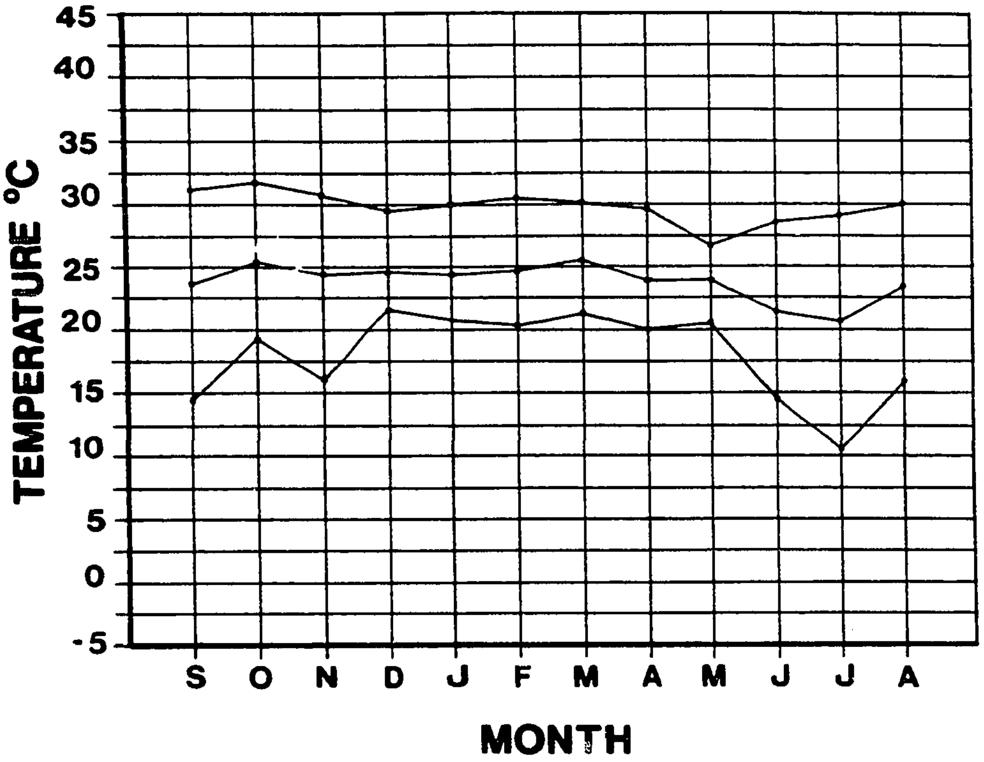


Fig. 6 Median monthly temperatures at Cocha Cashu (MNP), September 1980 - August, 1981: the three lines represent average monthly highs, lows, and averages. Highs and lows were recorded daily and monthly means calculated. Lowest temperatures were in July. Highest temperatures were in October.

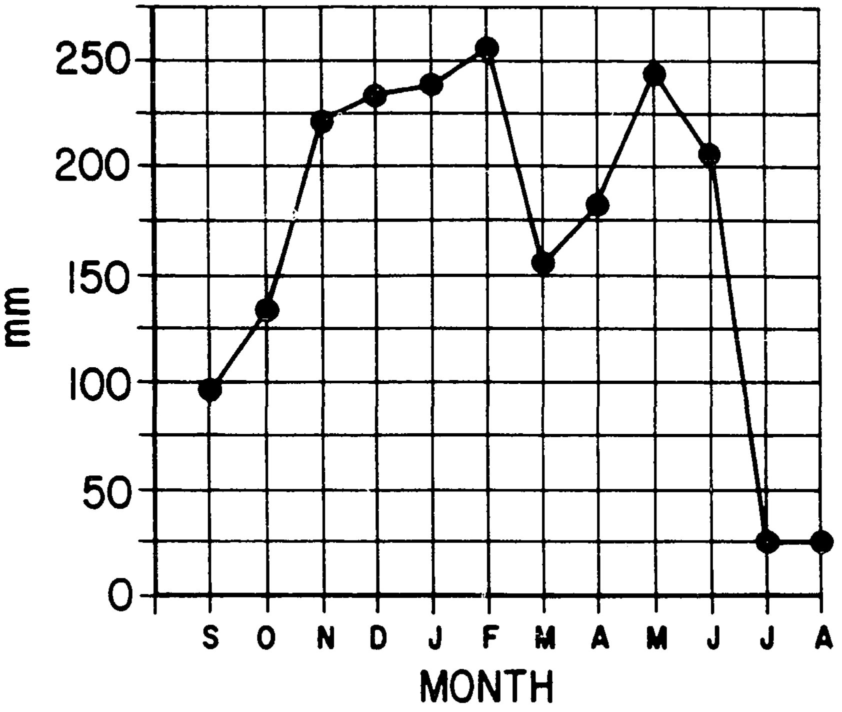


Fig. 7 Monthly precipitation at Cocha Cashu (MNP) 1980-1981. Rainfall was measured daily and summed for each month. The total rainfall for the year was 2000mm. The driest months were July, August, and September. The wettest month was February.

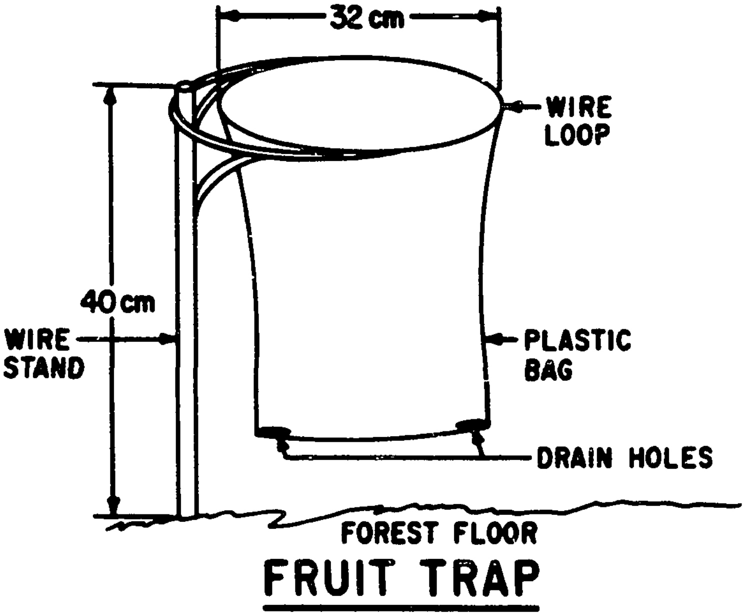


Fig. 8 Sketch of Fruit Trap. Traps were placed 25m apart in the forest at Cocha Cashu and 100m apart at La Golondrina. Light plastic bags were suspended from a meter-long wire hoop, providing a collecting area of $0.08m^2$. A total of 100 traps were set at Cocha Cashu and 40 at La Golondrina.

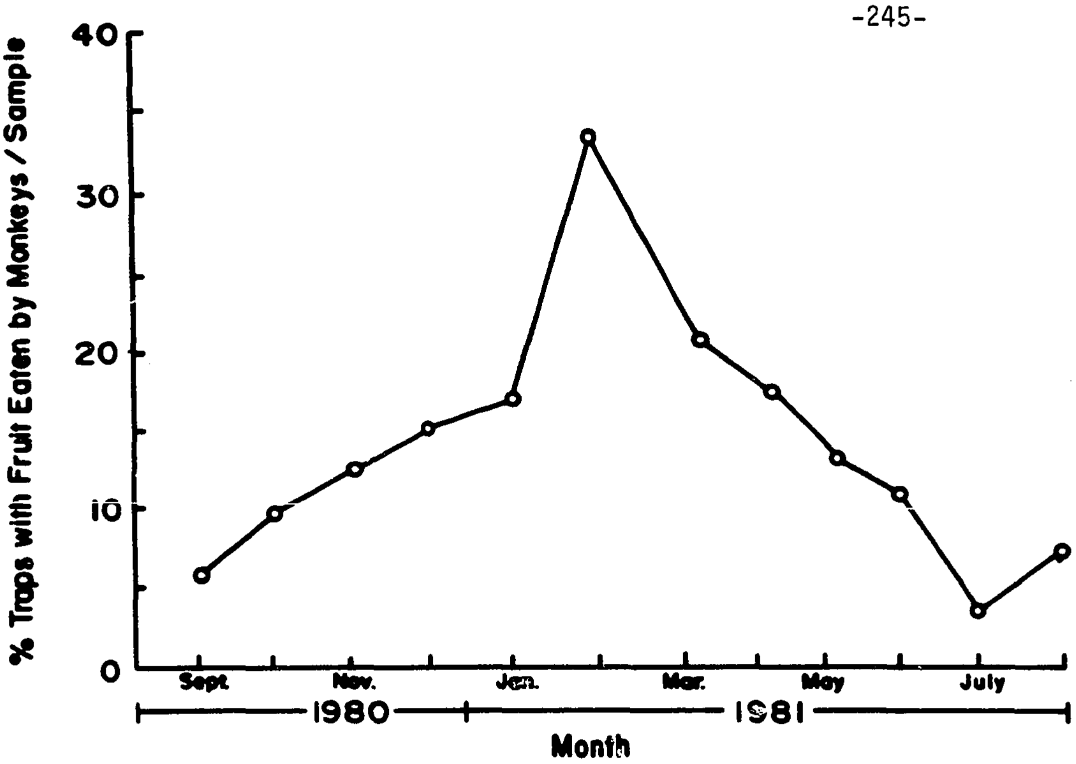


Fig. 9 Results from 100 fruit traps at Cocha Cashu(MNP), September, 1980 - August, 1981. Fruit fall was collected twice monthly and averaged for each month. Percentage of traps with fruit eaten by Aotus and/or Callicebus each month is shown.

(Data from C. Janson)

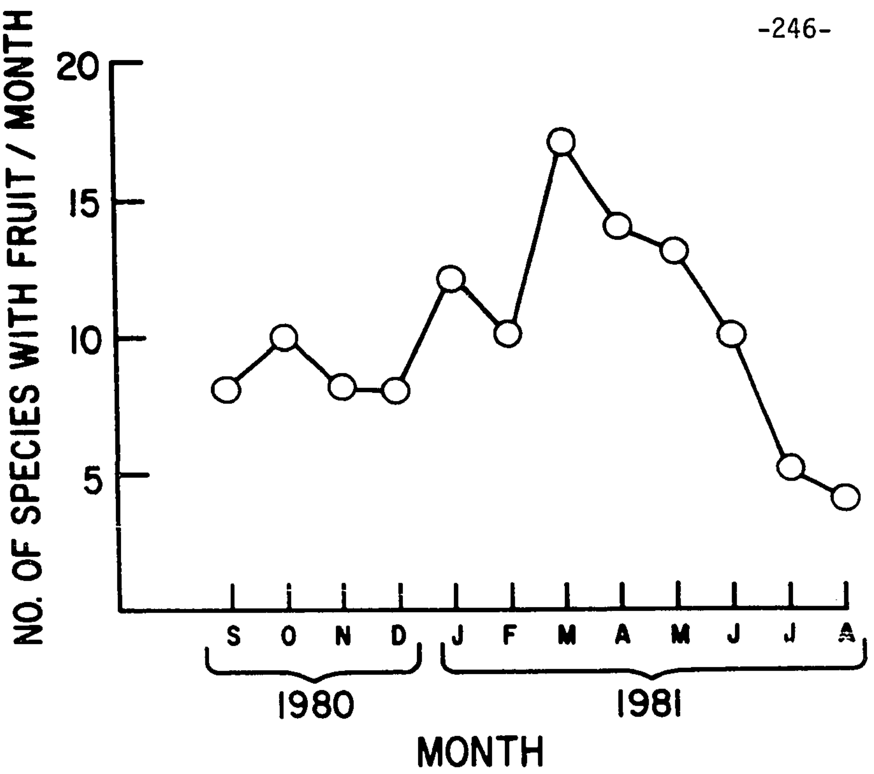


Fig. 10 Monthly fruiting of tree species from September, 1980 - August, 1981 at Cocha Cashu, (MNP). Fifty-one species represented by 1-4 individuals each were censused for a total of 175 trees. Each species was scored for each month is was observed with fruit. See Appendix I for species names and number of individual trees censused.

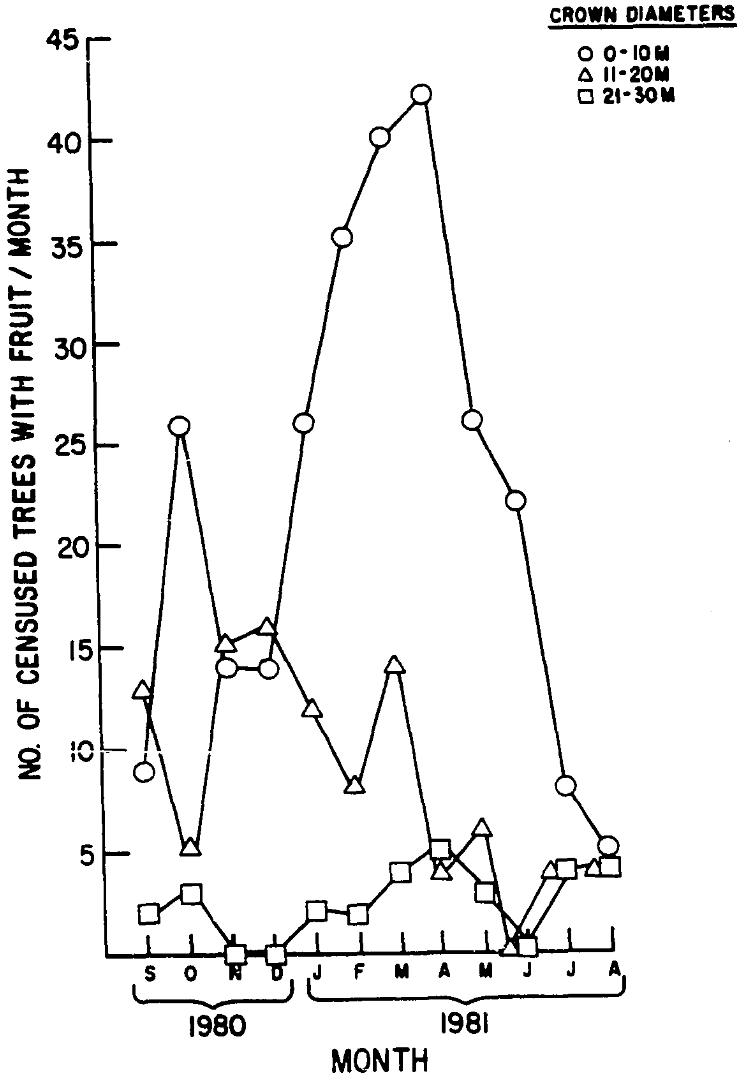


Fig. 11 Fruiting data and crown diameters of censused trees from September, 1980 - August, 1981 at Cocha Cashu, (MNP). Fifty-one species represented by 175 trees were censused for fruit and the crown diameter of each tree was measured. Number of individuals in each crown diameter category are arranged according to months in fruit.

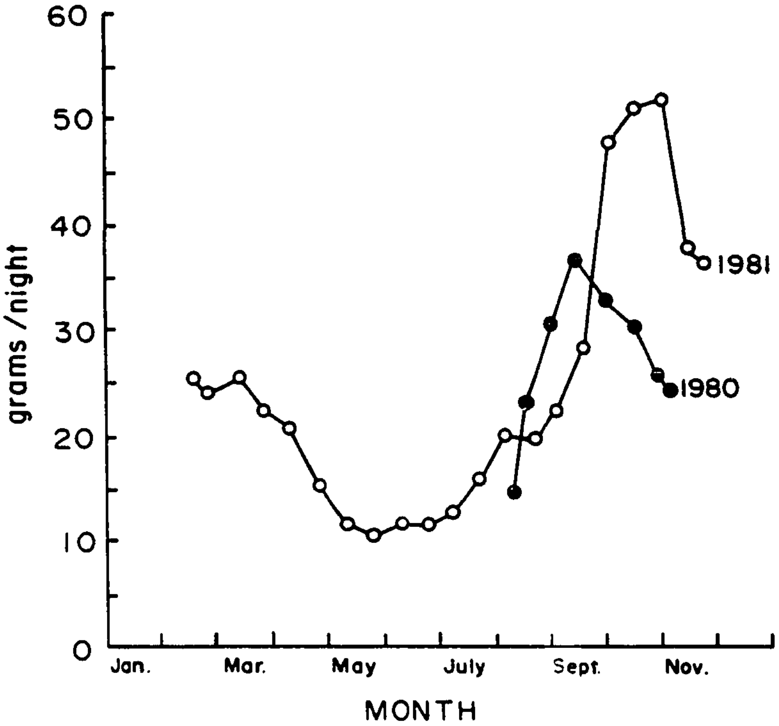


Fig. 12 Insect/Arthropod Abundance - Night Light Technique, Cocha Cashu. Invertebrates were collected bimonthly (seven days before and seven days after the full moon) in a fluorescent light trap. Weights of yield were averaged for each month. Traps were collected for 18 continuous months. Months of April - July were months of insect/arthropod scarcity, while yields of September - November were six times greater than the months of scarcity. (Data of Janson).

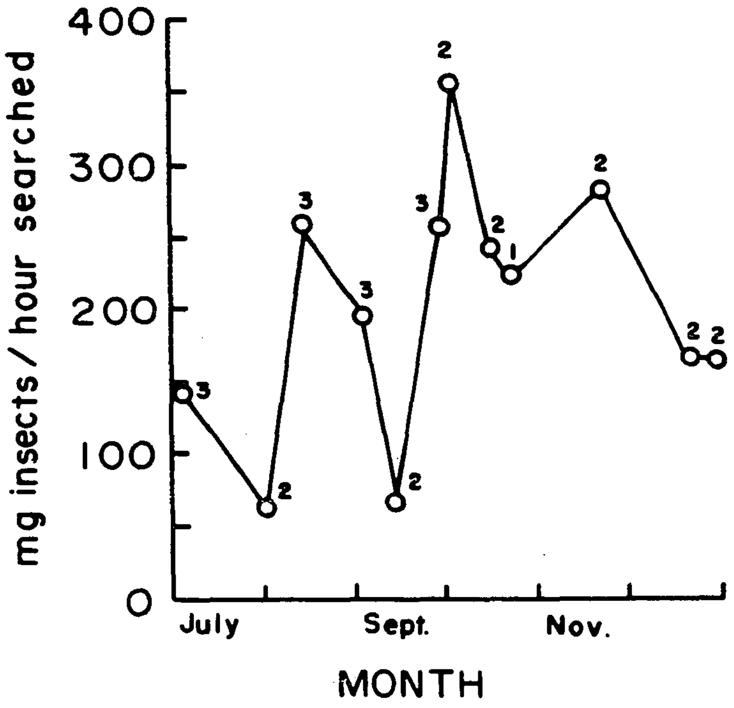


Fig. 13 Insect/Arthropod Abundance - Direct Search Technique, Cocha Cashu. Variation in arthopod biomass over a six-month period in 1981 as determined by the direct search method. Insects were collected on 12 days with 1-3 hour continuous searches on each of these days. Numbers over points indicate the number of hours of searching represented by the respective samples.
(Data of Brecht and Munn)

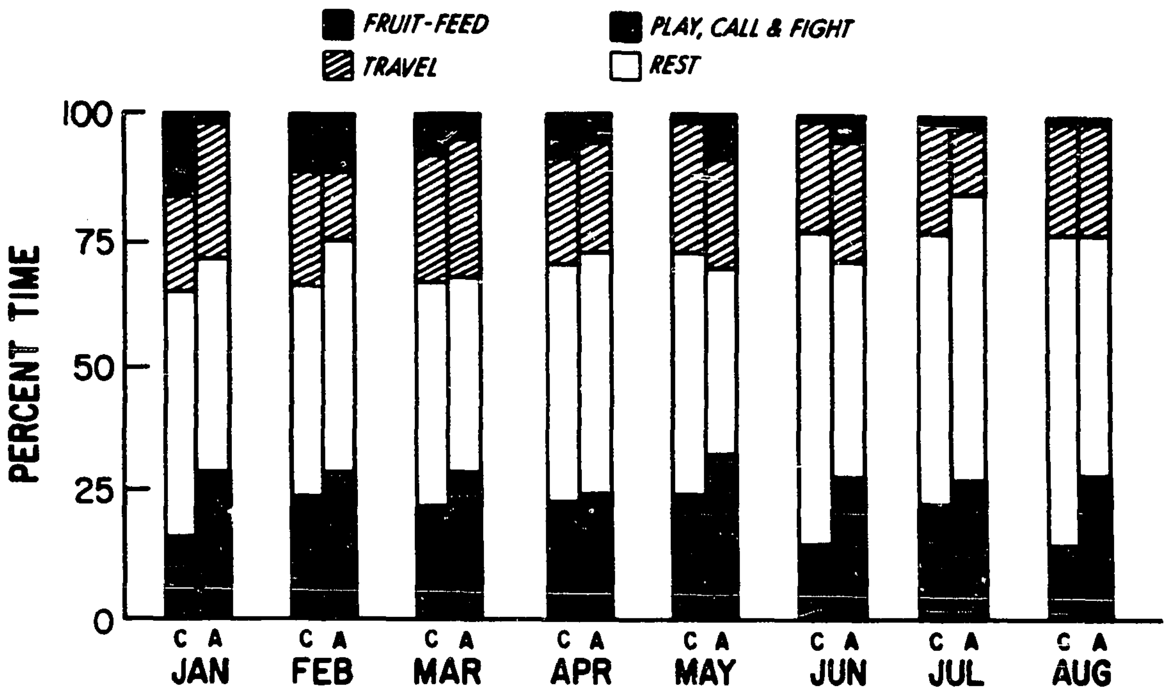


Fig. 14 Activity Budgets of <u>Aotus</u> and <u>Callicebus moloch</u>, Cocha Cashu (MNP). Data were taken from 12 hour, 5 day samples each month from January - August, 1981 for <u>C. moloch</u> Group II (C) and <u>Aotus</u> Group I (A). Percentages of total minutes were calculated for the activities: fruit-feed, travel, rest, and social behavior (including play, call, and fight). Other activities such as grooming, insect-foraging, and leaf-eating, were not included because these activities were difficult to observe in <u>Aotus</u> and were subsumed in both species in the category 'rest'.

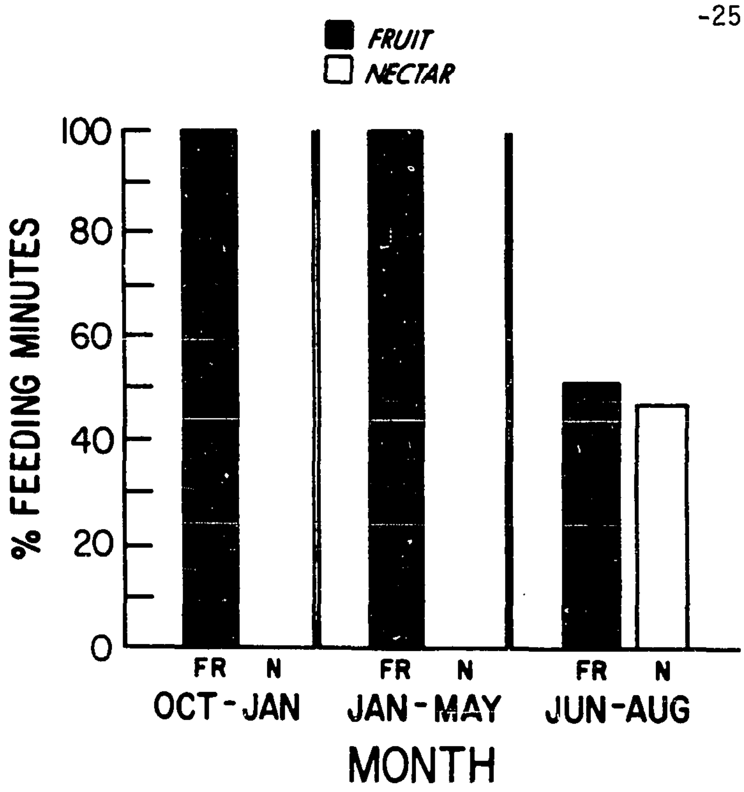


Fig. 15 Aotus diet in Peru (fruit and nectar). Data from Group I, October, 1980 - August, 1981. Insect-foraging and leaf-eating are represented in Figure 16.

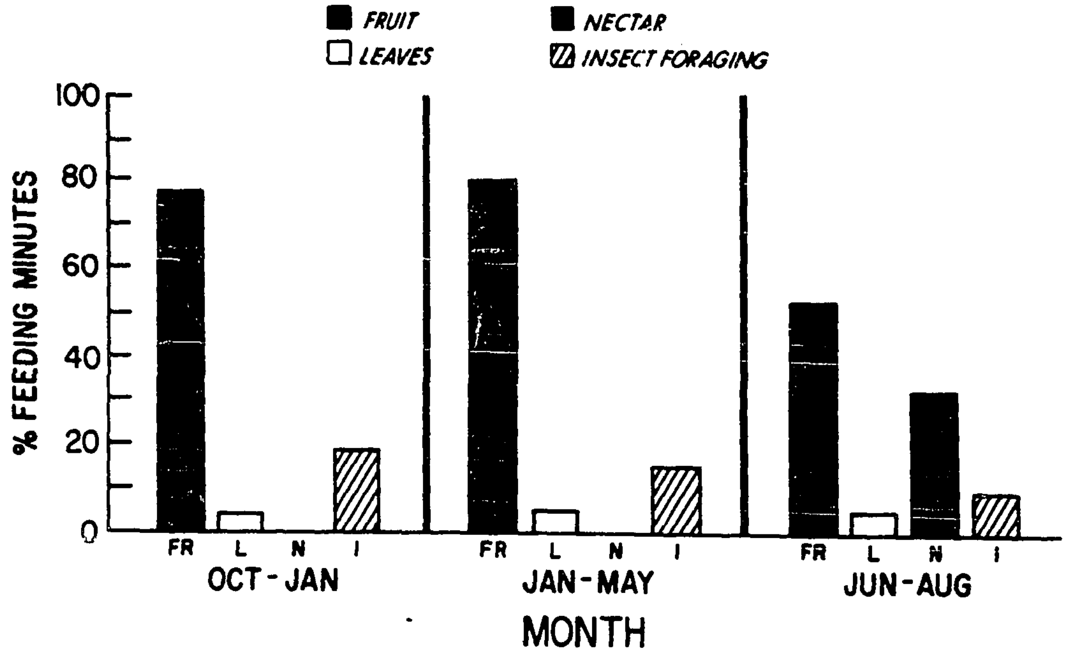


Fig. 16 Diet of Aotus in Peru, October, 1980 - August, 1981, including estimates of insect-foraging and leaf-eating which are based on analyses of feces collected.

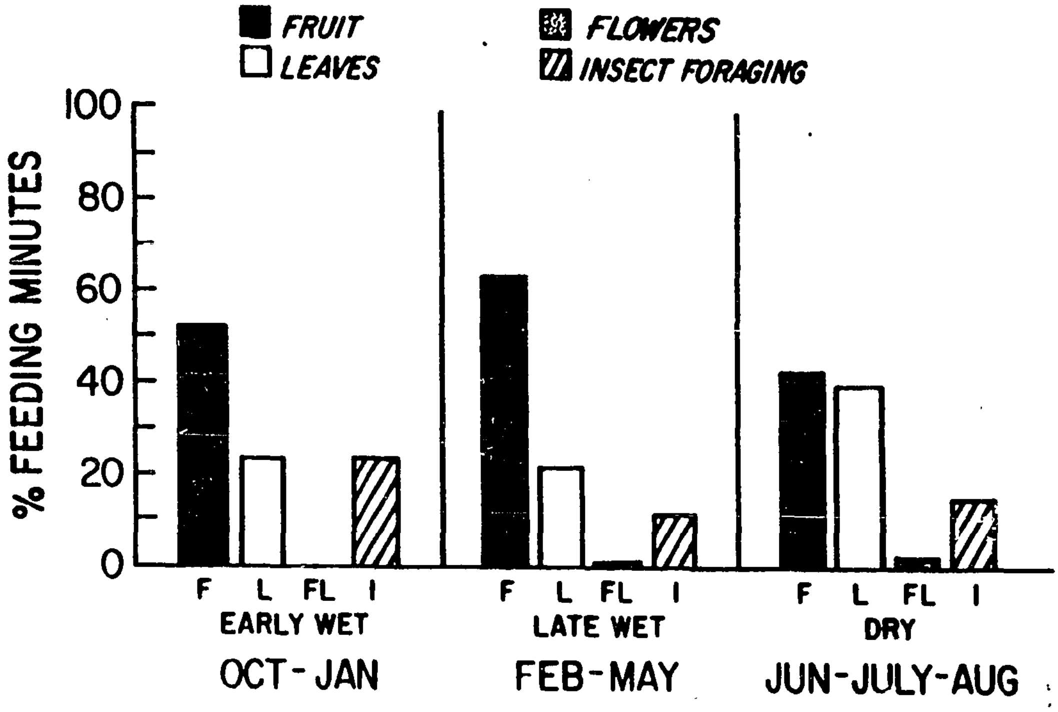


Fig. 17 Diet of Callicebus moloch in Peru, October, 1980-August, 1981. Data are from Group II. Note that leaf-eating increases during June-August.

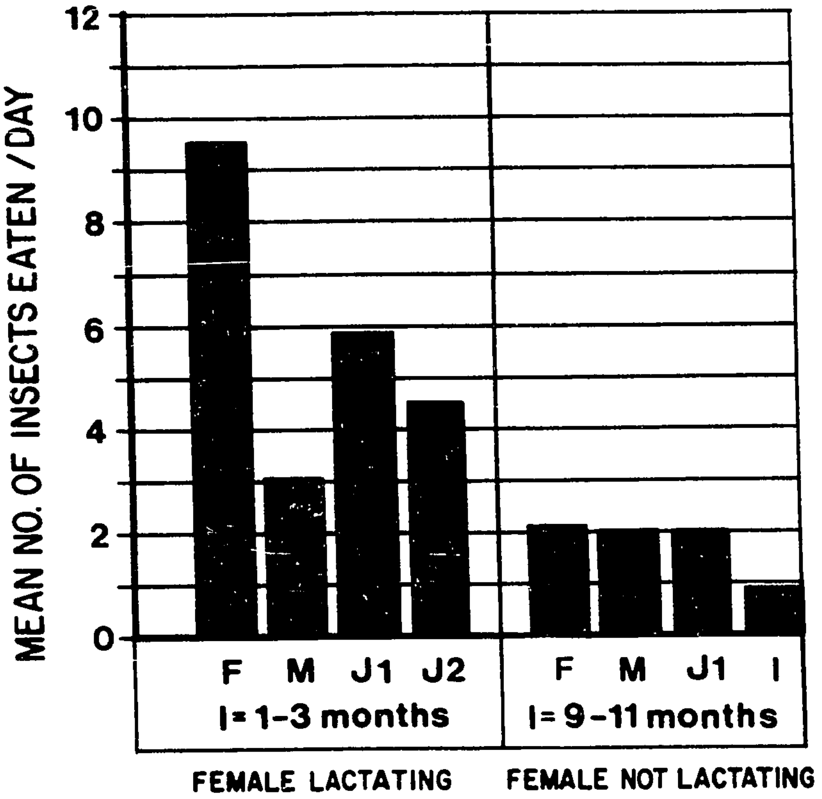


Fig. 18 Insect-foraging success by *C. moloch* at Cocha Cashu (MNP). F=adult female; M=adult male; J_1=subadult (2 years old); J_2=yearling; I=infant under one year of age. Note that when the female is lactating she eats three times the number of insects as the male (who is carrying the infant). The size of the insects caught by the female at this time of year is also larger (see text). At other times of year, when the female is not lactating and the male is not carrying the infant, insect-foraging success among group members is not significantly different. Data are from observations of Group II (22 days when the infant was 1-3 months of age, 22 days when the infant was 9-11 months of age).

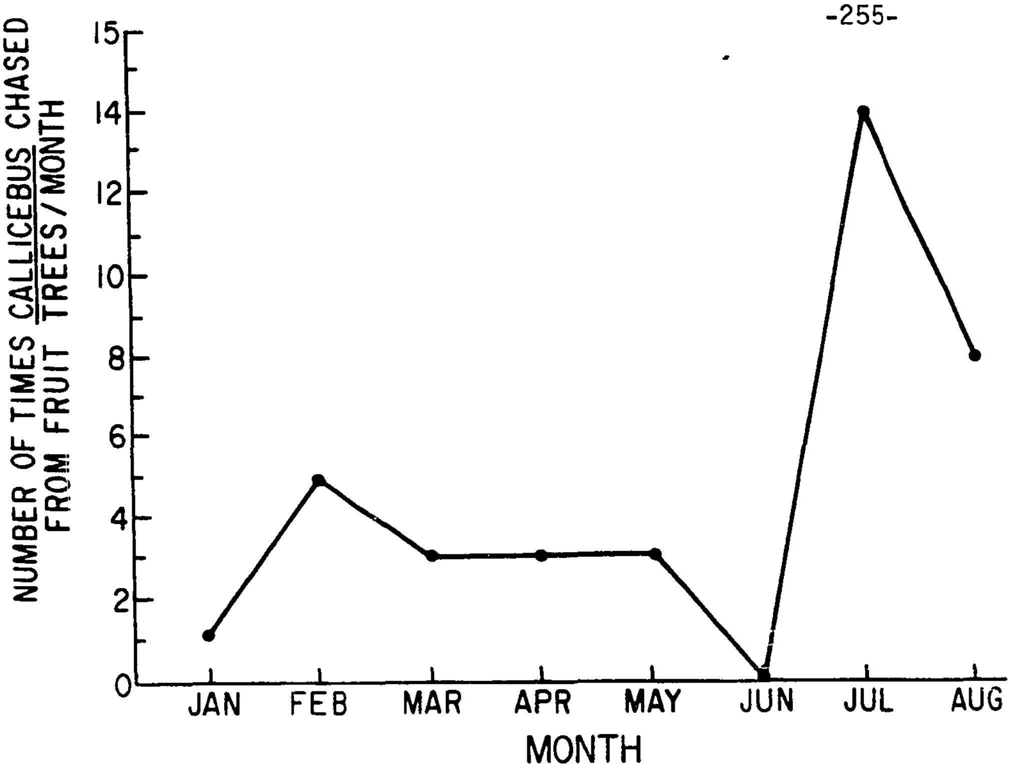


Fig. 19 Frequency of *C. moloch* displacement from fruit trees at Cocha Cashu (MNP). Data from Group II from January - August, 1981. *C* . *moloch* was chased by *Cebus albifrons* (27%), by *Cebus apella* (54%), and by *Ateles paniscus*(19%). In June, no large-crowned trees in the territory had ripe fruit, while in July a *Ficus* with a 35m crown diameter had abundant fruit.

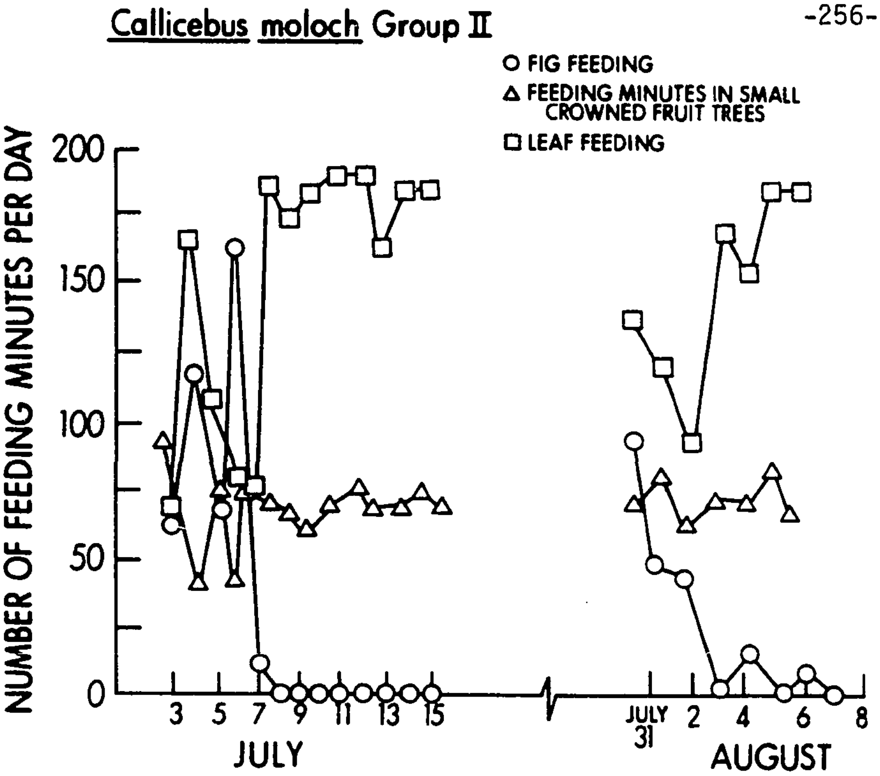


Fig. 20 Feeding by C. moloch Group II in July and August, 1981. Note that fig feeding is eliminated from July 8 through July 15. This C. moloch group was chased from a fig tree by other monkey species during these days (see Fig. 18). Leaf-eating increases at this time. Fruit-eating remains constant. In August, fig fruits in this territory are overripe and no longer edible. During the period from July 16 through July 31, the C. moloch group was not followed.

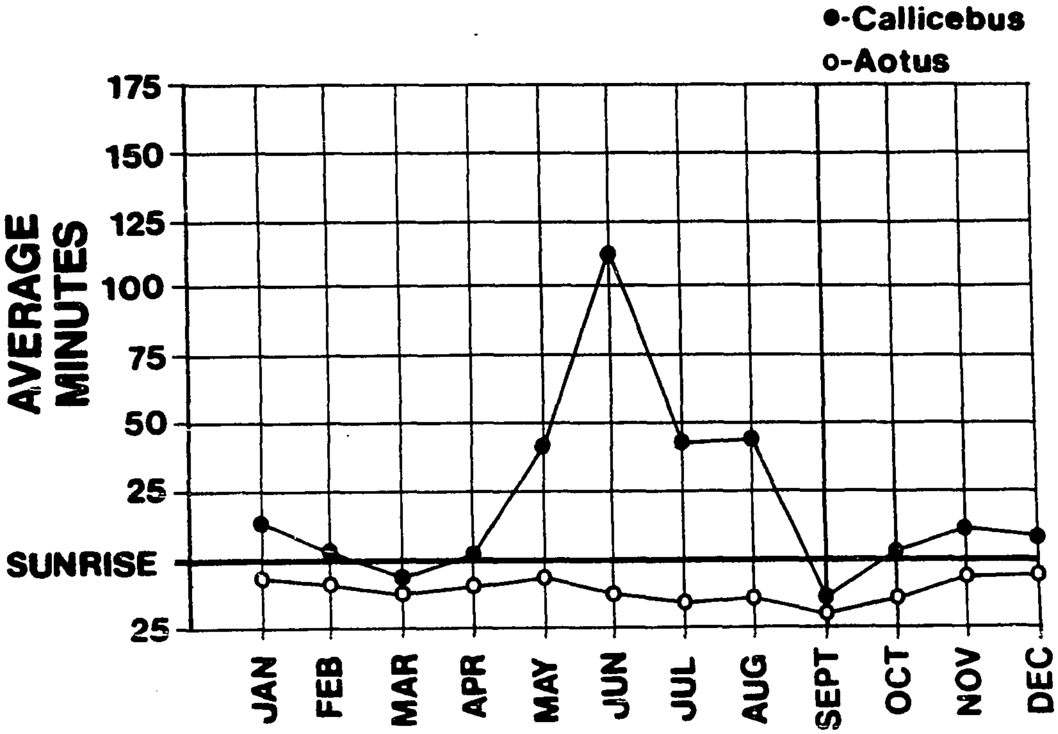


Fig. 21 Mean monthly times of entrance into and exit from sleeping trees for Aotus and C. moloch from September, 1980 - August, 1981. Data are from six days each month of Callicebus Group II from January - August, 1981, five days each month for Callicebus Group I from September - December, 1980, and 10-15 days each month for Aotus group I from September, 1980 - August, 1981. Exit time was determined by the first monkey out of the sleeping tree; entrance time was determined by the last monkey into the sleeping tree.

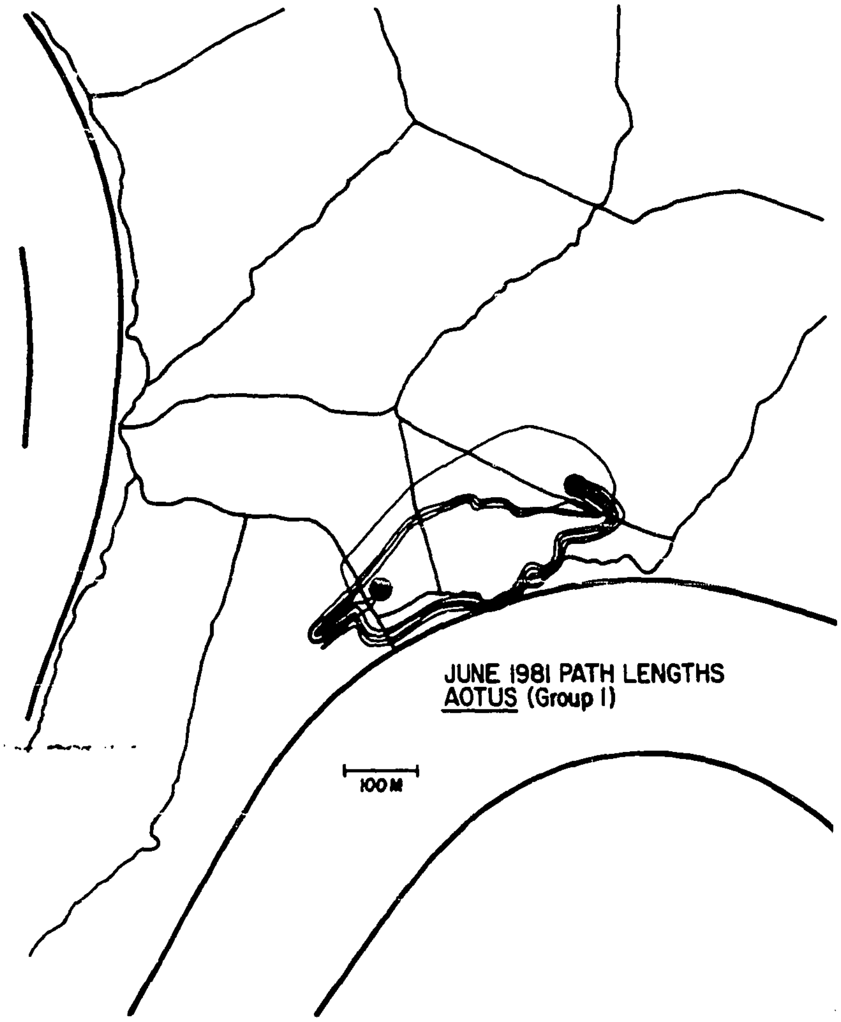


Fig. 22 Nightly paths of _Aotus_ Group I during a five-day sample in June, 1981, Cocha Cashu (MNP). Solid circles represent the only sleeping trees used during the sample. Note the habitual use of certain paths night after night, but use of different path one out of the five nights.

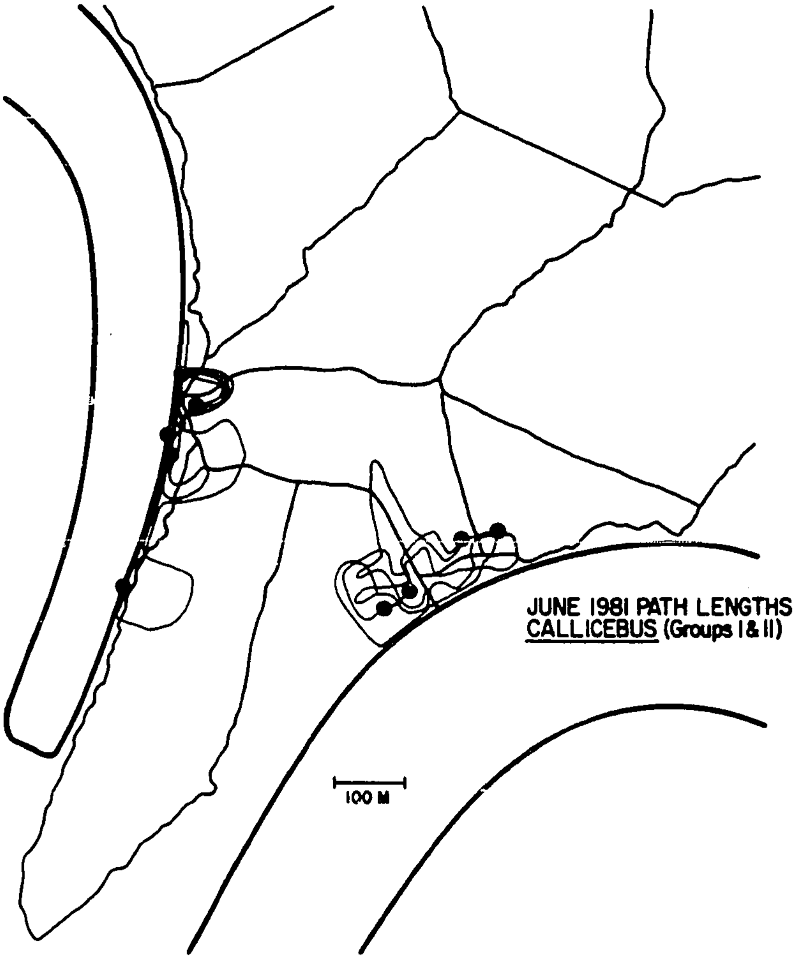


Fig. 23 Paths of C. moloch Groups I and II. Each group was followed from dawn to dusk for five consecutive days. June was a month of fruit scarcity and only a few scattered fruits were available in each territory. Solid dots represent all the sleeping trees used in the sample. Average path length of Group II was 443m.

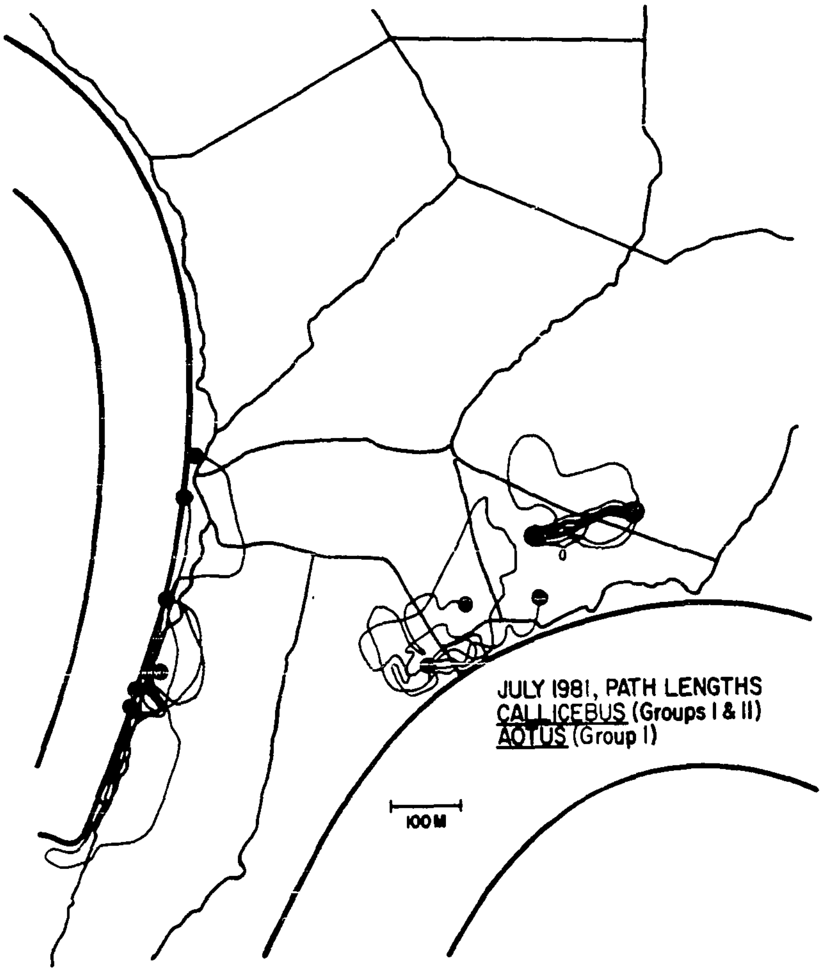


Fig. 24 Nightly (daily) paths of <u>Aotus</u> Group I, <u>Callicebus</u> Groups I and II. Each group was sampled for five days from dawn to dusk or dusk to dawn during July. Note that the paths of <u>Aotus</u> Group I did not overlap with <u>Callicebus</u> Group I during July. Large-crowned fruit trees were located in the territory, but only <u>Aotus</u> fed in them. <u>C. moloch</u> foraged in a different part of the territory for scattered fruits, insects, and leaves. <u>Aotus</u> Group I path lengths are to the right of the figure.

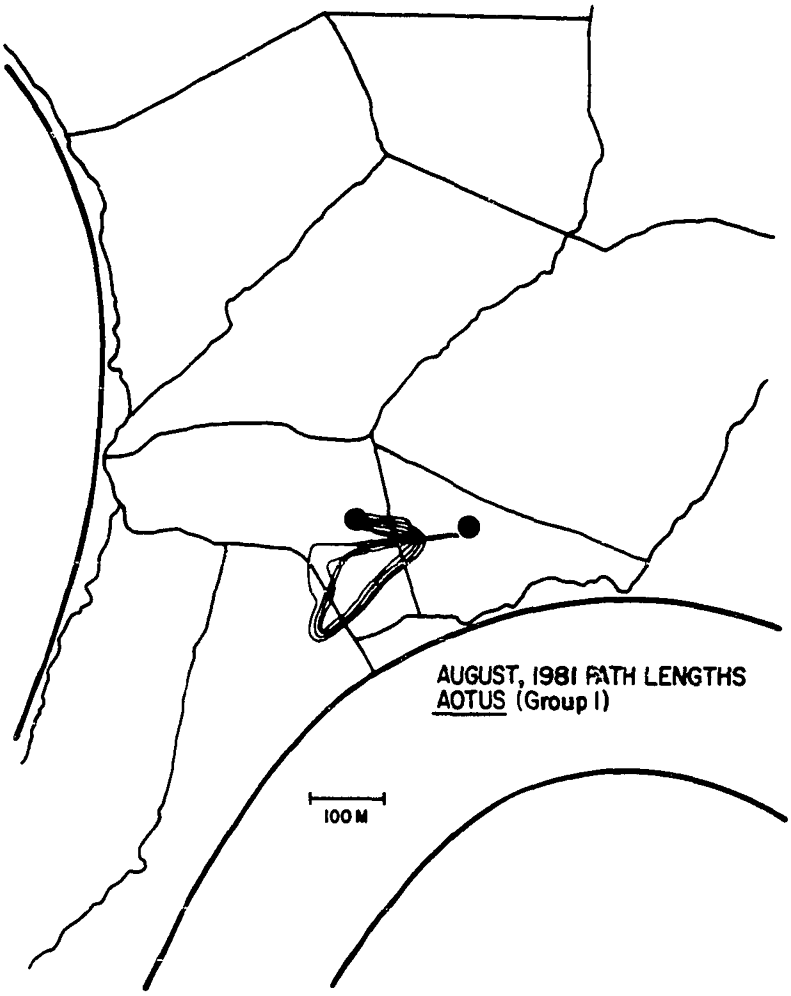


Fig. 25 Path of _Aotus_ Group I during a five-day sample in August, 1981. Only two large resources were available in the territory during August, a _Ficus_ tree and a _Quararibea_ tree in flower (nectar resource). Solid circles represent the only sleeping trees used during the sample. Note habitual pathways. Average path length of _Aotus_ Group I in August was 560m.

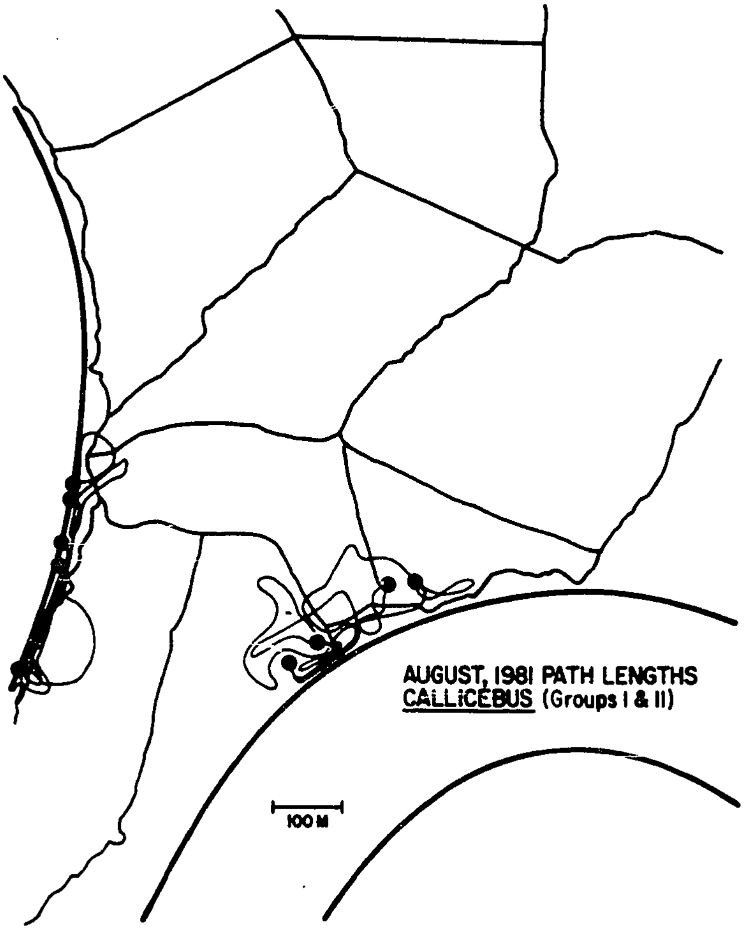


Fig. 26 Paths of C. moloch Groups I and II. Each group was followed from dawn to dusk for five consecutive days in August, 1981. The solid circles represent all the sleeping trees used during the sample. The average path length for Group II was 574m.

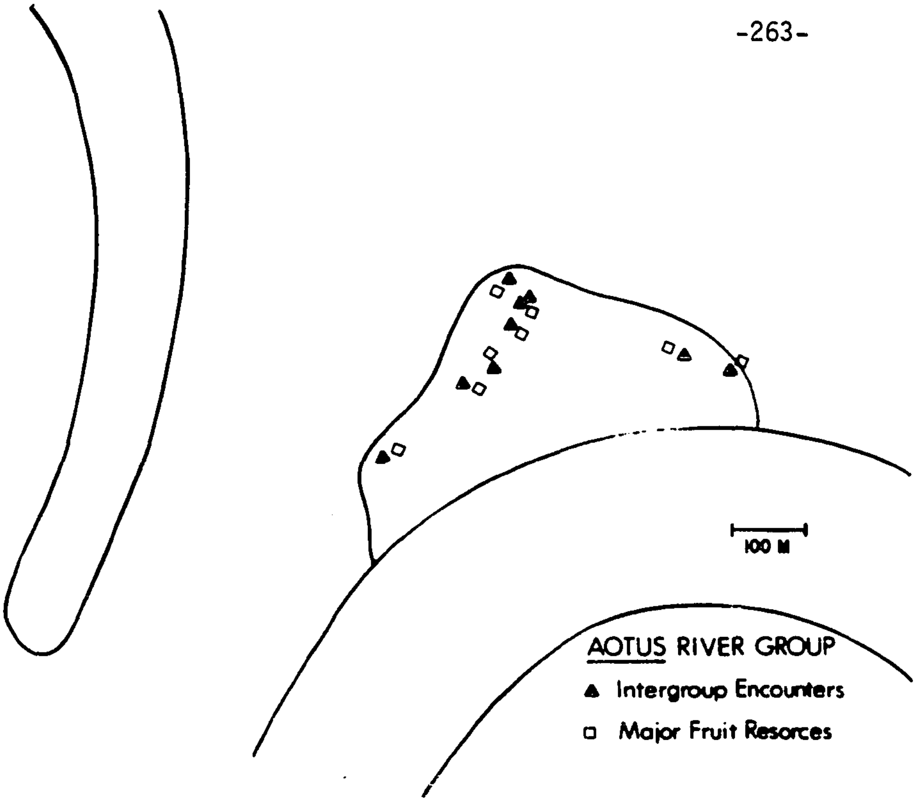


Fig. 27 Location of intergroup encounters by Aotus Group I (Cocha Cashu) and the proximity to large-crowned trees with ripe fruit. All aggressive interactions between groups from September, 1980 - August, 1981 have been mapped (N=9). Additional fights were observed between other groups.

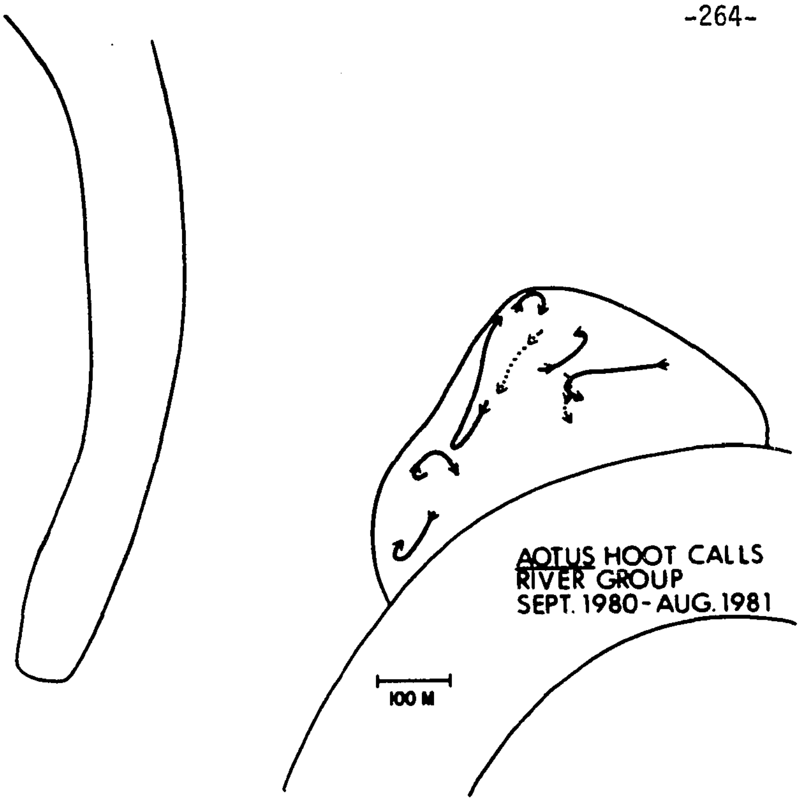


Fig. 28 Location of long-distance hoots by Aotus Group I Cocha Cashu (MNP), September, 1980 - August, 1981. Each arrow represents a calling monkey which traveled while it called for a one to three-hour period. Each arrow represents a different month.

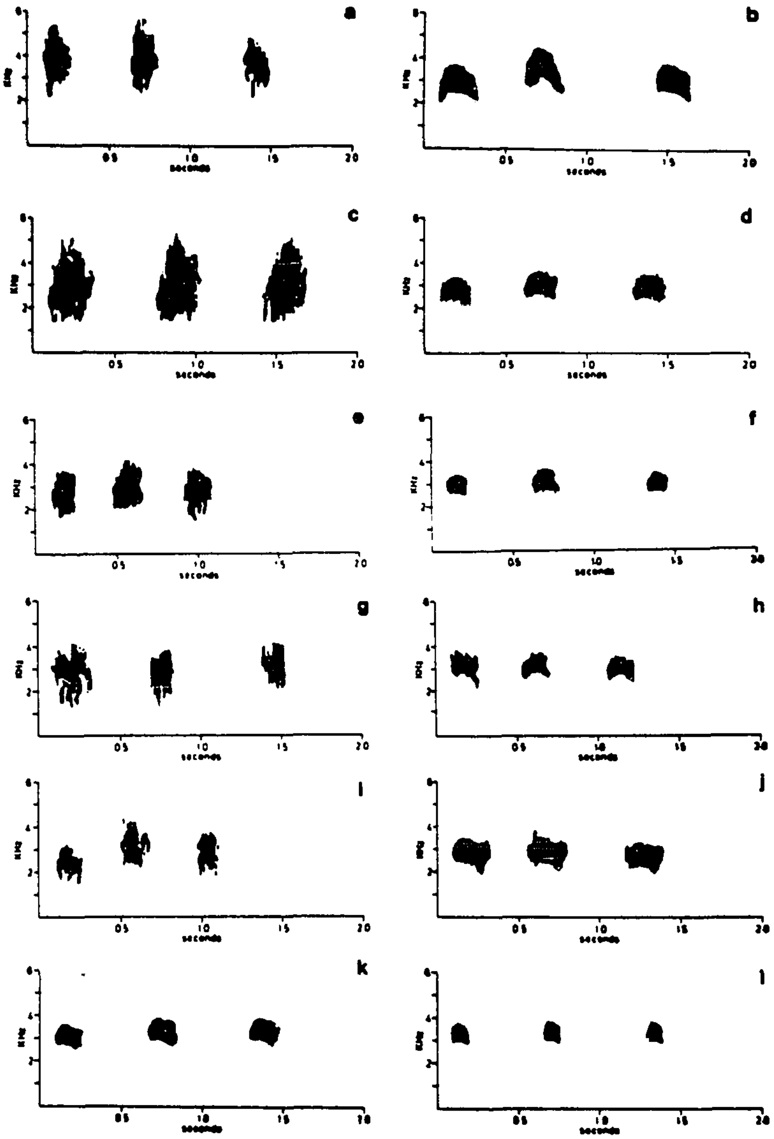


Fig. 29a Sonograms of hoots from 12 different groups of *Aotus*. A and B are from La Golondrina Ranch, Paraguay, C is an individual that traveled through many territories at Cocha Cashu, Peru, D is animal which called at Quebrada Romero 30 km from Cocha Cashu, and E through L are from calls produced by night monkey study group members at Cocha Cashu, Peru. Note that the structure of the first column has more spectral splatter (gruff bark) than the second column which are more pure tones.

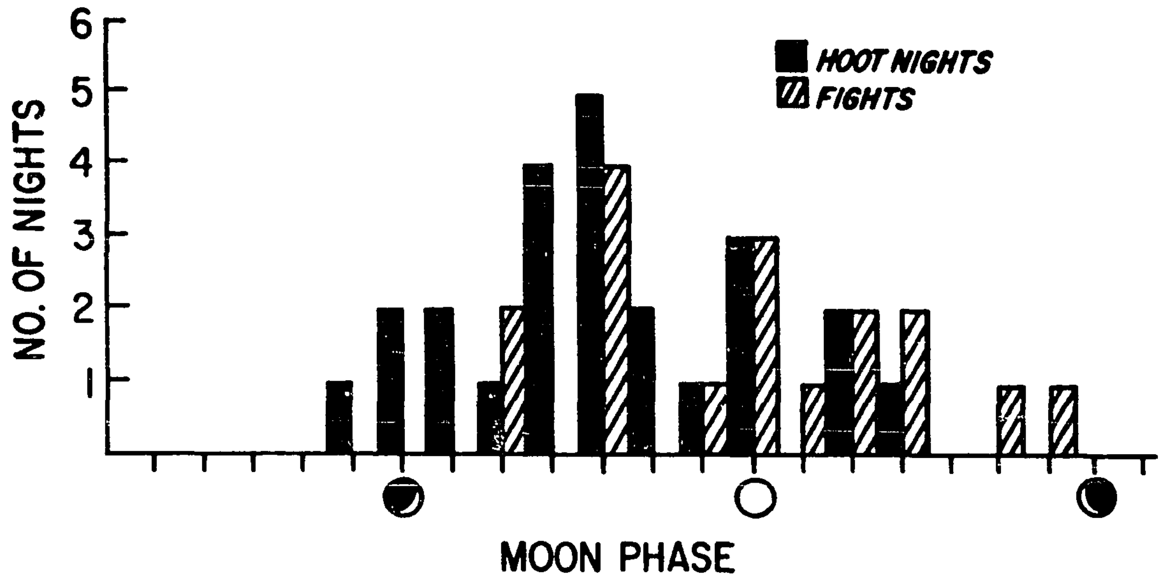


Fig. 29b Timing of nightly hooting and fighting in relation to phase of the moon (<u>Aotus</u> Group I). Composite data for an 11 month period from September, 1980- August, 1981.

The long-distance hoot calls occur predominantly during the second week of the lunar month. Agonistic encounters between groups take place around the time of the full moon being directly overhead. Because of the moon has to be directly overhead for optimum visibility, fights occurring later in the month take place later at night when the angle of the moon provides more light.

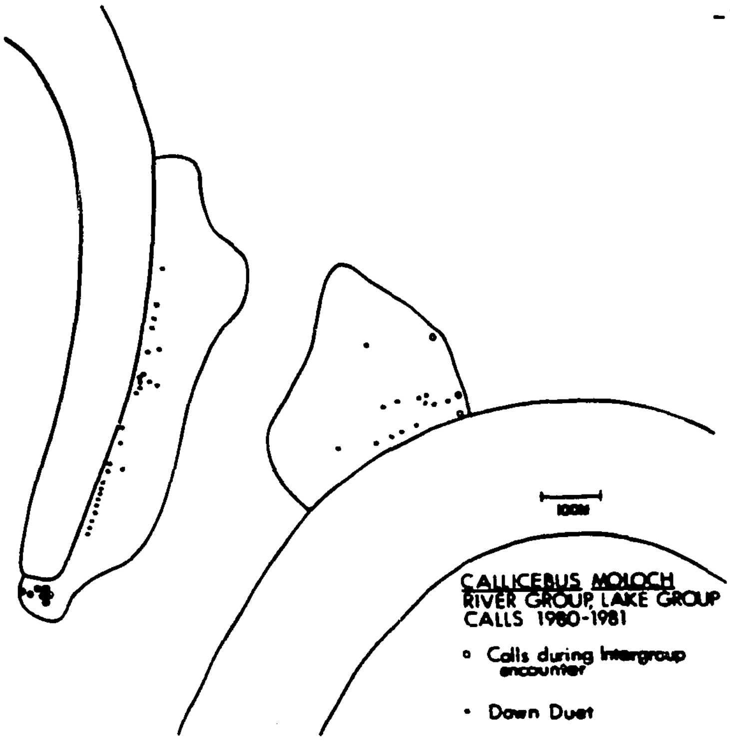
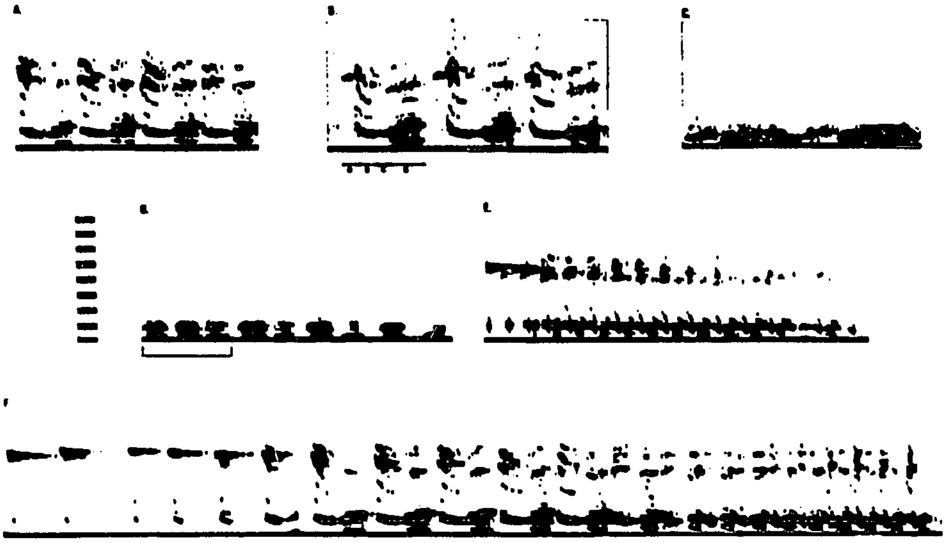


Fig. 30 Location of calls and intergroup fights by _C. moloch_ Groups I and II from September, 1980 - August, 1981. Fights with neighboring groups occurred only when a border tree had ripe fruit. Note that dawn calls did not occur at borders and appeared to be given more frequently at lake or river edges.



Spectrograms of *Callicebus moloch* vocalizations analyzed with the broad-band filter (effective resolution, 300 Hz). A, Pants. B, Bellows (a, pre-introduction; b, introduction; c, pause; d, climax). C, Moans. D, Honks. E, Chirrup-pumping (CP) sequence. F, Chirrup-panting-pumping (CKP) sequence. Frequency scale indicates kHz; time scale is 0.5 s

Fig. 31 Callicebus moloch ornatus dawn call sonogram (Robinson 1979).

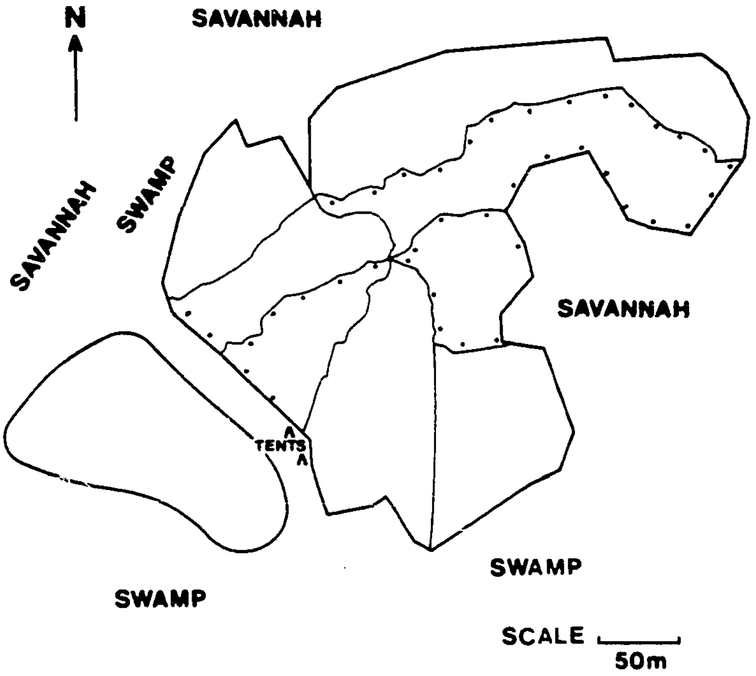


Fig. 32 Map of the study site at La Golondrina Ranch, Paraguay. Habitat island subtropical forests lie within the boundries of the closed lines. Lines within the foest represent trails and the dots along the trails are fruit traps. The space between the two forest areas is an old dirt road, but tree crowns above the road provide continuous arboreal pathways between the two areas.

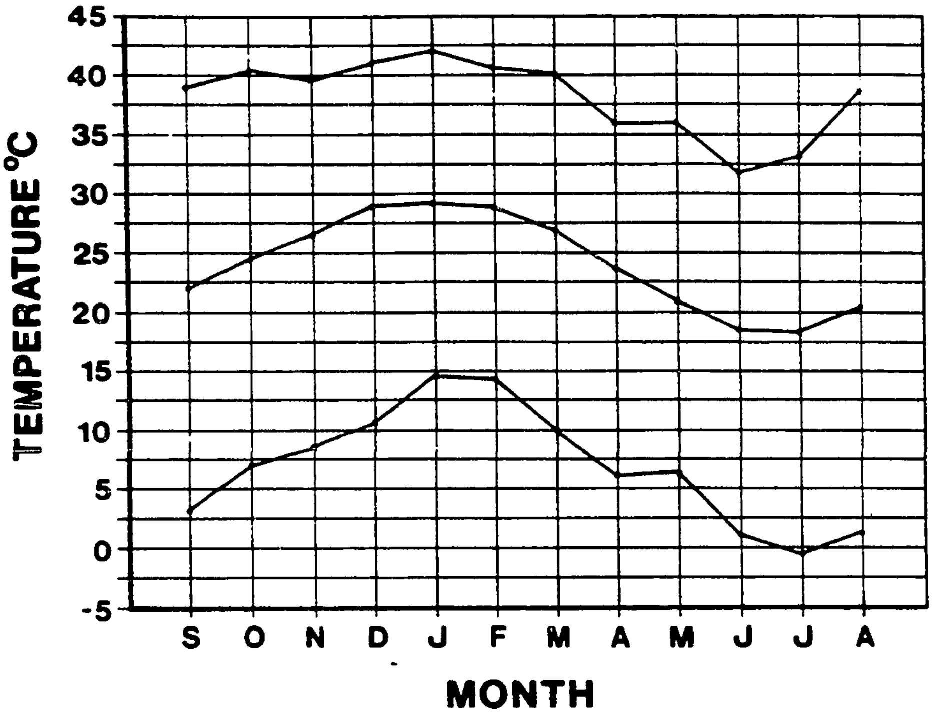


Fig. 33 Mean high, low, and average monthly temperatures for Asuncion, Paraguay for each month. Means are based on 40 years of data taken from the Parguayan Geological Department.

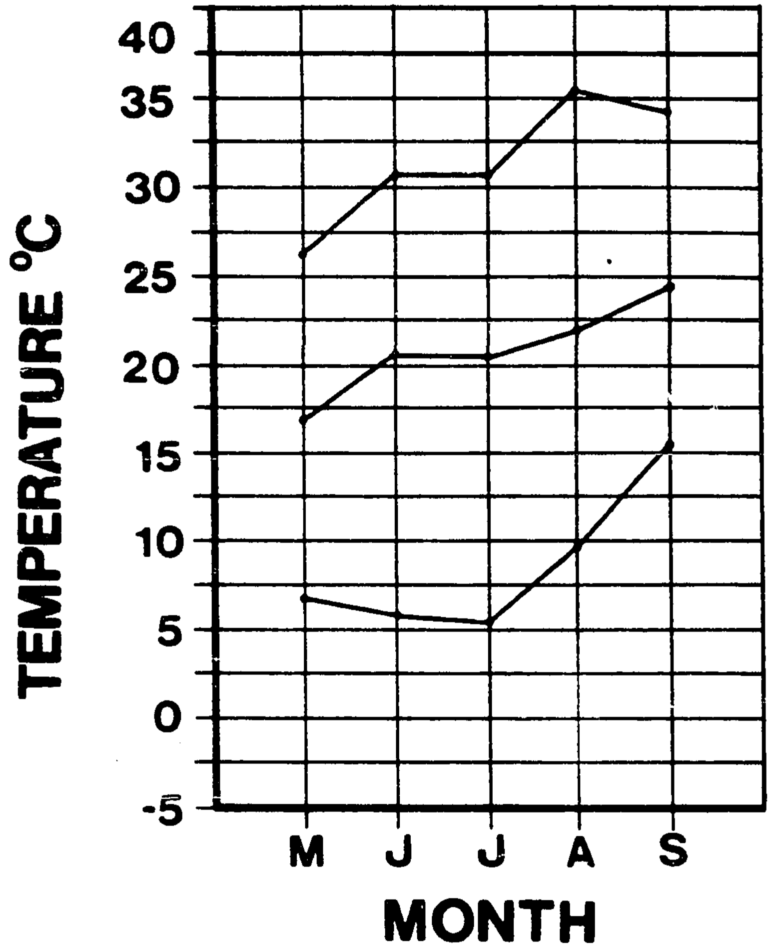


Fig. 34 Mean monthly high, average, and low temperatures for five months at La Golondrina Ranch, Paraguay (May - September, 1982).

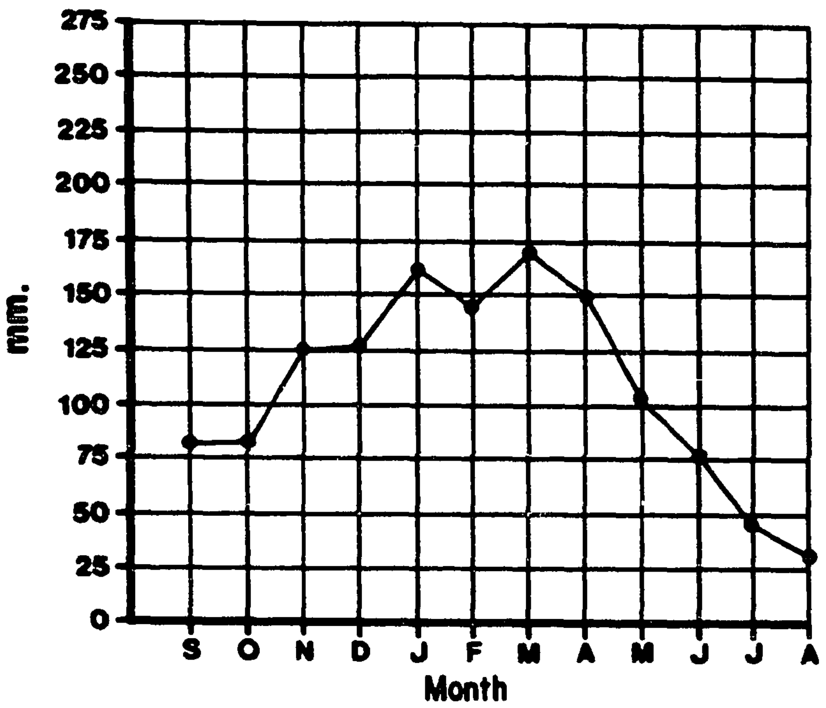


Fig. 35 Mean monthly precipitation in Asuncion, Paraguay; based on 40 years of data compiled by the Paraguayan Geological Department. Total average annual rainfall was 1300mm. The driest months were July and August.

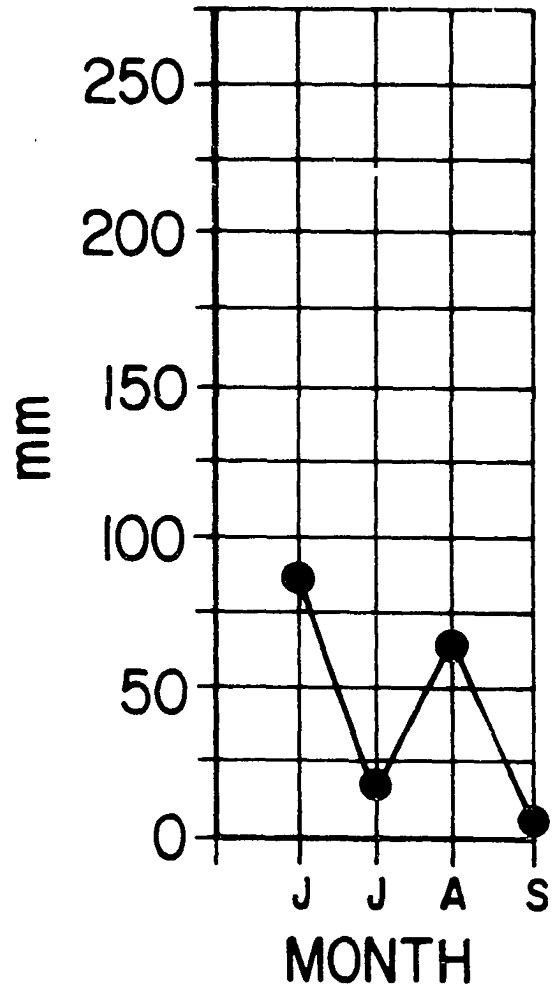


Fig. 36 Monthly precipitation at La Golondrina Ranch, Paraguay (June - September, 1982). Rainfall was measured daily and summed for each month. September represents only the first 15 days. In 1982, July and September were the driest months.

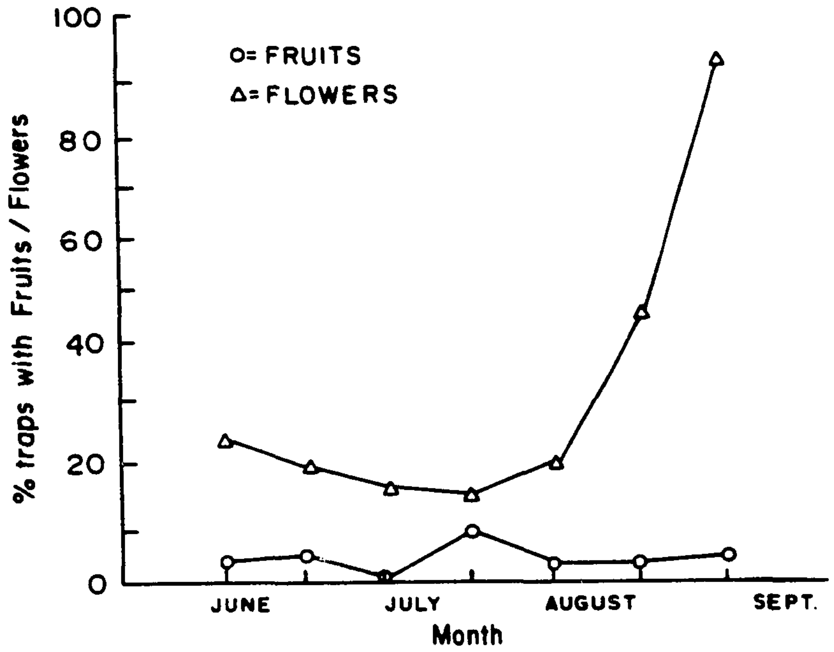


Fig. 37 Fruit trap results at La Golondrina Ranch, Paraguay. Forty traps were collected biweekly from June to September, 1982. Traps were distributed at 25m intervals in the forest, (Fig. 32) and at the periphery of the forest. The percentage of traps that contained fruits or flowers eaten by monkeys was calculated.

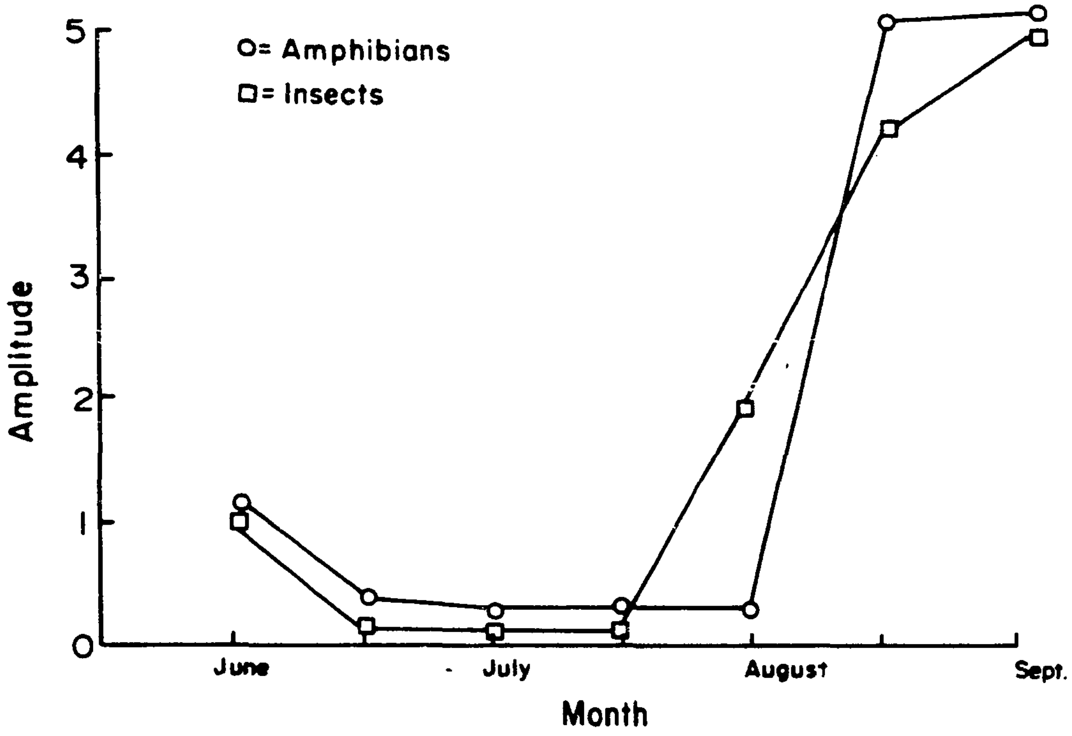


Fig. 38 Amplitude of insect and amphibian calls at La Golondrina Ranch, Paraguay. Biweekly tape recordings of night sounds were taken at three hour intervals throughout the night. All samples from each night's recordings were scored from 1-5 with 1 being not loud and 5 being extremely loud; scores were averaged to obtain a single value per sample night, as represented above. Note the sudden increase in amphibian and insect calling in mid-August. Increases in rainfall and temperature may have stimulated this activity.

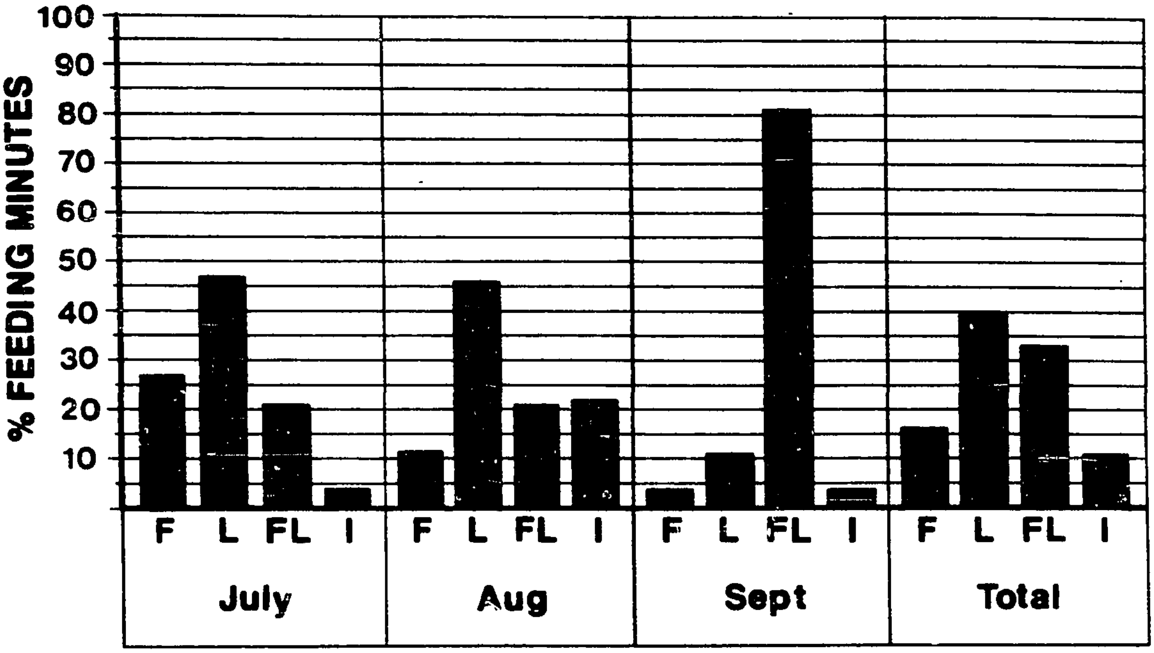


Fig. 39 Diet of <u>Aotus</u> Group I at La Golondrina Ranch, Paraguay from July - September, 1982. F=fruit; L=leaves; Fl=flowers and flower buds; I=insects. Note that leaf-eating remained high when fruits and insects were scarce, but dropped off when flowers and flower buds were available. Insect-feeding scores include foraging time while fruit- leaf-, and flower-feeding did not include time necessary to travel to these resources.

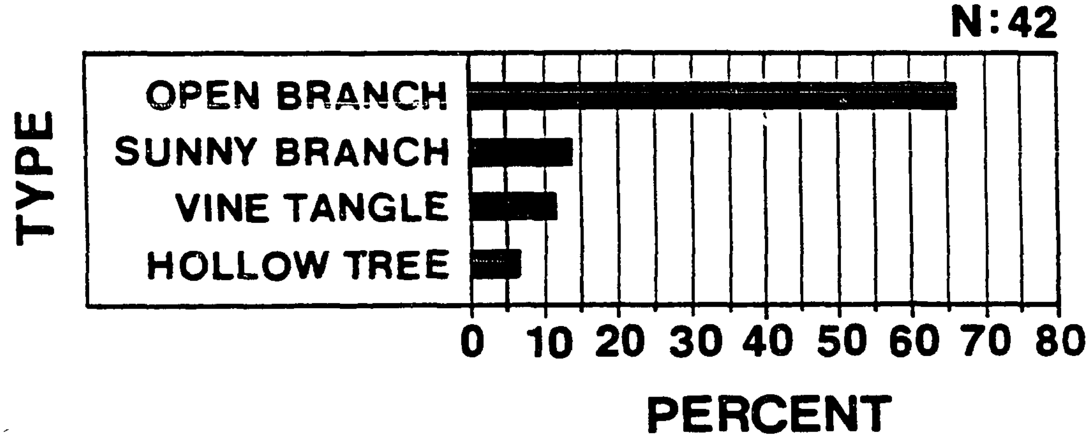


Fig. 40 Type of trees used by Aotus for sleeping at La Golondrina Ranch, Paraguay. Data are from Group I during the months of May - September, 1982. All trees were used by the group for daytime sleeping. A sunny branch was direct in sunshine with no intervening foliage; an open branch had other branches or leaves above it, (the monkeys were clearly visible from all sides on an open branch). Hollow trees were used only on the hottest days in September.

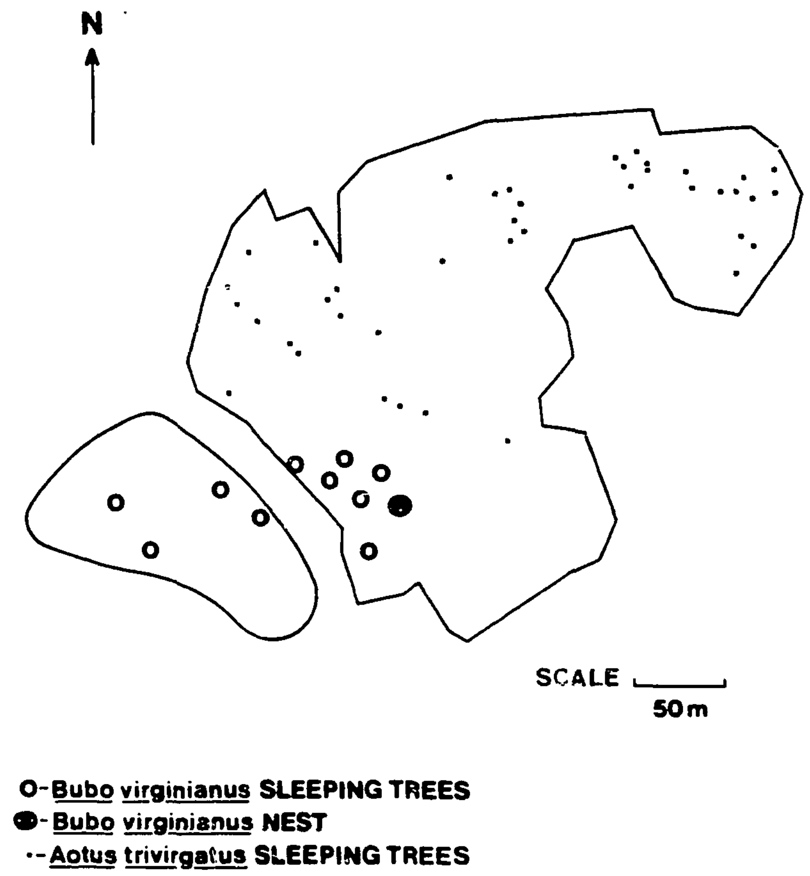


Fig. 41 Map of Aotus sleeping trees as they relate to the sleeping trees of the great horned owl pair in the study site at La Golondrina Ranch, Villa Hayes, Paraguay.

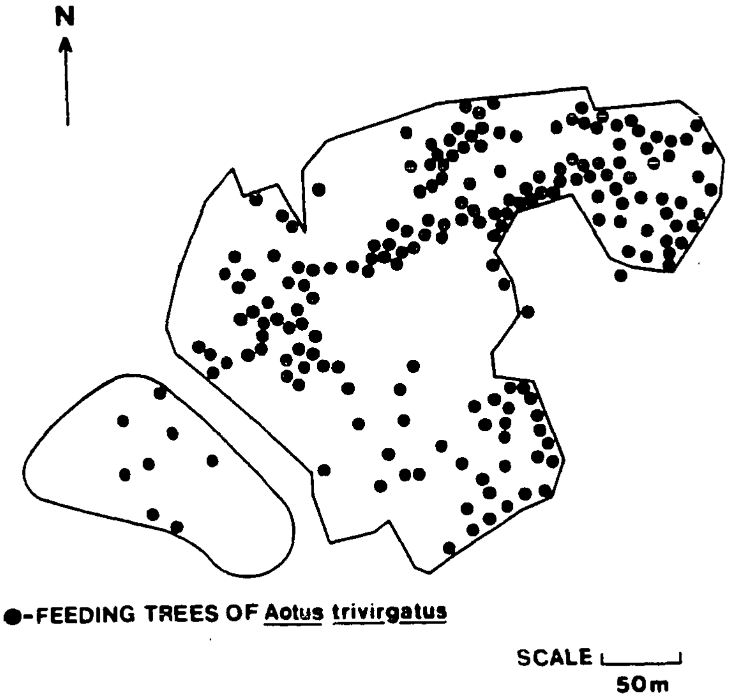


Fig. 42 Map of Aotus food resources used from June - September, 1982 at the study site of La Golondrina Ranch, Villa Hayes, Paraguay.

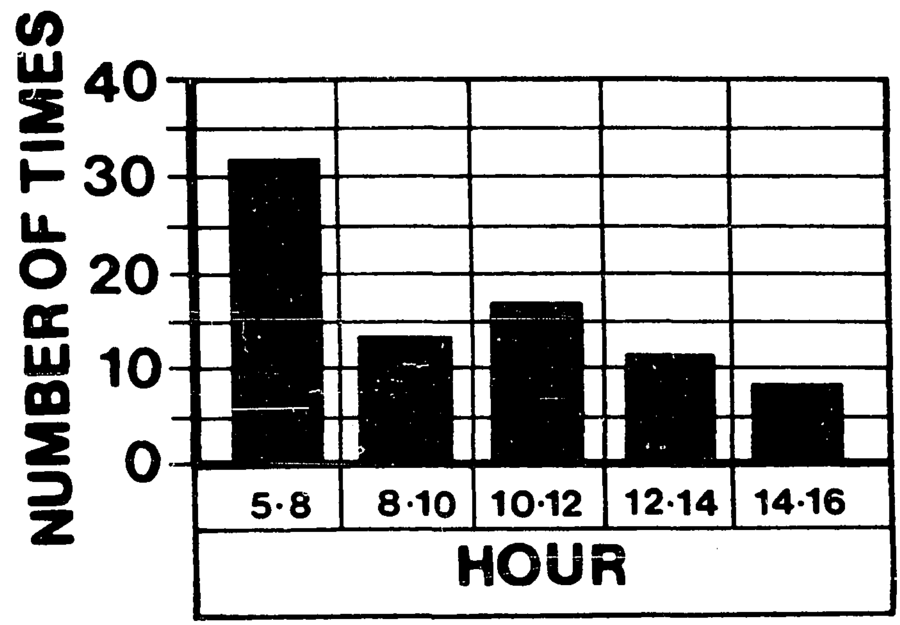


Fig. 43 Timing of entrance into sleeping trees by Aotus La Golondrina, Paraguay. Data from Group I, May - September, 1982, representing 40 days of observations. The monkeys often changed sleeping trees during the day, but the timing of change was unpredictable.

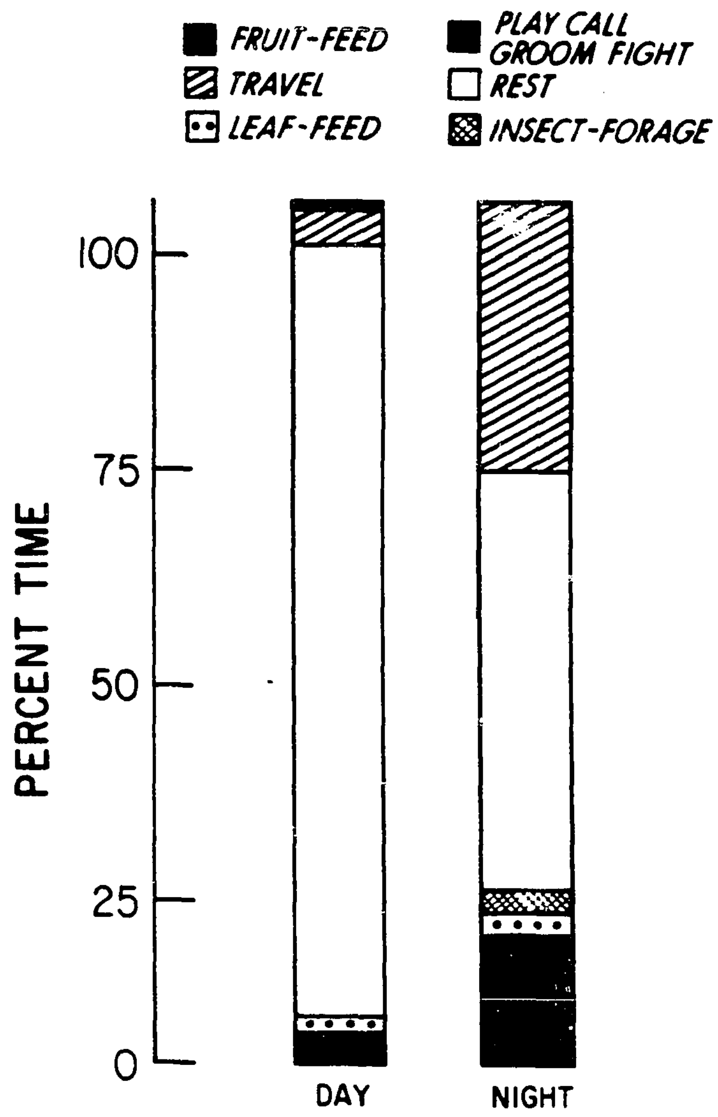


Fig. 44 Day and night activity of Aotus Group I at La Golondrina Ranch, Paraguay. Data are from four 24-hour samples; July 22, 23 and August 2, 4, 1982. More than one hour per day was spend feeding and less than an hour was spent traveling.

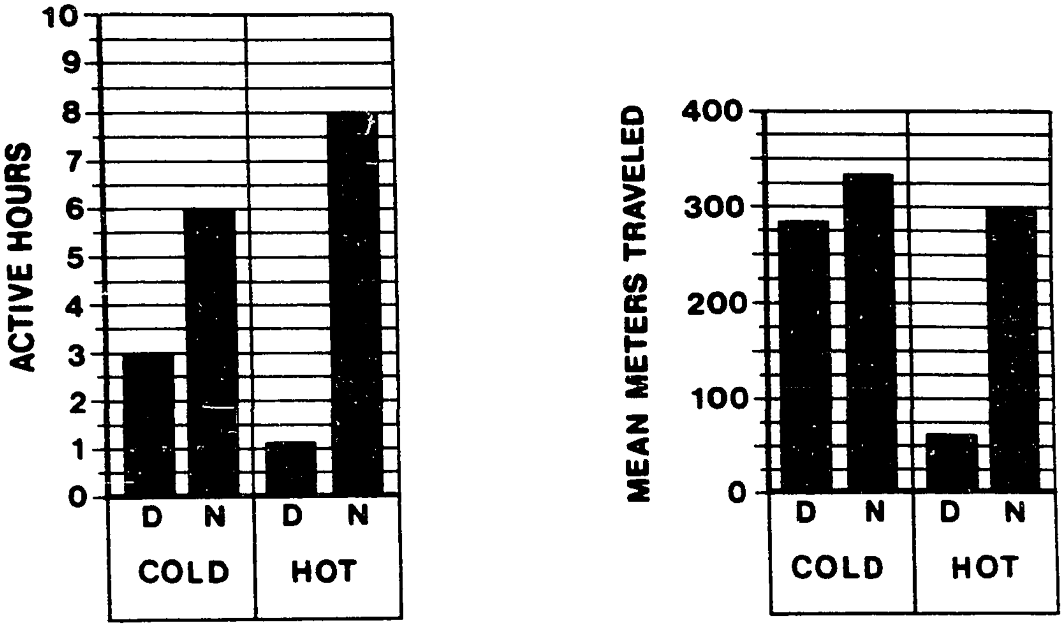


Fig. 45 Comparison of activity of <u>Aotus</u> in temperature extremes. Data from Group I includes only complete all-day (D) or all-night (N) data during the months of July-September, 1982. A day was considered 'cold' if lows ranged between 5°C and 12°C, and considered 'hot' if lows ranged between 15°C and 20°C. It should be noted that the lowest temperature ever recorded at Manu National Park was 11°C in the month of July and that the highs at La Golondrina Ranch, Villa Hayes, Paraguay, were much hotter than any recorded at any time of the year in Manu National Park, Peru.

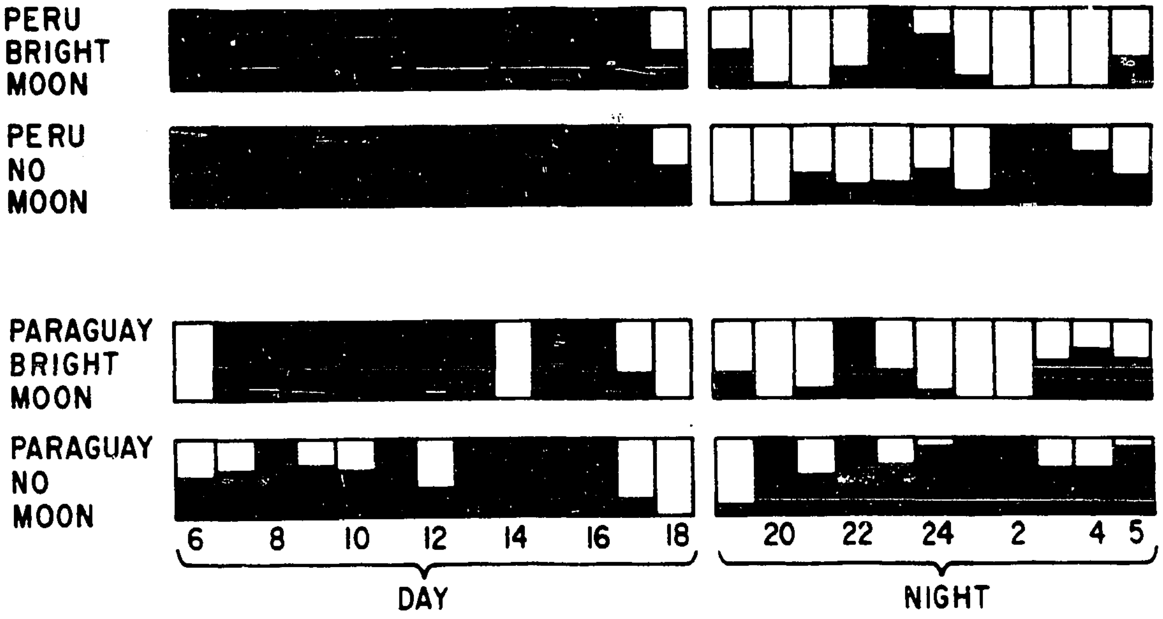


Fig. 46 Day and night activity of Aotus in Peru and Paraguay when the the moon was a) three days prior to vs three days immediately following the full phase, or b) three days prior to vs three days immediately following the new moon (darkest) phase. Solid black represents resting behavior, solid white represents activities including traveling, feeding and social behavior.

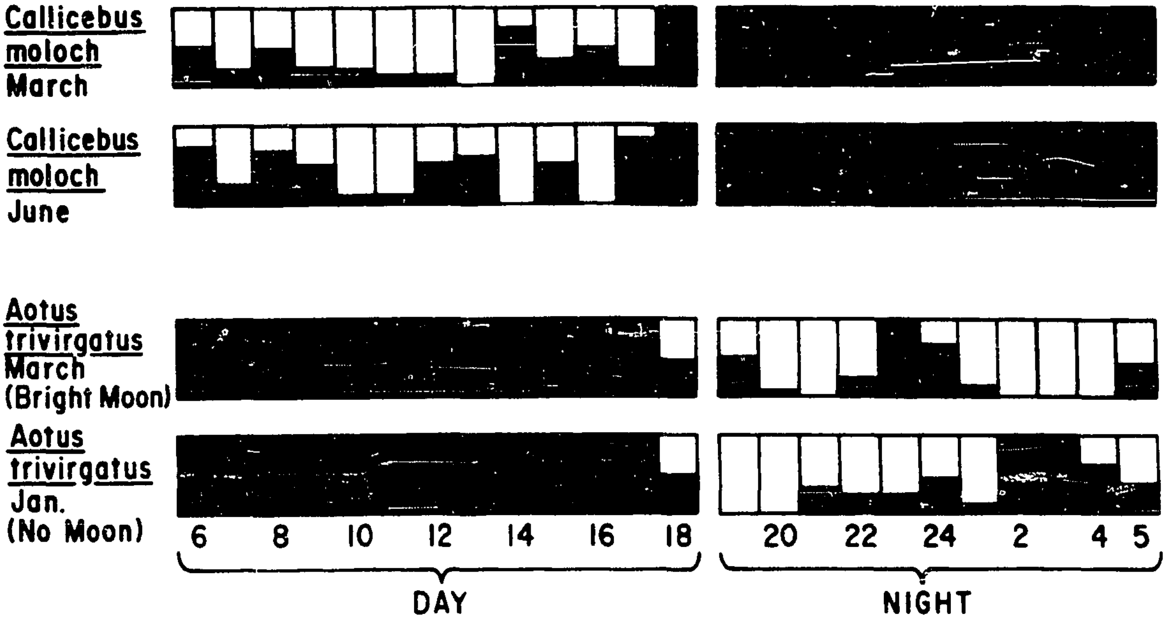


Fig. 47 Activity patterns of Callicebus in contrast with those of Aotus at Cocha Cashu, Manu National Park, Peru. Solid black represents rest, solid white represents activity (including feeding, traveling, and social behavior). March was a wet month with abundant resources, while June was a month with few foods available. Note that Aotus rested more during nights with no moon.

APPENDIX I

Phenology Census Results for Cocha Cashu, Peru
September, 1980 - August, 1981

Species	Number of Individuals Counted	Crown Diameter 0-10m	11-20m	21-30+m	Months with Fruit
Annona sp.	4	4			Apr May
Allophyllus glabatus	4	4			Apr May
Brosimum alicastrum	4			4	Mar - May
Brosimum lactescens	2		2		May June
Calatola sp.	4	4			Apr - Aug
Casearia decandra	4	4			Jan Mar
Cecropia sp.	4	4			Jan - June, Nov
Celtis iguanea	4	4			Apr May Sept
Clarisea racemosa	4		4		Sept Nov, Dec
Coussapoa ovalifolia	4	4			Sept Oct
Cupania cinerea	4	4			Feb Mar
Duguetia quitarensis	4	4			Mar Apr
Ficus erythrosticta	4	2		2	May Jul Aug Oct
Ficus kilipii	2			2	Jul Aug Sept
Ficus mathewseii	1			1	May
Ficus perforata	1			1	Oct
Ficus regularis	1		1		Sept Oct
Hirtella triana	4	4			May June
Guatteria acutissima	4		4		Sept - Nov
Inga edulis	3	3			Jan Feb Dec
Inga marginata	4	2	2		Jan Feb Dec
Inga mathewseii	4	4			Jan Mar Apr
Iriartea ventricosa	4	4			May June
Jacaratea digitata	4	4			Mar Apr
Laurac sp1	4		4		Sept Oct
Laurac sp2	4	4			June Oct Nov
Laurac sp3	4	4			Jan Feb Oct
Lecointea peruviana	4		4		Nov Dec Jan
Lunania parviflora	4	4			Apr
Leonia glycocarpa	4	4			Dec
Maytenus sp.	4	4			Dec
Malmea sp.	4	4			Mar
Myrcia splendens	4		4		Jan Dec
Myrciaria sp.	4	4			Apr June
Neea sp.	2	2			June
Oxandra acuminata	4	4			Jan Feb
Perebea guianensis	1	1			Jan - Mar

Phenology Census Continued

Species	Number of Individuals Counted	Crown Diameter 0-10m	11-20m	21-30+m	Months with Fruit
Paullinia hystrix	4	4			Sept Oct
Paullinia obovata	4	4			Mar
Protium neglectum	2	2			Feb - June
Protium tenuifolium	2	2			June
Quararibea wittii	4		4		Feb - May July
Sapium aereum	4	2	2		Jan Feb Mar
Sorocea briquetii	4		4		Nov Dec Jan
Sloania guianensis	4		4		Mar
Sloania obtusifolia	2			2	Jan Feb Mar
Spondias mombin	4	4			Jan Feb Apr
Trichilia poepigii	4	4			Jan Feb Oct Nov
Trichilia quadrajuga	4	4			July
Trichostigma octandra	4	4			Oct Nov
Xylopia sp.	4		4		Mar
Totals: 51 species	175	104	43	11	

APPENDIX II

Species Fed on by *Aotus* at Cocha Cashu, Peru
September, 1980 - August, 1981

Family
Genus species

- Anacardiaceae
  - *Spondias mombin*
  - *Tapirara quianensis*
- Annonaceae
  - *Annona neglecta*
  - *Duguetia quitarensis*
  - *Guatteria* cf. *acutissima*
  - *Malmea sp*.1 (flowers)
  - *Malmea sp*.2
  - *Oxandra acuminata*
  - *Oxandra sp*.
  - *Xylopia cuspidata* (*ligustrifolia*)
- Bombacaeae
  - *Ceibia pentandra* (nectar)
  - *Quararibea cordata* (nectar)
  - *Quararibea rhombifolia* (nectar)
  - *Quararibea wittii*
- Capparidaceae
  - *Crataeva benmenthii*
- Caracaceae
  - *Jacaratea digitata*
- Combretaceae
  - *Combretum assimile* (nectar)
- Curcurbitaceae
  - *Gurania sp*.
- Elaeocarpaceae
  - *Sloanea guianensis*
  - *Sloanea* cf. *obtusifolia*
- Euphorbiaceae
  - *Margaritaria nobilis*
  - *Sapium aereum*

Family
  Genus species

Flacourtiaceae
- *Casearia decandra*
- *Laetia corymbulosa*

Icacinceae
- *Calatola venezuelensis*

Lauraceae
- *sp.*1-5

Leguminosae
- *Acacia sp.* (tree leaf flush)
- *Inga edulis*
- *Inga marginata*
- *Inga mathewsii*
- *Lecointea peruviana*

Meliaceae
- *Trichilia poeppigii*
- *Trichilia quadrijuga*
- *Trichilia sp.*

Moraceae
- *Brosimum alicastrum*
- *Brosimum lactescens*
- *Cecropia sp.*
- *Clarisia racemosa*
- *Coussapoa obovalis*
- *Ficus erythrosticta*
- *Ficus* cf. *expansa*
- *Ficus kilipii*
- *Ficus mathewsii*
- *Ficus maxima*
- *Ficus perforata*
- *Ficus regularis*
- *Ficus sp.*1 & sp.2
- *Pourouma sp.*
- *Pseudolmedia laevis*
- *Sorocea cf. briquetti*

Myrtaceae
- *Myrciaria amazonica*
- *Myrcia splendens*
- *Psidium acutangulum*

Palmae
- *Iriartea ventricosa*

Family
Genus species

Phytolactaceae
Trichostigma octandra

Rubiaceae
Hamelia axillaris

Sapindaceae
Allophyllus glabratus
Cupania cinerea
Paullinia hystrix
Paullinia obovata

Ulmaceae
Celtis iguanea

Urticaceae
Urera eggersii

Violaceae
Leonia cf. *glycycarpa*

Vitaceae
Cissus ulmifolia

Aotus fed on fruit, unless otherwise stated.

APPENDIX III

Species Fed on by *Callicebus* at Cocha Cashu, Peru
September, 1980 - August, 1981

Family
  Genus species

- Anacardiaceae
  - *Spondias mombin*
- Annonaceae
  - *Annona neglecta*
  - *Annona sp*.
  - *Duguetia quitarensis*
  - *Malmea sp*.
  - *Oxandra acuminata*
  - *Xylopia cuspidata* (*ligustrifolia*)
  - *Guatteria* cf. *acutissima* (fruit and flowers)
- Araceae
  - *Anthurium brevipenduculatum*
  - *Monstera sp*.
- Aristolochiaceae
  - *Aristolochia sp*. (flowers)
- Bignoniaceae
  - *Arribidea verrucosa* (flowers)
  - *Callichlamys latiflolia* (flowers)
  - *Cuspidaria floribunda sp*.1 & sp.2 (flowers, leaves, immature pods)
- Bombacaceae
  - *Quararibea wittii*
- Burseraceae
  - *Protium neglectum*
  - *Protium tenuifolium*
- Celastraceae
  - *Maytenus magnifloria*
- Chrysobalanaceae
  - *Hirtella triandra*
- Cucubitaceae
  - *Gurania capitata* (fruit and flowers)
  - *Gurania sp*. (fruit and leaves)
  - *Fevillea sp*. (leaves)

Family
  Genus species

Elaeocarpaceae
  Sloanea guianensis

Euphorbiaceae
  Margaritaria nobilis
  Sapium aereum

Flacourtiaceae
  Casearia decandra
  Lunania parviflora

Graminae
  Bambusa sp. 1 & *sp*. 2 (leaf bases)

Guttiferae
  Chrysochlamys cf. *ulei*

Icacinaceae
  Calatola venezuelensis

Lauraceae
  sp. 1-5

Leguminosae
  Acacia sp. (leaves)
  Bauhinia sp. (flowers, leaves)
  Caesalpinia bondoc (leaves)
  Inga edulis
  Inga klugii
  Inga marginata
  Inga mathewsii
  Inga tenulostipulum (flowers)
  Lecointea peruvinana
  Schizolobium sp. (leaves, flowers)

Melastomaceae
  Miconia aulocalyx (leaves and fruit)

Meliaceae
  Guarea kunthiana
  Guarea macrophylla
  Trichilia elegans
  Trichilia pleeana
  Trichilia poeppigii
  Trichilia quadrijuga
  Trichilia sp.

Menispermaceae
  Cissampelos sp. (leaves and flowers)

Family
  Genus species

Moraceae
- *Brosimum alicastrum*
- *Brosimum lactescens*
- *Clarisia racemosa*
- *Ficus bullenii*
- *Ficus erythrosticta*
- *Ficus kilipii*
- *Ficus mathewsii*
- *Ficus regularis*
- *Ficus sp*.1 & *sp*.2
- *Perebea guianensis*
- *Pseudolmedia laevis*
- *Sorocea* cf. *briquetii*

Myristicaceae
- *Otoba parvifolia*
- *Virola* cf. *peruviana*

Myrtaceae
- *Calyptranthes sp*.
- *Eugenia punicifolia*
- *Eugenia sp*. 1
- *Myrciaria amazonica*
- *Myrcia splendens*
- *Psidium acutangulum*

Nyctaginaceae
- *Neea hirsuta*
- *Neea* cf. *floribunda*

Palmae
- *Iriartea ventricosa*

Phytolactaceae
- *Trichostigma octandra*

Piperaceae
- *Piper heptandrum*

Polygonaceae
- *Coccoloba lehmanii* (flowers and fruit)

Rubiaceae
- *Gleospermum sphaerocarpum*
- *Guettarda aromatica*
- *Hamelia axillaris*

Family
  Genus species

- Sapindaceae
  - *Allophyllus glabratus*
  - *Cupania cinerea*
  - *Paullinia hystrix*
  - *Paullinia obovata*
  - *Paullinia sp.*1

- Sterculiaceae
  - *Byttneria sp.* (leaves)

- Ulmaceae
  - *Celtis iguanea* (fruit and leaves)

- Urticaceae
  - *Urera eggersii*

- Violaceae
  - *Cestrum reflexum sp.*1 (orange Chinese lantern fruit)

- Vitaceae
  - *Cissus ulmifolia*

Callicebus fed only on fruits for all species listed above except as otherwise noted.

APPENDIX IV

Composition of Fecal Samples Collected from *Aotus* and *Callicebus*, Cocha Cashu, Peru 1981

Month	Species/ # Samples/month	Composition (Scale 0=none, 5=only item)		
		Leaves/vegetation	Fruit	Insects
April	*Aotus*/13	0	5	0
		0	4	1
		0	3	2
		0	4	1
		0	5	0
		0	5	0
		0	5	0
		0	5	0
		0	5	0
		0	5	0
		0	4	1
		0	3	2
		0	4	1
April	*Callicebus*/5	0	4	1
		5	0	0
		0	5	0
		2	2	1
		5	0	0
May	*Aotus*/14	0	5	0
		0	5	0
		1	2	2
		0	2	3
		1	2	2
		0	2	3
		0	3	2
		0	3	2
		0	5	0
		0	3	2
		0	3	2
		0	4	1
		0	3	2
		0	4	1
May	*Callicebus*/8	5	0	0
		4	0	1
		0	5	0
		0	5	0
		0	3	2
		5	0	0
		5	0	0
		0	5	0

Month	Species/ # Samples/month	Composition (Scale 0=none, 5=only item)		
		Leaves/vegetation	Fruit	Insects
June	Aotus/4	0	5	0
		0	4	1
		1	3	1
		0	5	0
		0	5	0
June	Callicebus/18	5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
July	Aotus/2	0	4	1
		0	5	0
July	Callicebus/20	5	0	0
		5	0	0
		5	0	0
		5	0	0
		5	0	0
		0	5	0
		0	5	0
		0	5	0
		0	5	0
		0	5	0
		0	5	0
		0	5	0
		0	5	0
		3	0	2

Month	Species/ # Samples/month	Composition (Scale 0=none, 5=only item)		
		Leaves/vegetation	Fruit	Insects
July	Callicebus/continued			
		0	3	2
		2	3	0
		2	3	0
		0	4	1
		1	4	0
		2	3	0
August	Aotus/3	0	3	2
		0	5	0
		0	5	0
August	Callicebus/6	5	0	0
		5	0	0
		5	0	0
		5	0	0
		3	2	0
		3	2	0

Thirteen percent of the Callicebus fecal samples collected (n=56) contained insect chitin. Fifty-seven percent were composed only of leaves and vegetation. Sixty-four percent of the Aotus fecal samples collected (n=36) contained insect chitin. It should be noted that amounts of insect chitin in each sample was rated only on the 0 - 5 scale, and therefore, the above numbers do not indicate the actual number of pieces of chitin contained in each sample. No samples from Aotus were composed entirely of vegetation. Because the sample sizes are small and because not all months of the year were sampled, caution should be exercised when interpreting these data.

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