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FEEDING ECOLOGY AND DEMOGRAPHY OF THE MOUSTACHED TAMARIN *SAGUINUS MYSTAX* IN NORTHEASTERN PERU

by

MARIA MARLENI RAMIREZ

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.

1989

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

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ABSTRACT

FEEDING ECOLOGY AND DEMOGRAPHY OF THE MOUSTACHED TAMARIN SAGUINUS MYSTAX IN NORTHEASTERN PERU

by

MARIA MARLENI RAMIREZ

Adviser: Professor Warren G. Kinzey

Feeding ecology and demography of the moustached tamarin, *Saguinus mystax*, were studied at two locations in western Amazonia, Peru, for a total of 1500 hours. The feeding and ranging habits of a group of moustached tamarins were observed for 13 months at the Blanco Stream site. A cropped population of tamarins was censused on two consecutive years to investigate the effects of cropping on the remaining population of tamarins at the Yarapa River site. At both study sites *S. mystax* formed mixed groups with the saddle-back tamarin, *S. fuscicollis*.

Anti-predator concerns appeared to be the governing factors in the exploitation of food resouces by the moustached tamarin, and also seemed to favor the maintenance of mixed groups with the saddle-back tamarin. Moustached tamarins preferentially used small-crowned trees in the absence of larger primate competitors, presumably to avoid predation risks on tall, large-crowned trees. The latter were only exploited when fruit was scarce. Exudates, although available year round were only consumed in the dry season. Vulnerability to predators seemed to increase during exudate exploitation. The frequent use of

habitats with abundant leaf cover for insect foraging may also help reduce predation risks. The cropping of *S. mystax* at the Yarapa River coincided with the depression of the growth rate of *S. fuscicollis*. This was probably due to emigration, increased mortality due to predation, and reduced fecundity resulting from decreased competitive ability with conspecifics in mixed groups. It is suggested that both tamarins maintain a mutualistic relationship, the major benefit of which is increased protection against predators.

The economics of territorial defense seemed to influence the selection of preferred fruit trees and sleep trees. Highest ranking fruit trees and most sleep trees were found at the periphery of the home range thus presumably reducing the costs of territorial defense.

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CHAPTER I.- INTRODUCTION

This dissertation examines the feeding ecology and ranging behavior of the moustached tamarin *Saguinus mystax* (Callitrichidae, Primates), and explores some demographic aspects of its association with the saddle-back tamarin *Saguinus fuscicollis* (Fig.1).

Since the distribution and abundance of food resources are thought to influence social organization, the study of the behavioral ecology of *S. mystax* will help us gain a better understanding of the influence of ecology over social life. Furthermore, the derived characteristics that make *S. mystax* a callitrichid such as small body size and twinning, the reported flexible social organization in tamarins, and the propensity to join in mixed species groups offer the opportunity to explore the advantages of sociality in this small primate.

A.- History of studies of *Saguinus mystax* in the Neotropics

The last two decades have witnessed a re-discovery of New World primates as objects of study by researchers of many disciplines. Although the first detailed field study of a primate was the now classic work of Carpenter (1934) on the howler monkey (*Alouatta palliata*), the next decades did not see much primatological work done in the Neotropics.

Most of the early field studies were carried out on the larger forms of platyrrhines: howlers, capuchins, spider monkeys (Chivers,1969; Eisenberg and Kuehn, 1966; Oppenheimer, 1968; Richard, 1970); while little attention was given to the smaller species in general, and to the Callitrichids in particular. Since then there has been a steady increase in the number of field studies and interest in these primates (Kinzey, 1987), and by 1988 most species of Callitrichids have been observed in the wild, even though still very few species have been the object of detailed studies.

Until 1973, Peruvian Amazonia was an important source of wildlife--particularly primates--to supply the international pet market and the biomedical community. Between 1962 and 1971 it was estimated that over 30,000 monkeys per year were exported from the Amazonian region of Peru (Soini, 1972). About 2,000 tamarins per year were exported during the same period. S. fuscicollis made up the bulk of tamarin exports, followed by S. mystax.

The utilization of the moustached tamarin, Saguinus mystax as a model for laboratory study of Hepatitis-A research (Whitney, 1978) resulted in increased demand for this tamarin, which was captured in Brazil and Peru (Dawson, 1975; Mittermeier et al., 1978; Castro, 1978). In 1973, a ban on exportation of wildlife imposed restrictions on the availability of moustached tamarins from Peru. As a consequence, a program of captive and semi-captive breeding was established at Iquitos, Peru, with the intention of breeding the tamarins for export. The initial failure to breed the moustached tamarin in captivity resulted in continued pressure on wild populations to stock the breeding programs, and for biomedical research.

Previous to the data collection for this study little information was available on colony maintenance or behavior of the moustached tamarin, data that were necessary if *S. mystax* were to become breedable in captivity. Most existing data were demographic, and gathered in connection with censuses and trapping of *S. mystax* in Northwestern Peru (Castro and Soini, 1978; Moya et al., 1979; Soini and Soini, 1983).

From June 1981 to November 1982, I conducted an ecobehavioral study of *S. mystax* at two sites in Peru (Fig. 2). At the Blanco Stream, a small tributary of the Tahuayo river, two marked groups of moustached tamarins were radio-tracked to learn about their daily activities, ranging patterns, habitat use, and general behavior. In addition, two censuses, were conducted in 1981 and 1982 at the Yarapa river, in an attempt to evaluate the effects of cropping more than half of a small population of moustached tamarins on the recovery of the remaining tamarins (*S. mystax* and *S. fuscicollis*).

Studies at the Blanco Stream site began with Castro and Soini's 1978 short study, which provided some basic data for *S. mystax* and *S. fuscicollis* at the site. This was followed by the study presented in this dissertation (June 1981-November 1982), on diet and habitat use in *S. mystax*, during which two study groups named Green and Red were trapped, permanently identified and followed by means of radio-tracking. Norconk (1986) studied the tamarins from November 1982-June 1983, and October- December 1983, and focused on interspecific behavior and ecology of S. mystax and S. fuscicollis. She followed the same groups. From January 1984-December 1984, Garber (1986, 1987, 1988) focused on aspects of resource use of both tamarins in the Green troop during discrete periods of time. In addition, Garber trapped and permanently marked 10 mixed-species groups. Norconk (1986) also observed an introduced population of moustached tamarins living on an alluvial island from July 1983-September 1983. A census of two cropped populations of S. mystax was conducted by Glander et al., (1984) in 1982 at two sites in Peru. Box and Morris (1980), and Heymann (1985, in press) studied spacing behavior and vocal behavior of moustached tamarins housed in an outdoor enclosure in Iquitos. Snowdon and Hodun (1985) studied the responses of group members to the calls of recently captured moustached tamarins, also in Peru.

B.- General background on Saguinus with special reference to S. mystax

In this section I will summarize the previous studies on S. mystax. I will also touch on Saguinus spp. data that in my opinion provides needed background information for this study.

1.- Morphology and Systematics.- The Callitrichidae [= Subfamily Callitrichinae, Family Cebidae of Rosenberger (1984)] is the New World family of tamarins and marmosets all of which share a suite of characters rare among anthropoids. These include: small body size, clawlike nails on all digits except the hallux, tritubercular upper molars, absence of a third molar and tendency to twin (Sussman and Kinzey, 1984). There are four genera within the Callitrichidae (Hershkovitz, 1977) which can be placed in two functional groups based on the morphology of the lower incisors and canine teeth (Sussman and Kinzey, 1984). In the marmosets (*Callitrix* and *Cebuella*) the lower incisors are long and narrow, reach the occlusal level of the incisiform canines and lack lingual enamel, thus forming an efficient gouge (Rosenberger, 1978; Sussman and Kinzey, 1984). In *Saguinus* and *Leontopithecus*, the incisors are spatulate, shorter than the canines, and covered with enamel on both lingual and labial sides (Sussman and Kinzey, 1984). Rosenberger (1984) gives this assemblage of primates, plus *Callimico*, a subfamilial ranking (Callitrichinae), and the vernacular name "marmosets". Rosenberger (1984) recognizes two tribes within the Callitrichinae: Callitrichini with *Callitrix* (including *Cebuella*), *Leontopithecus* and *Saguinus*; and Callimiconini with *Callimico*, thus aligning this genus with the "marmosets". His classification recognizes the monophyly of the "marmosets"(with the exception of *Callimico*) and their affinities with the Cebinae (*Cebus* and *Saimiri*).

Mittermeier and Coimbra-Filho (1981) recognize 11 species within the genus *Saguinus* (Table 1) although Hershkovitz (1977) gives the Panamanian tamarin a subspecific status and thus recognizes only ten species. As I write this thesis only four species have been the subject of field studies of 6 months or more (Table 2): *S. fuscicollis* has been studied at four locations, all in Peru (Crandlemire-Sacco, 1986; Garber, 1986,1987, 1988; Norconk, 1986; Soini and Coppula, 1981; Terborgh, 1983); *S.geoffroyi* was studied in Panama by Dawson (1976a) and Garber (1980); *S. oedipus* was observed in Colombia by Neyman (1980), and *S. mystax* was observed at one location in Peru (Garber, 1986, 1987, 1988; Norconk, 1986; Ramirez, 1984a, this study). A considerable body of demographic information has been collected from wild populations of *S. mystax* and *S. fuscicollis* in Peru (Soini and Coppula, 1981; Soini and Soini, 1982, 1983); and censuses at many locations in Peru and Bolivia have provided data on the status of tamarin populations (Freese et al., 1978, 1982; Neville et al., 1976).

Comprehensive reviews on tamarins have become available recently. Soini and Snowdon (in press) reviewed all field and captive studies of *Saguinus* up to 1983 while Sussman and Kinzey (1984) concentrated on data bearing on the ecological role of the callitrichids. Hershkovitz (1977, 1979, 1982) presents detailed descriptions of the species and subspecies of tamarins as well as reviews their taxonomy (Hershkovitz, 1983) and evolution.

2.- Body size.- The tendency to generalize for the whole callitrichid radiation, based on the existing data, from both captive and field studies, has overlooked the mounting evidence on the variability and diversity within the genus Saguinus, in morphology, behavior, and ecology. One example is body size. Saguinus have been regarded as of medium size within the callitrichids. However, data gathered from wild populations indicate a wide range of variation, from a minimum of 250 gm (adult body weight) in some populations of S. fuscicollis (Soini and Coppula, 1981) to a maximum of 650 gm in S. mystax (Soini and Snowdon, in press). Moreover, upper Amazonian populations of S. mystax and S. fuscicollis decrease in size along a cline from north to south (Soini and Soini, 1982). It has also been suggested that Saguinus sp. are monomorphic in body weight. However, adult females are somewhat heavier than adult males in all the wild populations that have been adequately sampled (Dawson, 1976b; Garber and Teaford, 1986; Neyman, 1978; Soini and Soini, 1982), and in two well sampled populations of S. mystax, the greater weight of non-pregnant adult females (4-7% heavier than the adult males) was a statistically significant difference (Soini and Soini, 1982).

3.- Distribution.- Saguinus are mostly South American in distribution with only one species (S. geoffroyi) extending into southern Central America. Soini and Snowdon (in press) have grouped the tamarins--based on their present distributions--in two disjunct clusters: the Hylean or Amazonian species, and the extra-Amazonian species. The latter include: *S. geoffroyi*, *S. oedipus*, and *S. leucopus* which occur parapatrically in primary and secondary tropical forest of various degrees of deciduousness. The eight Hylean species: *S.nigricollis*, *S.fuscicollis*, *S.mystax*, *S.imperator*, *S.labiatus*, *S. bicolor*, *S. midas*, and *S. inustus*, range north and west of the Mamore-Madeira, and the lower Amazon river, including the Guyanas but excluding Venezuela. Only *S. midas* ranges south and east of the Amazon to the area between the lower Xingu and Gurupi rivers (Hershkovitz, 1977). *S. mystax* lives in the Amazonian basin of eastern Peru and Northwestern Brazil south of the Amazon (Hershkovitz, 1977). The hylean species occupy mainly tropical lowland humid forests from sea-level to more than 800 m, all species are found in high ground forest, and some occupy seasonally flooded forests. However, swamp forests or other forests that inundate for long-periods of time are avoided by *S. mystax* or are occupied only marginally by *S. fuscicollis* (Soini and Snowdon, in press; personal observation).

4.- **Habitat preferences.**- For a long time it has been emphasized that callitrichids "thrive" in secondary forest, and even in small patches of forest (e.g. Eisenberg, 1978). The observation that the Panamanian tamarin population on Barro Colorado Island (BCI) has decreased in the last forty years as the forest matures has been interpreted as supporting this idea

(Thorington, 1978). The high to very high population densities reached by *S. geoffroyi* in secondary forest in mainland Panama (Dawson, 1976a; personal observation) seem to support this contention. While this is probably the case for *S. geoffroyi*, *S. oedipus* and *S. leucopus* which live in areas of Colombia and Panama (Bernstein et al., 1976; Hernandez-Camacho and Cooper, 1976; Dawson, 1976a; Neyman, 1978; Lindsay, 1979; Skinner, 1985) with moderate to severe forest disturbance, it is less clear that this is the case for the Amazonian species of *Saguinus* and other callitrichids, all of which have been found in primary forest. Furthermore, although almost all Hylean *Saguinus* have been observed in secondary forest, a positive correlation between this type of forest and an increase in their abundance has not been found (Freese et al., 1982).

On the other hand, severity of the dry season might affect the density of wide-ranging Hylean species. Populations of the saddle-back tamarin in highly seasonal forests such as Cocha Cashu (comparable to BCI in degree of deciduousness, and human disturbance) in southeast Peru occur at reduced population densities when compared with their Hylean counterparts (Soini and Coppula, 1981; Terborgh, 1983). Competition from the numerous primate species at this locality, and the profusion of predators might contribute to the low density of tamarins.

The preferential use of forest edge vs. non-forest edge has only been demonstrated for the Panamanian tamarin (Dawson, 1979). Although all species studied to date seem to regularly visit forest edge (*S. fuscicollis*, *S. nigricollis*, *S. imperator*, *S. midas*; respectively reported by Terborgh, 1983; Soini and Coppula, 1981; Izawa, 1978; Terborgh, 1983; Mittermeier and van Roosmalen, 1981) its more than chance use has yet to be demonstrated for all these species.

5.- **Diet.**- Gut morphology in *S. geoffroyi* groups this tamarin with other primates relying on a diet of fruits and insects (Frugivore-Faunivore) (Chivers and Hladik, 1980, 1984; Hladik and Hladik, 1969). All species of *Saguinus* have been observed to feed on insects, fruits, flowers, nectar and plant exudates. Although the methodology (stomach content, time samples) and the length of observations vary from one study to another, it is apparent that insects are an important dietary item in all species studied. The tamarin diet consists of 30-75% of insects, most of which are large orthopterans. Moreover, there seems to be a trend within the genus towards a greater reliance on insects in the smaller species. *S. fuscicollis* in Upper Amazonia (Pacaya River) and *S. imperator* at Cocha Cashu spent 50-75% of their feeding time foraging for insects (Soini and Coppula, 1981; Terborgh, 1983). On the other hand, in the larger *S. geoffroyi* 30% of their diet was insects (Hladik and Hladik, 1969), or spent 40% of their feeding time foraging for insects (Garber, 1980), while *S. midas* was observed foraging for insects in over 30% of the feeding sightings (Mittermeier and van Roosmalen, 1981). Dawson (1976a) cautioned that his figure of

50% of insect feeding for the Panamanian tamarin was most probably an overestimate.

Two types of insect-foraging technique are distinguishable: one involves mostly passive scanning with little substrate manipulation which ends with the capture of the visible prey. This technique is observed in S. imperator, S. mystax and S. labiatus which tend to forage for insects in the lower and middle canopy of the forest (Pook and Pook, 1982; Terborgh, 1983; Yoneda, 1981; this study). S. fuscicollis displays a greater repertoire of insect foraging techniques and tends to occupy a broader vertical range. The saddle-back tamarin is essentially a manipulative forager, searching in many kinds of substrates, mainly in the shrub and subcanopy strata (Soini and Coppula, 1981), or from the ground level to beyond 40m (Terborgh, 1983), or searching at the base of large trees (Yoneda, 1981).

Fruit has been reported to be the most important tamarin plant food source for most of the year (25-69% of the diet), with the larger species including a greater proportion of fruits in their diet (Dawson, 1976a; Garber, 1980; Hladik and Hladik, 1969; Mittermeier and van Roosmalen, 1981; Soini and Coppula, 1981; Terborgh, 1983). Terborgh (1983) characterized fruit feeding trees used by tamarins as small crowned, mid-canopy trees which bear fruit in small quantities over many weeks. Studies of S. geoffroyi, S. mystax, S. fuscicollis and S. imperator (see Table 2 for study sites) showed that the tamarins relied on a few plant species to provide for most of their food (Dawson, 1976a; Garber, 1987; Norconk, 1986; Soini and Coppula, 1981; Terborgh, 1983). When fruit was scant in the dry season, the diet was supplemented with nectar and exudates: both tamarins at Cocha Cashu (Janson et al.,1981), S. mystax on Padre Isla (Norconk, 1986), and S. fuscicollis at the Pacaya (Soini and Coppula (1981). Garber (1987) reported goal-directed travel to nectar feeding sources for both tamarins at the Blanco site, and he hypothesized that these tamarins maintain a cognitive map of feeding tree distribution within their range.

Seed ingestion has been reported for S. geoffroyi, S. oedipus, S. midas, S. fuscicollis and S. mystax (Dawson, 1976a; Fooden, 1965; Garber; 1986; Ramirez, 1984a). Garber (1986) has presented evidence suggesting that the saddle-back tamarin and the moustached tamarin may be important dispersal agents for certain tree species.

6.- Use of space.- Tamarins occupy ranges that vary from 8-50 ha. Range size is commonly about 30-40 ha in area. The only exception to date is S. oedipus which occupies very small ranges in remnant forests. All tamarins have been observed to defend their home range against the apparent intrusion of conspecifics. However, the portion of home range that qualifies as a territory: more or less fixed, defended and exclusive (Brown and Orians, 1970) varies from 0% overlap (Saguinus spp., Terborgh, 1983) to 43% overlap (S. oedipus, Neyman, 1980) of the home range. Furthermore, intraspecific variation in territorial defense appears to be influenced by ecological conditions, such as severity of the dry season. Groups living in forests with marked seasonality in fruit availability shared a large portion of their range with neighboring groups--than groups in less seasonal environments--and practiced site defense rather than territoriality at the time of maximum scarcity [*S. geoffroyi*, Dawson (1976a) and *S. fuscicollis* Crandlemire-Sacco (1986)], although the evidence is circumstancial in the last case. On the other hand, Norconk (1986) observed more confrontations when fruit bearing trees were scant.

Tamarin's day ranges are long for their body size (Milton and May, 1976) varying between 1.0 and 2.0 km. Furthermore, home range size does not seem to affect path length (Norconk, 1986), thus, groups with reportedly the smallest home ranges traveled average daily paths (Neyman, 1980), while the shortest path was traveled by tamarins (*S. nigricollis*) with one of the largest home ranges (Izawa, 1976). Group size--even when tamarins live in mixed groups--does not seem to affect home range size (Norconk, 1986).

7.- Social organization.- *Saguinus* live in small groups which range in size from 2-13 individuals; most groups however have between 5-7 individuals (Soini and Snowdon,in press; Sussman and Kinzey, 1984). Large, temporary aggregations have been observed infrequently, and only at sites where a single species of tamarin is present (Castro and Soini, 1978; Dawson, 1976a;

Izawa, 1976, 1978). As a rule, groups of tamarins consist of at least one adult of each sex, but more commonly more than one, plus young of up to three or four different ages (Goldizen, 1987; Sussman and Kinzey, 1984). The sex ratio tends to be slightly biased in favor of males in *S. oedipus*, *S. geoffroyi*, *S. fuscicollis*, *S. mystax* and *S. labiatus*, and in the majority of groups only one female breeds (Goldizen, 1987; Sussman and Kinzey, 1984). Although callitrichids have been regarded as strictly monogamous--a belief derived mostly from captive studies--(Epple, 1975; Kleiman, 1977), mounting evidence from field studies suggests more complex mating practices (Dawson, 1976a; Neyman, 1978; Terborgh and Goldizen, 1985).

Terborgh and Goldizen (1985) studied frequency of mating in six groups of individually marked *S. fuscicollis*, which displayed a high degree of variability in mating systems, both between groups and within groups over time. Thus, mating in some groups was polyandrous, with both males having access to the adult female; in another case both adult males copulated with the two adult females in the group; and in one case the two adult females gave birth within the same group while living with one male; and in the last variation both adult males copulated with two adult females in the group. Group composition in *S. labiatus*, *S. fuscicollis* and *S. mystax* suggests that at least some groups might be polyandrous (Garber et al., 1984; Goldizen, 1987; Soini and Coppula, 1981; Soini and Soini, 1982).

Promiscuous and polyandrous matings have been observed in captive groups of *S. fuscicollis*, *S. mystax* and *S. oedipus* (Epple, 1975; Hampton et al., 1966; Malaga, 1985). Captive studies on the behavior and reproductive biology of *S. fuscicollis* and *S. oedipus* are numerous and have shed light on some of the mechanisms involved in the reproductive inhibition of non-breeding females in family groups. Experiments with scent secretions suggest that scent marks from the reproductively active female contain chemical signals that inhibit reproductive activity in other females living in a group (Epple, 1975; 1978; Epple and Katz, 1980, 1984; French et al., 1984; Savage et al., 1988). Fertility suppression appears more pronounced in *Saguinus* species than in the other callitrichids studied to date (e.g. *Callithrix jacchus*, *Leontopithecus rosalia*) (Savage et al., 1988).

It is widely observed that in the Callitrichidae, family members participate in infant carrying (Sussman and Kinzey, 1984). However, infant carrying in the wild has been quantified only for *S. fuscicollis*, and the adult males did most of it (Goldizen, 1987; Goldizen and Terborgh; 1986). Captive studies, although showing much individual variation, are in agreement with the observations on *S. fuscicollis* (Epple, 1975).

Intergroup migrations have been reported as common in *S. geoffroyi* (Dawson, 1977), and *S. oedipus* (Neyman, 1978) and also occur--although with much less frequency--in *S. fuscicollis* (Soini and Coppula, 1981; Terborgh and Goldizen, unpub.). Since in only one case marked tamarins have been observed for several years (Goldizen, 1987; Terborgh, 1983; Terborgh and Goldizen, 1985) kin relations of migrants are largely unknown. These observations have led to this mating system being referred "communal breeding" (Sussman and Kinzey, 1984) or "cooperative polyandry" (Terborgh and Goldizen, 1985).

8.- Mixed groups.- In the forests south of the Amazon river it is common to find two sympatric species of *Saguinus* which join in mixed groups (Castro and Soini, 1978; Garber, 1988; Izawa and Bejarano, 1981; Norconk, 1986; Pook and Pook, 1982; Ramirez, 1984b; Terborgh, 1983; Yoneda, 1981). Mixed groups observed to date include *S. fuscicollis*, and any one of three species: *S. mystax*, *S. imperator*, or *S. labiatus*. The species in mixed groups differ in body size by 20-40%, in locomotion, vertical use of the forest, foraging techniques, and size of prey taken.

On the other hand, similar-sized species (less than 20% difference in body weight) of tamarins are either (a) parapatric, as seems to be the case with *S. oedipus* and *S. geoffroyi*, which occupy the understory of the forest in habitats of the Choco of Colombia and in Panama, and might practice similar foraging techniques (Neyman, 1980); or (b) although in sympatry, the species are separated by micro-habitat segregation as seems to be the case of *S.imperator* and *S.labiatus* or *S. mystax* and *S.labiatus* in Bolivia (Izawa and Bejarano, 1981;Izawa and Yoneda, 1981), where both pairs of species have similar foraging techniques, vertical use of the forest and locomotion; or c) they replace each other in a discontinuous manner, as is the case of *S. nigricollis* and *S. fuscicollis* in parts of Colombia and Peru (Freese et al., 1982; Moynihan, 1976; Soini, 1972), both of which forage at all levels of the forest while concentrating on large prey.

Use of plant resources appears superficially similar in all species of tamarins studied to date--including species that form mixed species groups--in that ripe fruits are taken from terminal branches, mainly in the subcanopy of the forest (Mittermeier and Van Roosmalen, 1981; Soini and Coppula, 1981; Terborgh, 1983). Species of tamarins that do not form mixed groups, have similar body size (less than 20% difference), practice similar foraging techniques which probably result in similar prey taken, and utilize similar strata of the forest, all of which seems to preclude the formation of mixed species groups.

C.- Habitat use

Since food acquisition and range use will be documented for *S. mystax*, I will briefly review the theoretical background on habitat use in primates.

Food is perhaps the single most important resource that animals must garner in order to survive and reproduce, and as such influences every aspect of their lives. Traits of morphology and physiology determine the sets of behaviors open to an animal, or its behavioral capabilities (treated at length in Rodman and

Cant, 1984). Behavioral capabilities--especially of morphology, see Milton (1984) and Kay (1984)--enable solution of problems associated with food acquisition, and in interaction with the available food resources determine the manner of solution (Cant and Temerin, 1984; Oates, 1987), with diet as the outcome. For example, the relatively high metabolic rates and limited gut volumes of most small-bodied primates such as tamarins necessitate a diet high in nutrient quality and available energy (Garber, 1987).

The distribution and abundance of resources exerts a strong influence on patterns of home range use by primates (Clutton-Brock, 1977; Oates, 1987). Other resources, such as sleeping sites and water holes also influence ranging patterns. Range size is influenced by both dietary requirements and the distribution of food in space and time (Oates, 1987). If a group of primates is able to find all the food it requires within a small area, it will often forage over a relatively fixed range (Cheney, 1987). On the other hand, patchily distributed food resources result in larger, variable ranges (Clutton-Brock and Harvey, 1977). Foraging strategy theories have recently emphasized the role of memory and learning in feeding patterns (Garber, 1987; Oates, 1987). It has been proposed that the use of a circumscribed home range results in familiarity with it and perhaps more efficient exploitation of food resources. A number of studies have found evidence of goal directed travel to food patches which suggests that primates might possess mental maps of the environment (Altmann and Altmann, 1970; Milton, 1980; Robinson, 1986; Whitten, 1982).

Defense of the home range, or at least part of it, is common in primates (Oates, 1987). Territoriality or the defense of a fixed, exclusive area will evolve where the resources are limited but are distributed in such a way that can be economically defended (Brown and Orians, 1970). Unlike in many birds, territories in primates are all-purpose (sensu Hinde, 1956). The main benefits of territoriality are the undisputed access to resources and the provision of a place for mating and/or raising of offspring unhindered by conspecifics, which results in improved reproductive success (Odum and Kuenzler, 1975). Territory establishment and mate acquisition are interdependent prerequisites for successful breeding in some bird species, with the breeding advantages prevailing over the exclusive access to resources (Brown, 1964). Demographic data in tamarins (Neyman, 1980; Soini and Soini, 1983) and the Kloss gibbon (Tilson and Tenaza, 1976) suggest that territories must be established before breeding can take place. Body size, home range size, diet and degree of mobility all can affect whether an organism will defend a territory, as well as providing predictions about the size of the defended space. For example, vervet monkeys displayed territorial behavior when resources were scant (Harrison, 1983), while west African green monkeys with large home ranges practiced resource defense (Kavanagh, 1981).

D.- Scope of this study

In the next three chapters of this dissertation I will describe the use of space and food resources by the moustached tamarin at the Blanco Stream site. In addition, I will explore the nature of mixed species associations of S. mystax and S. fuscicollis by looking at the effects of artificially cropping S. mystax from a mixed population at the Yarapa river.

It is widely believed that ecological factors such as distribution and abundance of food resources have a profound effect on the social life of primates (Clutton-Brock, 1977; Terborgh, 1983). To gain some understanding of the adaptive strategy of S. mystax it is necessary to study the behavioral aspects of their ecology such as activity patterns, food selection and ranging behavior. These aspects of behavioral ecology need to be related to the resources available, and, as much as possible to the nature of competition and predation pressure (van Schaik, 1983; van Schaik and van Hooff, 1983).

The ultimate objective is to find out what ecological factors are relevant and how they affect social life. There is evidence however, that recent history as reflected in demographic patterns and social relationships affects social organization. Obviously, the standard length of most primatological studies--and this study--will be limited in showing which features of social life are consistent over time.

Insight into the ultimate benefits of sociality can be gained by studying the demographic effects of removing one species of tamarin from a mixed species population of S. mystax and S. fuscicollis.

In the following sections I will address a number of questions which include:

What are the characteristics of food sources? How do they influence use of space? What is the extent of exudate feeding? What are the relations with conspecifics and predators? What are the constraints on range use? What can we learn about the association of S. mystax with S. fuscicollis from data on artificial cropping?

It is hoped that the answers to all these questions will contribute to a better understanding of the pressures shaping the behavior of tamarins.

In Chapter II, I describe the two study areas and the different methods utilized in the field, and for data analysis. Chapter III contains the results and discussion of the demographic data at both study sites; as well as results and discussion of activity budgets, diet and use of space at the main study site. In Chapter IV a summary of the modus vivendi of the moustached tamarin, as gleaned from this study, is followed by a discussion on predation risks confronted by the moustached tamarins, which ends with an assessment of the benefits of living in mixed groups.

CHAPTER II.- THE STUDY SITE AND METHODS

The feeding behavior and demographic aspects of S. mystax , and its association with S. fuscicollis were studied at two locations in western Amazonia, Peru: the Blanco Stream of the Tahuayo River (1,150 hours: over 800 hours sampling the behavior of the tamarins and the remainder in primate censusing and forest surveying) and Yarapa River (350 hours, most of which were spent in primate censusing) for a total of 1500 hours between June, 1981 and November, 1982 (Fig. 2). At the Blanco Stream, after the initial survey a site was chosen to build a house in the local style and an area of about 2 sq km was designated as the main study area. A trail system was cut through the forest and I proceeded to census the tamarin population. Subsequently, two groups of moustached tamarins were trapped, fitted with color-coded collars and released for observation. One individual in each group was fitted with a radio-transmitter. After a period of habituation the monkeys were followed daily from the moment they left the sleeping tree until they retired to a sleep tree for the night. Observations were collected successfully on five consecutive days each month for 13 months for one of the groups (Green group); the second group (Red) was followed successfully for only two months. The tamarin carrying the radio-collar in the Red group died and the rest of the tamarins-always wary of my presence-were impossible to follow for any length of time without the help of the radio-transmitter. Most of the observations presented in this dissertation for the Blanco Stream site derive from 13 months of intensive data collection between October 1981 and November 1982.

At the Yarapa River site two censuses of the population were taken at intervals of twelve months: in July 1981 and July-August 1982. In addition five groups of tamarins were trapped, tagged with color-coded collars and released during the 1981 census. No radio-transmitters were used at this site.

A.- Description of the Blanco Stream Site

1.- Location.- The study site is located at Fundo Nuevo Conquistador, on the left bank of the Blanco stream. The Blanco stream (4^{o} 15'S,73^{o} 04'W) is a narrow, meandering, white water tributary of the Tahuayo River, which in turn is a primarily black-water tributary of the Amazon River (Fig.2). The closest large city is Iquitos, approximately 110 km away. During the rainy season Iquitos is 5.5 hours away by 40 hp speedboat. At most points the Blanco stream is about 6-8 m wide narrowing progressively towards its headwaters in the Yavari-Mirin hills near the Brazilian border. Water levels on the stream change rapidly, and during most of the dry season (from June to August) the stream dries up completely for several days at a time,precluding navigation.

The Blanco stream site was chosen because of the relatively pristine condition of the forest (due to its remoteness) and the abundance of tamarins (Castro and Soini 1978).

2.- The forest.- Following Holdridge's (1967) classification of plant formations, the life zone is that of tropical wet forest. Both banks of the Blanco are lined with primary forest which is only minimally disturbed by human habitation at the study site. Most of the forest is on high ground and never inundated. The riverine vegetation near the confluence with the Tahuayo River is flooded for a few weeks at the time of high water in March-April. At this time, and because of the differences in color of the waters, it can be observed how the Tahuayo ingresses the white waters of the Blanco for a few kilometers. In turn the Tahuayo is pushed back by the formidable volume of the Amazon river. At the study site the riverine forest is flooded frequently for a few days at a time, and although the flooding coincides with the overall rainy season for the region, it is more dependent on local rains at the headwaters than on the high water mark of the Tahuayo or Amazon Rivers. Thus, sections of forest near the stream edge were inundated as early as November.

3.- Habitats at the study area.- Six different habitats can be distinguished within the study area: stream edge forest (sometimes inundated), high ground forest (not inundated),low forest, vine forest or bajial, palm swamp forest or aguajal, and forest clearings (Fig. 3)

a.- Stream edge.- Near the stream edge the vegetation is generally low with trees commonly 6-10 m tall, although a few trees over 25 m can be found. Cecropia sp., Inga spp. and "Quillusisa" (Vochysia sp., Quararibea sp.) are common along the stream banks. The undergrowth varies from sparsely growing saplings to patches of dense growth with many vines and densely branched trees which can cover extensive areas along the stream edge. This type of habitat covered a considerable portion of the Red group's range. On the other hand, the Green group's range included a very small area of stream edge forest.

b.- High ground forest.- High ground forest covers most of the study area which has been largely undisturbed by local inhabitants, except for a small amount of felling of some large trees. Most of the tree species are evergreen with only a few deciduous species. The tallest trees occur in this habitat, a few reaching 40 m (e.g. Pithecellobium sp., "remocaspi"; Parkia sp. "pashaco"), but trees 17-22 m tall, are more common (e.g. Pourouma spp., "uvilla"; Hymenaea spp., "azucar-guayo", Iriartea sp.,"cumala") which form a continuous canopy layer. Beneath this a storey of a few short (up to 10 m tall) slender trees can be distinguished. The undergrowth is sparse and composed of a few saplings and palms (Lepidocaryum sp. "irapay"; Geonoma sp. "palmiche"). In most areas from 2-10 cm of leaf litter can be observed. This type of forest seldom inundates, except at low lying areas in between slopes and then usually for only a few hours at a time.

c.- Low forest.- Low forest grows on flat terrain. The vegetation is dense, composed of slender and medium-sized trees and lianas which reach up to 20 m, but more commonly are 10-15 m high which unite in an uninterrupted canopy; very rarely a few 30 m trees are observed. The undergrowth is dense and composed of tree saplings, some shrubs (Rubiaceae, Melastomataceae) and a few palms. Portions of the low forest are inundated frequently during the rainy season as a result of the overflow of streams. Most of the soil surface is bare with little or no litter accumulation and with many exposed roots.

d.- Vine forest.- The vine forest, or bajial, as the Spanish name implies, grows on low lying ground (from 2-4 m below the ground level of the high forest) usually bordering a stream. When the stream overflows it inundates the bajial for periods from 3-8 days from October through May. Very dense, tangled low vegetation that impedes movement covers the area. Most of the vegetation is composed of woody lianas and short low branched trees intercalated with a few trees that branch above 8 m.

e.- Palm-Swamp forest.- The palm-swamp forest or aguajal grows throughout the area intercalated with the high ground forest. The soil is water-logged and the vegetation sparse and composed mostly of palms which average 20 m high and some trees reaching over 30 m . The most common palms include Mauritia flexuosa "aguaje", species of Iriartea sp. "pona", and Huasai sp.

"chonta". The understorey is open with occasional stands of Heliconius sp. Aguajales are usually found on terrain that is generally 2-3 m below the level of the high ground forest.

f.- **Forest clearings.**- Forest clearings are either the result of naturally occurring falls, cultivated fields "purmas", or "supaychacra"(devil's farmland) as they are called locally. Cultivated fields were found only close to the Blanco stream and occupied approximately 4 ha of the main study area . "Supaychacras" are naturally occurring open areas within the high forest which are characterized by sparse, low trees and shrubs (2-7 m tall) of sclerophyllous appearance growing on bare, light colored soil.

4.- **Climate.**- The changes in temperature throughout the year were minor. The hottest days were recorded in June and September (38^{o} and 40^{o} ^{o}C) while the coldest temperatures were recorded in July and August (19^{o} and 20^{o} ^{o}C). The amount of rainfall and the changes in stream water level showed the most obvious seasonality. During the thirteen months of intensive observations it rained every month, but there were peaks in April-May and November-December. It rained the least from June to August (Fig 4). In September the first heavy rains announced the beginning of the rainy season which extended until April-May. Records of temperature and rainfall are summarized in Table 3. The stream level changed considerably from day to day, but from September through May there were a few meters of water in the stream most of the time. Even though there was water in the stream from June through October 1982 there were days when only a few centimeters of water covered the bottom. Although the study site is only 40 km from the mouth of the stream, in August 1981, it took three days to reach the study site by a combination of paddling, carrying the canoe over logs, and walking over the stream bed.

5.- **Forest phenology.**- There appeared to be a lag between the onset of the rainy season and fruit production. Although rainfall increased in September 1982, fruit production as measured by the index of fruit abundance (Fig. 5), did not increase until a month later. New leaves however were observed on many trees a few days after the first rains.

6.- **Primate fauna** .- Eleven species of primates were observed within the main study area. The most common primates were S. mystax, S. fuscicollis, Cebuella pygmaea, Aotus sp., Callicebus moloch cupreus and Pithecia monachus. Cebus apella and Cacajao calvus rubicundus were observed rather infrequently. C. albifrons, Saimiri sciureus and Ateles sp. were seen only a couple of times. Lagothrix lagotricha was reported to occur further inland, and had been hunted in the past.

7.- **Predators.**- Eagles (Accipitridae) and Hawks (Falconidae) were not uncommon; tayra, (Eira barbara, Mustelidae) and small felids were also seen in the area.

8.- Human influence.- Human habitation was negligible and only six families comprising a total of about 30 people lived scattered along the 70 km of the stream. Only four families were permanent residents, the rest were transient hunters and/or members of a logging crew. Slash and burn subsistence agriculture was practiced by the residents as well as fishing and hunting. Monkeys were infrequently hunted, although *C. calvus* was occasionally hunted to keep the infants as pets. At the study site about 1 ha of somewhat disturbed forest was burnt for cultivation and another hectare of secondary forest was cleared for the same purpose during the 16 months of the study.

B.- Methods at the Blanco Stream Site

1.- Data recording .- A field notebook was used to record observations. Pages were pre-labeled according to pre-established categories (See section B6). Additionally continuous notes were taken ad-libitum.

2.- Climate.- Records of temperature and rainfall were taken from September 1981 through October 1982. Temperature was measured with a maximum-minimum thermometer placed in the house under the shade and most probably reflects well the conditions in the forest. Rainfall was measured with a rain gauge placed outside the house in an adjacent forest clearing. To standardize comparisons of temperature and rainfall from month to month I included records for temperature and rainfall for 15 continuous days for every month on Table 3. Since I had to leave camp every month on supply trips of various lengths, daily records of temperature and rainfall are not complete.

3.- Trail system .- A trail network of 18 km was opened after locating some of the tamarin groups living in the vicinity and after learning some of their movements (Fig 6). Most trails followed predetermined compass bearings. Trails were named and marked with plastic flagging every 50 m.

4.- Census.- With the objective of locating two study groups and deriving a density estimate of the tamarin population, censuses were conducted in June, July and October 1981. Eight kilometers of trail were covered during each census, making a total of 104 km. Between June and October, 1982, censuses of the tamarin troops were repeated and 63 km of trail were covered. Between June and August 1981 several researchers helped with the census.

Trails were walked by teams of two observers and also singly. On most days three trails were covered simultaneously. Routes followed included straight trails and one circular route which bordered an area of about 1.5 sq km. Four census routes were established and they were censused repeatedly. Census walks were made from 6:00 to 10:00 a.m. and in the afternoon from 13:30 to 16:30. Groups were located either by their vocalizations or by visual detection. Groups were classified as either reproductive or incipient following Soini and Soini(1982). Soini and Soini(1982) characterized reproductive groups as composed of 3-12 individuals: a pair of adults (female lactating, post-lactating or pregnant) plus up to three successive litters; incipient groups were characterized as small, non-reproductive groups, with 2-3 individuals which were usually young adults; juveniles or infants have never been observed in incipient groups

After locating a group, an effort was made to count and classify all individuals. Age-class categories were based on size and although we could discriminate between adults and juveniles or infants, it was more difficult to distinguish between closer or intermediate size categories (e.g. small subadults from large juveniles).

All sightings were entered on a map of the area (map location method). Multiple sightings were particularly useful in distinguishing one group from another. The number and composition of the associated S. fuscicollis was another criterion. The size of the group was accepted as accurate after several consistent counts had been accumulated.

Density figures were based on complete counts of four identifiable groups of tamarins--observed repeatedly--living in an area of 100 ha. Three groups were classified as reproductive and one as incipient. Two of the reproductive groups (Red Group and Green Group) and individuals belonging to two other groups were trapped and marked with bead collars (see trapping and marking). Density figures were calculated at the end of the study. Information gathered from intensive observations indicated that about 15% of the census area was shared with other groups of tamarins. Calculations were made as follows: total number of tamarins found living entirely within the study area + proportion of that number that would live in 15 hectares.

Density figures for the other primate fauna are estimates based on opportunistic counts during the study period. Every time that a primate group was sighted--even in the course of intensive observations--an effort was made to count and classify all group members.

Biomass for tamarins was estimated by using body weights obtained during trapping. Average body weights for each of the age-sex classes were employed in the calculations. Average body weights for the other primates were obtained from Terborgh (1983).

5.- Trapping and marking.- The trapping method here employed has been used extensively in the capture of S. mystax and S. fuscicollis (Encarnacion et al., 1977). Basically, the tamarins are habituated to feed on ripe bananas inside a trap. Thereafter trapping is attempted.

In 1981 after locating several groups of tamarins in the forest, baits made of bunches of ripe bananas were tied to trees at several of the observation sites. Captive tamarins of both species were used as decoys. Baits were left very early in the morning and checked at midday, early in the afternoon, and late in the afternoon. After the monkeys had fed twice in a day or two days in a row at a particular site a platform was built and the bait was left on top of it. Once the monkeys fed on top of the platform, a multiple trap was set on it and bananas were placed inside the cages. At this stage a person concealed inside a palm blind 3-4 m away from the platform checked on the total number of tamarins in each of the groups that came to the trap, how many entered and fed on the bananas, and whether moustached tamarins were feeding on the bait (usually, saddle-backed tamarins were the first to get "hooked" on eating the bananas).

Before dawn the next day bananas were placed in each of the compartments of the multiple trap and a person would then hide inside the palm blind. Each of the doors of the multiple trap could be opened or closed from inside the blind. The monkeys occasionally could be trapped all at once, but more frequently it took several hours until all members of a group were caught. After this, the tamarins were removed from the trap one by one and an intramuscular injection of Ketalar (0.1 cc/500 gm) was administered to the inner thigh. Immediately after, the tamarin was released into a yute bag to wait for the drug to take effect, which took about two minutes. Thereafter, the following body measurements were taken with the help of a Pesola scale, a ruler, and a caliper: weight, body length, tail length, measurements of the genitals and their appearance: pigmentation, suprapubic gland (degree of development and production of secretions); condition of the nipples and breasts: size, secretions; length of the canines and general condition of the dentition; presence of scars. All monkeys (except the infants) were tattooed on the abdomen with a two digit number. Animals of subadult and adult characteristics were fitted with chains bearing code-colored beads (3 beads, one for each: group, sex, individual). Afterwards the tamarins were returned to the traps to recover. After the animals appeared to have recovered completely--which took about three hours on average-- the doors of the trap were opened from inside the blind and the monkeys quickly jumped out. One individual in each of the two groups trapped was fitted with a radio-collar instead of the bead collar. The radio-collar transmitted signals at a specified frequency. The signals were picked up by an antenna and relayed to a receiver, which amplified the signal (SM-1 transmitter on BT collar, LA-12 receiver, and 3 element antenna from AVM Instrument Company, Dublin, CA 94568). The radio-collars were covered with brightly colored tape to aid in identification of the carrier.

The tamarins that did not enter a trap or escaped during handling were identified as to sex and approximate age. Tamarins that did not enter a trap generally sat near by or on top of the trap and it was easy to assign them to an age category (based on size) and in most cases to sex them.

During capture special care was taken to keep handling of the monkeys to a minimum. During the numerous trapping campaigns of the Proyecto Primates it had been observed that individuals of some populations manifested a trapping syndrome locally known as "tembladera". This is usually manifested by a series of very strong convulsions that usually ended with the death of the animal. Sometimes the prompt release of a tamarin from the hand grip allowed it to recover (L. Moya, pers. comm.). Considering this observation, every effort was made to allow less than a minute between the moment when we grabbed a tamarin and the administration of anesthetic, immediately after which the tamarin was released into a yute bag.

Special care was given to back-carried infants. Back-carried infants were quickly removed from the back of the carrier--we wore new gloves during this procedure--and placed inside the trap. Once the measurements of the carrier were taken, it was immediately returned to the trap. It has been suggested that handling of infants can prompt rejection by the carrier which may result in the death of the infant (L. Moya, pers. comm.). Even with the precautions at the Blanco site, one infant was mauled to death by its carrier (a young adult female) upon awakening from the effects of the drug. In this case it seems more likely that the confinement inside the trap upon awakening, combined with the general excitement of the tamarins in other compartments (rather than olfactory cues) contributed to this behavior.

Re-trapping of tamarins to change radio-collars when the batteries ran out proved very difficult. The tamarins did not seem to pay much attention to any type of decoy: I tried both species of tamarins, and adults and juveniles of both sexes. Various baits, e.g., bananas of different varieties, wild fruits being consumed at the time by tamarins, and even large grasshopers caught live, tied by one leg and kept jumping inside the trap, failed to entice the tamarins. Only two individuals belonging to the Green group were re-trapped during the next four months after many days of baiting traps at different sites. Unfortunately, in one case the radio-collar only signaled for little over a month and in other not even for 24 hours. (See Chapter II D3, for comments on trapping success at both study sites).

6.- Sampling techniques for activity budgets and diet.- The behavior of each of the two marked study groups was sampled intensively for five consecutive days each month. To make observations comparable and allow the researcher to recover from fatigue, the five-day samples were separated by three days and taken in the same order. The Red group was followed first. Every sample day I located the sleep tree of the previous night and began noting observations as soon as it was light enough to discern activities. This was usually about 6:00 hours. Observations were recorded for as long as the animals were active. While tracking equipment was used, group location was uncomplicated. However, from March 1982 until the end of the study, the Green group had to be located the day before starting the next sampling period. This was accomplished by walking throughout the known ranging area until the animals were located, and they were followed until they entered their sleeping tree, so their location was known the next morning.

The small size of the tamarins and quickness of movement combined with the considerable height at which they move made sampling of activities a difficult task. Focal sampling (sensu Altmann, 1974) proved impractical since any one individual could not be observed continuously for more than one or two samples. Furthermore, the bead collars could not be distinguished most of the time. Thus, the main advantages of focal sampling, namely, the ability to record activities of a known individual for an extended period of time and at short intervals so as to get data on duration and sequence of activities, were lost. Radio-tracking could have been the ideal tool to keep track of at least one individual, however, the radio-collar bearing tamarins (a female in both groups) usually moved in front of the group and I found out that I could not follow her close enough to see what she was doing without disturbing the rest of the group. Thus, a compromise strategy was to follow the group slightly behind and on the side as this angle provided the best view of all members of the group. In this way scan-samples (sensu Altmann, 1974) of the activities of all members of the group were taken at five minute intervals. Determination of the activities usually took from 3 to 6 seconds for each individual.

From the start it was obvious that intra-group behavior was very difficult to observe and quantify so I decided to concentrate on getting as much ecological data (mostly feeding) as I could, but always being alert to any details of behavioral interactions, which were recorded ad-libitum.

Data were collected on six different activity states: plant feeding, insect foraging, traveling, resting, vocalizing and miscellaneous.

a.- Plant feeding.- Feeding on plants included inspection and handling of vegetable matter, bringing it to the mouth, chewing, licking and ingesting. When I could not see clearly if the tamarins were feeding, the time spent on fruit or exudate trees was assigned entirely to feeding. During plant feeding additional information recorded included: food categories (fruit, flower, seed, leaf, bark, exudate); part that was eaten(mesocarp, exocarp, aril,whether seed was swallowed). This was determined by direct observations of the tamarins combined with inspection of the fruit remnants around the tree. The exact minute when tamarins entered and exited a fruit or exudate tree was noted, in order to provide the total time spent feeding on a particular plant source.

b.- Insect foraging.- Foraging for insects included all activities connected with finding (scanning "intently" around, turning and inspecting leaves, looking underneath twigs and branches) and ingesting animal matter. Activities associated with foraging for insects seemed to follow a pattern in which scanning "intently" usually was followed by pouncing or quickly grabbing something that was transferred to the mouth. The prey was identified from direct observations and/or from the remains that occasionally reached the forest floor. Foraging included slow locomotion and brief periods of sitting while scanning.

Insect foraging bouts were defined as foraging sequences that usually started with scanning of surroundings, and ideally finished when the tamarin captured a prey and ingested it. On many occasions, however, insect foraging bouts finished unsuccessfully when an attempt to catch prey failed or when the search was abandoned. The search was considered abandoned when the tamarin began another activity, e.g. fruit feeding, inactivity, etc. Inactivity was initially very difficult to distinguish from long-distance scanning, but if it lasted over ten seconds, then it was decided that the foraging bout had ceased. Samples of foraging sequences were taken throughout the study.

c.- **Traveling.**- Travel was tallied when the animal was moving from one tree to another, apparently unrelated to foraging for insects or fruit feeding.

d.- **Resting.**- Inactive while animal sitting or lying down on its side. Included short periods of inactivity (a few minutes at a time) when the tamarin would be sitting on one spot seemingly alert to what was going on around. This last was not always easy to distinguish from scanning while foraging for insects, although sitting periods during insect foraging were usually brief(less than 20 seconds).

e.- **Vocalizing.**- Whenever moustached tamarins vocalized an effort was made to identify the caller, as well as its location . Notes were taken on the circumstances of the call.

f.- **Miscellaneous.**- included activities such as allogrooming, play, territorial behavior (fights, chases), marking, etc.

Additionally, at each scan interval the following were noted:

- the height at which the activities took place according to 5 m blocks.
- the type of support, whether bough (> 10 cm diameter) branch (< 10 > 4 cm), or twig (< 5 cm).

- the type of habitat: high forest, low forest, aguaje-palm association,low vine forest(bajial). I also distinguished the aguaje-High forest transition.

- the location in space: I took a compass reading of the position of the group as a whole in relation to known trees and trails.

- whether or not S. fuscicollis was moving nearby. Depending on the habitat type I could detect saddle-back tamarins within a 10-40 meter radius around the moustached tamarins. The spatial center of each group was estimated and the distance between centers was calculated. The activity of saddle-back tamarins as well as the height at which it was performed were determined by observing the first sadle-back that came into view. Ad-libitum samples of insect foraging sequences in the saddle-back tamarin were also taken.

Between scans, samples of the duration of a foraging sequence were taken. A foraging sequence started with scanning of the substrate and ended with the capture and ingestion of an invertebrate or with a change of activity towards non-foraging. The supporting structure during a foraging sequence was also noted: tree,vine, palm, as well as the substrate:leaves, branch surface and the success of the search. Whether the search was successful or not was only discernible if the tamarin pounced on an invertebrate (although I couldn't always be sure that it was an invertebrate). Foraging success was rated as positive or negative (+ or -).

Ad-libitum observations included: identification of infant carrier, order of progression, marking behavior, behavior during a territorial encounter. In territorial encounters an effort was made to identify the position (front, back) and role played by the different tamarins in the confrontation as well as the length of the episode.

The results presented in this section derive entirely from 57 full days of observation of the Green group distributed in 13 monthly samples from October 1981 through November 1982, making approximately 700 hours of observation (Table 2). Only two five-day monthly samples were gathered for the Red group, plus a number of short observations in the following months. The death in December of the radio-collared tamarin belonging to the Red group, our unsuccesful attempts at re-trapping, and the fact that the members of this group still reacted strongly to the presence of the observer after almost three months of observation made continuous following of this group without the aid of radio-telemetry a very frustrating proposition.

7.- Ranging.- At the start of the study radio-tracking was very important in getting accurate information on ranging in these tamarins which otherwise were easily lost. The first day of the sample, the sleep tree of the previous night would be marked with dated flagging tape. As the animals began to move I followed their route, taking compass bearings of the direction of their movement from the sleep tree, then trees along the way were marked accordingly with flagging tape for future identification. At the start of the study I simply tied plastic flagging to trees along the route of the tamarins. I noted the date and time on the plastic strip. Additionally when crossing trails I checked the distance to the nearest tag and noted the direction of movement. I later returned and plotted this information on movement on an accurate map.

8.- Plant sampling.- To document the differences in forest structure, ten plots of vegetation, each 20 m by 20 m were selected within the main study area. The height and girth at breast height were recorded for all trees with a girth of at least 10 cm. In many cases a height finder was used to calculate height. Two vegetation plots of each habitat type--except edge forest and forest clearings which were sampled only once--were included in the samples.

To examine fruit phenology a total of ten trees representing six species were located at the beginning of the study and were monitored every 5-8 weeks. Since very little was known of the dietary preferences of the tamarins I interviewed the local inhabitants about monkey foods, with little success, which accounts for this very small initial sample. During the course of the study twenty additional trees--representing 20 species--were included in the sample as more fruit species eaten by the monkeys were discovered. Crowns of trees were scanned with binoculars and whether they had flowers or fruits was noted according to the following scale: whole crown covered, half crown,less than half crown. Additionally the fruits were classified as ripe or unripe and an effort was made to discover the proportion of each according to the folowing scale: all ripe or all unripe, half and half, few ripe/unripe.

To investigate fruit abundance I conducted a 4 km trail census every month. I randomly selected a route within the Green Group's study area and walked it counting the number of fruiting trees encountered. I looked for fruiting trees by scanning the forest floor for evidence of fruit drops. Walks were usually taken immediately after each of the sampling periods. Upon finding a tree I usually estimated crown size and crop size. Crown size was estimated by a combination of several methods: measuring the fruit shadow below the tree, scanning the crown with binoculars and, when needed, my field assistant climbed up a neighboring tree and estimated crown and crop size. Crop size was classified according to the scale used to examine fruit phenology.

Collection of tamarin plant foods was usually accomplished 1-7 days after the 5-day sampling period for the month. A botanical sample was collected by my field assistant who climbed the tree. I collected data on: tree height, crown size, fruit abundance, status of fruit available: ripe, unripe and proportion of each (according to the fruit phenology scale), presence of flowers: yes or no. Each tree species was subsequently tagged with a numbered metal ID tag. Plant samples were identified by the staff of the New York Botanical Garden and by Alwyn Gentry of the Missouri Botanical Garden.

9.- Analysis of data

a.- Activity budgets.-For the purpose of data analysis each of the individual activity states counted as an activity record for the five minute interval. Percentages for each activity were then calculated in relation to the total activity records for each five minute interval. These percentages were added and divided by the total number of five-minute intervals in each sample hour. These hourly percentages were then added and divided by the total number of hours of activity for each day, to obtain the mean percentage of time spent at each activity. For example when observing a group of five animals, and during the scan three animals were feeding on fruits while two were sitting inactive, then for that scan 60% were feeding and 40% resting and so on for each scan. For each hour of observation, activity records were noted with accuracy for all tamarins in seven out of a possible 12 scans on average. Only full sample days (from rising of the monkeys until they entered their sleeping tree) were used for the calculation of activity budgets.

b.- Feeding.- I have used data on the duration of feeding episodes (see Chapter II B6a), rather than scan sample data for the detailed analysis of feeding data. Scan sampling tends to underestimate short visits to fruit trees (those that occur between scan intervals) and underestimates long visits that start and finish outside of a scan interval (e.g. a visit from 7:11 to 7:19 will be recorded at the 7:15 scan although it lasted for 8 minutes. In addition, by using exact length of plant feeding episodes I can compare my data with the only other tamarin study that includes this kind of data (Terborgh, 1983).

Feeding time on plant materials has been calculated following a method similar to that of Terborgh (1983) in his treatment of feeding data for tamarins. Total feeding time for a visit to each tree was obtained in monkey-minutes of use by adding the number of individuals feeding throughout the length of a visit. These total monkey-minutes of feeding divided by the number of individuals in a group gave group-minutes of feeding for a given tree. These in turn were added for the different food trees of the day giving total daily feeding time on plant material.

c.- **Ranging.**- To estimate path length I used two methods. In November and December 1981 I retraced the route followed by the monkeys and measured it by counting strides of known length. This was transferred to a map of the area. Later on, when I was more familiar with the site, I traced the route directly on the map, since many times it proved impractical to retrace the travel route for each day. During data analysis detailed maps showing location of fruit trees, routes followed, and site of territorial encounters were prepared. Daily distances traveled were measured from the maps.

In the calculation of home range, a 25 X 25 m grid--the small grid was chosen to avoid overestimating the size of the home range--was overlaid on a map of the area containing the tracings of the tamarins' movements. All quadrats entered by the moustached tamarins were included in the calculation of the home range. Sightings of neighboring moustached tamarin groups within quadrats of the Green group's home range were used to estimate the percentage of range overlap.

Quadrat use was estimated by counting the number of times that the moustached tamarins entered 50 X 50 meter quadrats superimposed on the travel route maps.

d.- Fruit abundance.- To give a numerical idea of fruit abundance I gave each fruit tree encountered during the census walks two numerical values- one for crown size: 1(1-3 m), 2(>3-5 m), 3(>5 m); and another for crop size : 1 (few fruits), 2 (half crown had fruits), 3 (whole crown covered with fruits). Using these values I estimated an index of fruit abundance (ranging from 1-9) by multiplying crown size x crop size for each month.

e.- Habitat distribution within the range of the study group.-The boundaries of the different habitats within the study area were obtained during the daily reconnaissance of the area and by noting the different habitat types at each stop on the trail system. A detailed habitat map was prepared while in the field (Fig. 7). A grid with 25 m/side was overlaid on the map and the area covered by each habitat type was thus calculated.

In the case of the Green Group's range, high forest covered more than half the study area (58%) with the low forest covering 26%, palm swamp about 8%, vine forest 5% and cultivated fields only 3%.

f.- Distribution of fruit trees within the range of the study groups.- a map with the distribution of fruit trees utilized by the tamarins was superimposed on a map showing the distribution of the different habitat types.

g.- Statistical tests.- All statistical tests were performed on untransformed data. SAS statistical package was utilized at the Computer facilities of the Graduate Center, City University of New York. Wilcoxon tests, and Spearman rank correlation tests, will be represented in the text by W: and rs respectively. Chi-square value is represented by x.

Two databases were used for analysis: the main database contained hourly records for each day for the different activities and path length; the second database contained plant feeding time per day (fruit feeding, exudate, other) and number of food trees visited, number of species visited , and path length.

C.- Description of the Yarapa River site

1.- Location.- The Yarapa River is a black water tributary of the Amazon (Fig 2). The study site is located about 15 km from the mouth of the river (04°31'S, 73°22'W). S. mystax is found only on the right bank of the lower Yarapa and on both banks near the headwaters. It is absent from the inundated forests of the lower left bank (Moya et al., 1979). The main study area includes approximately 2 sq km of forest on the right bank of the Yarapa River (Fig 8).

2.- The forest.- Following Holdridge (1967) the life zone corresponds to that of a tropical wet forest. The forests of the Yarapa river have been subjected to human encroachment for a long time due to its size and proximity to the Amazon river. Most of the forest along the river edge is secondary and its banks are utilized for rice cultivation especially in the lower Yarapa. Fruit orchards are distributed away from the river edge in small plots surrounded by secondary forest.

Further inland the forest has been disturbed to different degrees usually along a gradient that goes from heavily exploited to minimally disturbed as one moves far away from the river edge and navigable streams.

3.- Habitats at the study area.- The main study area is covered by a combination of vegetation growing on abandoned fields "purmas", cultivated plots, a grassy area, vine forest, moderately disturbed tall forest, secondary forest, and swamp forest. Most of the terrain is flat and traversed by three streams.

a.- Vine forest.- About one-third of the study area is covered by the vine forest which is inundated annually for about 8-10 weeks during the rainy season. The vegetation in this habitat shows a preponderance of woody lianas, a broken tree layer with trees 5-10 m high, and an abundance of the "nejilla" palm, _Bactris_ sp. Most of the vegetation in the "purmas" consists of thick undergrowth and low trees (maximum 7 m tall).

b.- Secondary forest.- The secondary forest, with trees as tall as 12 m is restricted to the area along trail B, and blends well with the tall forest.

c.- Tall forest.- The tall forest, a moderately disturbed forest, with trees 17-20 m tall, occupies most of the southeastern portion of the study area.

d.- Palm-swamp forest.- The "aguajal" occupies most of the east and southern section of the forest.

e.- Forest clearings.- The purmas, cultivated plots and the grassy area all have cultivated fruit trees which are regularly utilized by the tamarins. In addition, _Spondias mombin_ and _Pourouma_ sp. are common in these habitats. The camp site is surrounded by a grassy (man-made) area which houses some cattle. The cows made limited use of the forest around the house.

4.- Climate.- Essentially the same as at the Blanco Stream site.

5.- Primate fauna.- Besides *S. mystax* and *S. fuscicollis* other monkey species observed included: *S. sciureus*, *C. pygmaea* and *Pithecia hirsuta*. *Callicebus moloch* and *Aotus* sp., are also known to occur in the area. Both species of tamarins were the most abundant primate species in the area with *Saimiri sciureus* perhaps the second most common primate.

6.- Predators.- Hawks are common as well as *Eira barbara*; *Felis yagouaraoundi* is also present.

7.- Human influence.- Human habitation is high compared with the Blanco stream site and, although mostly restricted to the river edge, many small cultivated plots (about 1 ha) are found in higher terrain. Also, the palm swamps are exploited heavily for the extraction of "aguaje" fruits (*Mauritia flexuosa*) which are later sold in the local markets.

Hunting of primates is an infrequent activity now. *Ateles* sp. and *Alouatta seniculus* lived in the area as recently as twelve years ago, but they seem to have been hunted to extinction in the lower Yarapa, although they are still reported to occur near the headwaters. The tamarins are not hunted but are occasionally caught and kept as pets.

In terms of habitat modification, the only discernible changes between 1981 and 1982 were the clearing of about 3% of the forest for agriculture and the fact that part of the habitat of the tamarins was affected by one of the largest floods in Amazonia during the last ten years. Interviews with local inhabitants indicated that the forest cover had not decreased more than 5% between 1978 and 1981.

D.- Methods at the Yarapa River site

1.- Trail system.- An existing trail system of about 10 km was cleared and extended for a few kilometers. The trail system was mapped, measured and plastic flagging was placed every 50 m.

2.- Census and Trapping.- The same methods utilized at the Blanco site were employed at this site. A total of 184 km of trail were censused in July 1981. The 1981 census was supplemented by the trapping of several groups of the moustached tamarins. During trapping I followed the same procedure as at the Blanco site.

Twenty-two individuals from five different groups were captured, tattooed and released. All adult-sized tamarins (14) were fitted with color-coded bead collars; however, these were of limited use in the identification of individuals in the census of 1982. Altough many tamarins appeared to have retained the collars, only a few could be readily identified since some of the beads were missing and others were worn and faded.

In July-August 1982 a total of 116 km of trail were censused. Re-trapping was not attempted at this time due to lack of manpower. Although 50% of the groups were first detected by auditory means and 39% by direct observation, it was possible to approach the tamarins most of the time, after which they were followed and reliable countings could be obtained.

3.- Trapping success.- Success in trapping moustached tamarins was affected by such factors as exposure of the tamarin population to domestic cultivars and season of the year. At the Blanco stream site two groups of moustached tamarins (Red Group and Green Group), and several individuals from neighboring groups were trapped in early October. Only three individuals were re-trapped in the next 14 months. At the Yarapa site five groups of moustached tamarins were trapped in July 1981.

The dry season appears to be the best time to attempt trapping, due to the general decrease in fruit availability. As soon as the first rains started, the moustached tamarins of the Blanco Stream did not pay attention to the bait (or even the decoys) I was using. The previous exposure of tamarins to the bait is also important. It appears that moustached tamarins living close to cultivated fields will more readily accept bait of bananas at any time of the year. Moustached tamarins at the Blanco site had very little exposure to cultivated fruits. In contrast, tamarins at the Yarapa River and elsewhere were lured into traps with bananas with less difficulty, even in the wet season. In general however, the reports from the trapping teams at the Proyecto Primates indicated a much lower success at trapping tamarins at this time of the year.

At the Blanco site only two groups were captured after 154 person-days of effort at the end of the dry season. Trapping and re-trapping efforts directed at other groups living within the study area, combined with the habituation and later observation of the marked groups were continued for the next six months. However, only two individuals of neighboring groups were trapped in all this time, while three decoys died of illness. Finally, in April 1982 I gave up trapping attempts on neighboring groups or re-trapping of the tamarins in the Red group.

On the other hand, the trapping success at the Yarapa river was related to the fact that trapping took place at the appropriate time of the year, the population had previous exposure to cultivated fruits, and the population was denser than at the Blanco site.

4.- Analysis of data

a.- Population density.- Was calculated from complete counts of tamarins located within the designated study area. Although some of the groups probably ranged beyond the designated study area I am fairly confident that most of their ranges were included in the census area. The river and the extensive palm-swamp formed natural boundaries on the north and south respectively. Local inhabitants reported that tamarins were rarely seen in the vicinity of the palm-swamp and my own observations at the Blanco site indicate that both tamarins made limited use of this habitat.

Map location combined with trapping were also used by Moya et al. (1979) and by Soini and Soini (1982). Since it was important to have accurate estimates of pre-cropping densities for the Yarapa, and Moya (personal communication) had indicated that the density figures given in their report were an overestimate, I checked the original field notes. It was found that in some cases, nonsimultaneous sightings of groups of the same size detected within a very small area had been considered as observations of different groups, when more likely there was only one. Thus, new density figures were calculated after excluding double counts of such groups. It was estimated that 12 groups of S. mystax totaling 61 individuals had been located within the study area by L. Moya et al. between July and September 1978. Only five S. fuscicollis from different groups were removed from the population.

b.- Juvenile productivity (JP) = # of breeding females per year X # of infants per litter that survive to juveniles. Calculations made on groups captured complete. (n= number of groups).

CHAPTER III.- RESULTS

The results presented in the next section deal with characteristics of the population of moustached tamarins observed at the Blanco Stream. The characteristics of the population at the Yarapa River will be presented in section J. In section K I will explore the mechanisms of population growth at both study sites.

A.- Demographic variables of S. mystax at the Blanco Stream site

1.- Population density.-The moustached tamarin was the second most abundant primate species at the Blanco stream study site (Table 5). Population size of S. mystax increased from 22 to 26 individuals per sq km (or 19 to 23 individuals in known groups) during the 1981-1982 season (Table 6). S. fuscicollis, although occurring at slightly lower densities, also increased in numbers during that period. Both species of tamarins were found in all habitats.

Compared to other sites in Upper Amazonia for which density data are available, moustached tamarins were moderately abundant at the Blanco Stream site in 1981. Population density in upper Amazonia has been found to range from 17->33 individuals per sq km (Soini and Soini,1982). Subsequent reports for 1983 (Norconk, 1986) and 1984 (Garber, 1988) indicate that the S. mystax population at the Blanco Stream site continued to increase in size such that at the end of the third year of more or less continuous observations there had been an increase of 11 individuals per sq km. Thus, between 1981 and 1984 the moustached tamarin population at the Blanco site increased by about 50% (Table 6).

Saddle-back tamarins were found in permanent and semi-permanent mixed associations with the moustached tamarins. Mixed groups of the tamarins shared a large portion of the fruits available and jointly defended territories against conspecifics (Ramirez, 1984a; Norconk, 1986). The Saguinus fuscicollis population increased during my study and kept growing such that by the end of 1984 (Garber, 1988), it had increased by 55% (Table 6).

In addition to the tamarins there were ten other species of primates (Table 5). Overall, tamarins were the commonest primates at the Blanco site and despite their small size they constitued almost half of the resident primate biomass (Table 5).

2.- Group size.- Group size in S. mystax ranged from 4-8,(n=9 ; 1981 mode=5-6; 1982 mode= 7) for reproductive groups at the Blanco Stream site (Table 7). One association of two adult females (non-parous) was observed repeatedly at the site until 1982. In 1981 most groups (67%) had five independently locomoting individuals. Modal group size for other areas in Amazonia is 5 (range= 3-12). Censuses at the Blanco Stream site in 1975 revealed groups varying in size from 3-6, with a modal group size of five (Soini and Soini, 1982). *S. fuscicollis* associated in mixed groups ranged in size from 3-8 individuals.

The majority of groups of tamarins in the study area had increased in size by the end of the study (Table 7).

3.- Natality.- Observations for the Green and Red groups show that they increased in size from 1981 to 1982 by virtue of births (Table 8).

a.- The Green group.- At the time of trapping in October 1981 there were two infants approximately 2-3 weeks old. All adults in this group were classified as young based on their dental characteristics and the condition of the genitals. All individuals appeared in very good condition and body weights were at the upper end of the range when compared with data available for other areas (Soini and Soini, 1982). Female #27 was obviously lactating (her breasts were full of milk), while female #28 appeared to be non-parous. Female #27 was pregnant when captured again in March 1982. I estimated that infants should have been born in April but since none were observed and the female appeared to lose weight I assumed that the infants were stillborn or died during or soon after birth. If gestation period is similar to other *Saguinus*, 140-150 days (Soini and Soini, 1982); this means that Female # 27 got pregnant within 1.5-2.0 months after giving birth to live infants, and while she was still lactating.

Female #28, captured again in October 1982, remained non-parous as indicated by her nipple condition. A few weeks later infants appeared in the group (Norconk, 1986). Presumably, female# 27 was the mother of the infants. Thus, female #27 appeared to have three pregnancies in 19.5 months. The third pregnancy must have occurred at the end of May or early June, which leaves over 2.5 months between the time when she was trapped and the presumed time of conception. Interbirth intervals for wild populations vary from 8-14 months with a median of 11-12 months (Soini and Soini, 1982). Trapping records however, seem to indicate that most females either breed once a year, or if they breed twice a year only one litter survives (Soini and Soini, 1982).

b.- The Red group.- Two infants were trapped during the capture of this group in October 1981, female# 23 was lactating while female #26 was in the last stages of pregnancy. Female #26 gave birth to twins a couple of weeks later. This female was found dead in January and the infants were never seen again. This is one of two reported cases (Goldizen, 1987), of the occurrence of more than one reproductively active female in a group. I have only heard of one other case where four infants were found in one group of moustached tamarins. They were all clinging to one male when captured near the Maniti river (E. Mermao, pers. comm.). Trapping records for 49 complete groups, revealed only one parous female per group (Soini and Soini, 1982).

4.- Birth season.- Infants at the Blanco site were born from late September through December and also in May. In November most groups had newborns. Births for other areas in Amazonia peak from November through February (Soini and Soini, 1982), although pregnant females are found throughout the year.

5.- Dispersal.- Immigrations or emigrations into the focal groups were not registered during the study. The Green group continued to increase in size during the next two years (Table 8) and grew to have thirteen tamarins, soon after which it split into two units (Garber, 1988). Presumably the new unit of tamarins emigrated from the area. This is one example of how new groups are formed. However, there are indications that this may not be the most common mechanism (See Discussion of demographic findings, section K).

B.- Activity budgets of S. mystax at the Blanco site

Activities of the tamarins were influenced by the availability of resources. Fruit appeared to influence various aspects of the tamarin's life. Availability of fruit at this site determined two seasons: a wet season from November to June, and a dry season from July through October.

1.- Day length.- Moustached tamarins were active an average of 10 hours per day (x=10:10, n=52), but there was considerable variation throughout the year (max=11:30, min=8:59), (Table 9). Overall, moustached tamarins had shorter days of activity during the dry season from July until October (x=9:42), than during the wet season from November through June (x=10:37) (W: p= .0001, n=52). Most of the changes in the length of active day appear to correspond to changes in daylength at this latitude.

A tamarin day always started soon after sunrise (x=6:20, range 5:55-7:10 a.m.). Moustached tamarins left their sleep tree later in the dry season than during the wet season (W: p< .05, n=52). Heavy rain or a drop in temperature always delayed their departure from the sleep tree. When the tamarins entered their sleep tree activity ceased, although occasionally I observed brief grooming bouts. S. mystax entered their sleep tree significantly earlier during the dry season (x=16:06) than during the rainy season (x=16:56) (W: p< .0001, n=52). Thus, shorter days of activity were accomplished by leaving the sleep tree slightly later and retiring to it earlier.

2.- Yearly activity budget.- Moustached tamarins spent more than a third of their "active" hours resting, another third was used in food-gathering activities; more than a fourth of their day was spent in traveling from one place to another, and less than a tenth was used for various social activities (Table 10 and Fig. 9).

3.- Seasonal variation in activity budgets.- Although there was considerable monthly variation in the total amount of time spent on different activities, a seasonal pattern only emerged for insect foraging and travel, but not for time spent feeding on plant parts, time spent resting, or miscellaneous activities (Table 11, and Fig.10).

a.- Plant feeding.- Moustached tamarins spent only slightly more time feeding on plants in the wet season months than in the dry season months, and the differences were not statistically significant. Consumption of different plant parts, however, showed clear seasonal trends, apparently related to changes in fruit productivity. Details will be presented in Section C, on diet.

b.- Resting.- Moustached tamarins spent on average, similar amounts of time inactive in both seasons. However, shorter days of activity in the dry season (Table 9) resulted in a real increase in the amount of time spent resting over a 24-hour period.

c.- Insect feeding.- From November to June, *S. mystax* spent about 17% of their time looking for and ingesting insects. With the advent of the dry season, foraging for insects became a very conspicuous activity, and at the end of the dry season, which extended into November in 1982, it occupied almost a third of the tamarin's waking hours (W: $p < .01$, $n=57$). The increase in time spent feeding on insects during the dry season may be related to a decrease in the amount of time spent feeding on plants and time spent in travel. There was a negative correlation between time spent feeding on plants and time spent feeding on insects during the dry season ($rs= -.544$, $p<.001$, $n=20$). Through the year there was a negative correlation between time spent feeding on insects and time spent traveling ($rs= -.65$, $p< .0001$. This negative correlation was stronger in the dry season ($rs= -.7$, $p< .0002$).

The overall increase in insect feeding during the dry season resulted in a net increase in the amount of time associated with feeding, wet season mean 28.4% (166 feeding minutes) vs. 32.8% (206 feeding minutes) in the dry season.

d.- Travel.- Moustached tamarins spent more time traveling during the wet season than during the dry season (W: $p< .0001$, $n=57$). Tamarins traveled a much longer path during wet season months than during the dry season (W: $p> .0001$, $n=57$), (Table 12) . Longer path lengths may be related to a greater abundance of fruits and to the fact that tamarins visited a greater number of fruit trees in the wet season than in the dry season (W: p<

.01, n=57), (Table 13). There was an overall positive correlation between distance traveled and number of fruit trees visited (rs= .589, p< .0001, n=57) for the whole year; but the correlation was stronger for the dry season (rs=.683, p> .0009, n=20).

e.- Miscellaneous.- activities such as grooming and vocalizations occupied similar amounts of time throughout the year.

4.- Daily activity budget.- Tables 14,15, and Fig.11 summarize the pattern of daily activity budgets. On an average day, and upon leaving the sleep tree, moustached tamarins traveled to a tree and did most of their daily plant feeding (mostly fruit feeding) within the next few hours by visiting several fruit trees in succession. Foraging for insects became evident within one hour after leaving the sleep tree, and it was a sustained activity for the entire day (Table 14). Travel, although a conspicuous activity throughout the day, peaked between 7 and 8 and between 16 and 17 hours. Periods of inactivity were distributed throughout the day but peaked around midday, when food gathering activities and travel were depressed, but social activities such as grooming were more common. Vocalizations peaked early every morning, and during territorial confrontations, which were also more common in the morning hours.

The effect of season on daily feeding patterns will be presented under the respective subheadings in Section C, on diet. There were also seasonal differences in travel. Travel in the dry season, although reduced (Table 11) was maintained at a steady pace through the day (Table 15). However, the midday lull in travel was shorter. Moustached tamarins started periods of inactivity (although brief) earlier in the day in dry season months than in wet seasons months (Table 15).

See section D for discussion of activity budgets.

C.- The Diet of S. mystax at the Blanco site

In the next section I will report on annual and seasonal diets of S. mystax and relate them to the temporal and spatial distribution of known resources.

Saguinus mystax fed on a variety of arthropods (insects, spiders) and fruits throughout the year, while exudates and nectar were consumed seasonally (Fig 12). Most of the tamarin's feeding time was spent in insect feeding (63% of feeding minutes), followed by fruit feeding (34% of feeding minutes); consumption of exudates was seasonal and occupied a small portion of feeding minutes (3%). Ingestion of nectar and leaf buds occupied only a minute fraction of feeding minutes (0.4%).

1.- Resources available to S. mystax

a.- Fruit availability.- The index of fruit abundance indicated a greater availability of fruit trees and fruit species from November through June than from July-October (Figure 5 and Table 16), (W: $p< .005$, $n=13$, for number of trees). From July until September there was a profound reduction in the number of fruit trees and the size of the crops available in the forest. In September, the 4 km census walk revealed only one tree with fruits (Table 16). In October and November the number of fruits slowly started to increase again.

Over 60% of the fruit trees and species (combined) encountered during the census were utilized by the moustached tamarins which seems to suggest that S. mystax fed on the most abundant fruits available to them.

b.- Fruit phenology.-Most trees monitored produced fruits during a discrete period of time (Table 17), although there was considerable intraspecific variation from one individual fruit tree to another. For example, Maripa sp., fruited for four months while numerous individuals of the same species were in fruit for only a month. Parkia oppositifolia (tree #34) displayed a similar pattern.

A low percentage (3%) of monitored trees bore fruit more than once during the period of observation and some did not at all. Most trees, however, were observed for less than a year.

c.- Exudate availability.- exudates were available year around within the Green group's range. Trees exploited by the three resident groups of Cebuella pygmaea produced a steady supply of exudates, yet they were seldom utilized by S. mystax. Exudates oozing from beetle-attacked trees and wind-broken trees were available within the range of the Green group. Exudates surrounding the seeds of legumes were also available from February until October, but were only marginally utilized.

d.- Spatial distribution of feeding trees.- Plants utilized by S. mystax were distributed in all types of habitats. Most trees, however were found in the tall forest, and progressively fewer in the low forest, palm swamp, vine forest and overgrown fields. The proportion of food trees in each habitat was roughly equal to the proportion of that habitat within the range of the Green group (Table 18).

e.- Insect abundance.- I did not obtain independent information on insect abundance. Sampling of arthropod populations in southeastern Peru (Tambopata, a more seasonal forest) indicated year long availability of insects in different kinds of habitats, from floodplain to bamboo forest to terra firme forest (Pearson and Derr, 1986). The authors found greatest abundance in terms of biomass in the wet season and particularly in the early wet season. At Cocha Cashu, in a forest subjected to a similar rainfall regime as Tambopata, arthropods showed marked seasonal variation in density. Night light censuses revealed a period of insect scarcity from April to July, and a period of abundance from September through November when arthropods were six times more abundant than during the period of scarcity (Janson,in Wright, 1985).

2.- Plant feeding

During the study, two hundred and twenty three trees were utilized by the moustached tamarins for plant feeding. Most plant feeding time was spent on fruits (92% of plant feeding minutes), and exudates comprised 7% of plant feeding time. However, exudates were an important item in the diet towards the end of the dry season (October and November). Nectar and flowers were infrequently consumed (1% of plant feeding time), and only a very small fraction of feeding minutes were spent on young leaves and bark/lichens (0.1% of plant feeding minutes each).

a.- Life forms.- Trees were the most commonly exploited life form for fruits (66% of the species utilized), although fruits from vines (24% of the species) were also eaten (Table 19). Fruits from palms (one unidentified species) were only rarely included in the diet. Most of the exudate sources were trees.

b.- Taxonomy of plant resources.- Tamarins fed on fruit of 72 plant species during the study. Tamarins exploited the largest number of species in the families Moraceae, Leguminosae (sensu lato) and Convolvulaceae. The fruits of the Moraceae were the most important overall, both in number of species utilized (Table 20) and in the percentage of time spent feeding on them (Table 21). Saguinus mystax spent on average 25 % of plant feeding time per month feeding on members of the Moraceae. Moraceae were especially important during 5 of the 13 months of observations, when tamarins spent between 29% and 82% of feeding time per month consuming Pourouma spp., Naucoleopsis sp. or Ficus sp. (Table 21).

In terms of feeding time, legumes were very important for the tamarins during three months April, August and September (29%-39% of feeding time). It is significant that the ingestion of the exudate or aril surrounding the seeds of some legumes (e.g. Parkia spp.) was consumed in quantity only during the dry season, when fruit resources were scarce (Table 21). The first ranking species accounted for 42% of all fruit feeding during the period of observation. Moustached tamarins used from 1-16 trees of the first ranking species during each sample.

c.- Species and tree diversity .- The plant portion of the tamarin's diet was relatively diverse. On an average day tamarins fed on the product(s) of at least six species (range=1-11, n=57), by visiting between 3 and 12 trees, but most commonly moustached tamarins used 8 trees/vines per day (Table 13). During a five-day sample period tamarins consumed between 8 and 20 species, by visiting between 14-29 trees/vines (Table 13). The five highest ranking species contributed between 54 and 96% of feeding minutes to the monthly diet (Table 21). However, the highest ranking individual food trees belonged to different species in 8/13 months (see Table 25).

The diet was richer in species and total number of trees visited in the wet season, but poorer than expected in the dry season; the differences, however, were not statistically significant (W: p= .728, p= .611, n=57). There were, however, seasonal differences in the number of fruit trees/species visited (See next section). Month to month variation was great, even within the same season, and this may account for the lack of overall seasonal trends. For example, between December and January the number of species consumed almost doubled (from 8 to 15, based on equal number of sample days), and paralleled the overall increase in number of fruit species.

In all months, except October, most plant-species were used for the fruit resource. In all cases, with two exceptions, each species/tree was exploited for one resource only. Spondias mombin and Quararibea cordata were each exploited for fruits and exudates, and exudates and nectar, respectively.

d.- Item diversity.- This was greatest during the dry season, by the addition of exudates and nectar to the diet (Fig. 12). In terms of feeding time, it was only in contrast with the rest of the year--when exudate consumption was very sporadic and amounted to very little--that exudates appeared to have any importance in the diet. During most of the year, over 99% of plant feeding time was spent on fruits.

3.- Fruit feeding

a.- Fruit types.- Fruits were the predominant plant food item throughout the year although there were seasonal changes in the emphasis on fruit. Fruits consumed by moustached tamarins can be characterized as being typically small, sweet, meaty drupes, yellow or purple in color (Table 22).

Fleshy fruits (I include capsules with soft exocarp and fleshy mesocarp because of their likeness to drupes) were by far the preferred fruits (over 90% of all plant species). Drupes were produced by more than half of the species consumed and on average over one third (x=36%, range 0-88%) of feeding time per month was spent eating drupes. Moustached tamarins spent about 10% of plant feeding time eating capsules. In all cases of fruit consumption the fleshy mesocarp or aril was ingested. Seeds were sometimes swallowed, while the skins of some fleshy fruits were discarded. There was no evidence for seed predation, but seed dispersal, as evidenced by apparently intact seeds found in feces, was observed for Byrsonema sp., Inga sp., and Parkia oppositifolia.

b.- Fruit size.- Most fruit species (71%) were small 0.6-2.0 cm (range=0.6-8.0 cm, n=59)in diameter (Table 22). Ingestion rates were determined for 11 species of fruits. S. mystax could ingest up to nine fruits per minute (1.5 cm in diameter). Larger fruits with tough exocarp required a large initial investment of time.

c.- Tree size.- About 90% of the fruit trees/vines utilized were small crowned species and 61% were subcanopy species (Table 23). Approximately 24% were emergent forms, most of which had medium to large crowns. Even those emergents utilized, however, had relatively narrow crowns.

d.- Gathering technique.- Moustached tamarins approached each fruit tree as a group and in most cases they entered it all at once to start feeding. However, on many occasions when feeding on relatively exposed tree crowns tamarins would combine feeding with glancing around, or one individual would be seen sitting in the fruit tree without feeding while looking around as if guarding. In most cases, S. mystax remained in the fruit tree only for the time necessary to feed, immediately after which they exited the tree. A few species, such as Maripa sp. and Parkia oppositifolia, were used extensively for resting.

e.- Fruit handling.- Fruits were usually held with both hands, brought to the mouth and the exocarp was torn off with the teeth and discarded in most cases. Mesocarp, aril and sometimes the seed were ingested by the tamarins. The majority of fruits appeared to be easily opened by the tamarins. However, the leathery pods of Parkia oppositifolia appeared to require extra effort, in order to gain access to the exudate surrounding the seeds.

f.- Fruit monitoring by S. mystax.- During short visits to fruit trees (visits of < 1 minute) moustached tamarins appeared to be testing the ripeness of fruits. During such visits tamarins would bite into the pericarp of a fruit and discard it, after which they would leave the tree. When I checked the discarded fruits most were not sweet. Rejected fruits usually appeared ripe as judged by the color of the exocarp (although some had green exocarps) but in 10 out of 12 rejected fruits I could detect no sugary taste. When there were many trees of the same species in fruit, as in the case of Pourouma sp. the preferred fruit tree at any one time was the one with the sweetest (to my taste) and apparently ripest fruits. Other unused Pourouma sp. trees discovered in the study area were tasted and in all cases (n=5) the fruits were tasteless even though they may have appeared ripe.

Although these observations seem to indicate that S. mystax occasionally taste fruits and in the process assess nutritional value there is evidence indicating that visual and olfactory cues are used most of the time to determine ripeness. Most fruits consumed by tamarins advertise their ripeness with bright colors, yellow-orange fruits made up 50% of the fruits consumed by the moustached tamarins (Table 20).

Moustached tamarins appeared to monitor individual trees of Pourouma sp. Pourouma sp. fruits are purple early in the ripening process and apparently do not advertise their ripeness by different shades of purple.

g.- Temporal patterning of fruit feeding.- Moustached tamarins spent an average of 95 feeding minutes per day eating fruits (range= 18-194) (Table 15). Time spent feeding on fruits varied through the year, and seasonally. S. mystax spent less fruit-feeding-minutes than expected, in the wet season (x=92, range=18-185) than in the dry season (x=98, range 23-194) the differences, however, were not statistically significant (W: p= .621, n= 57).

On a daily basis, S. mystax did about 60% of fruit feeding during the first hours of the morning (Table 15 and Fig. 11); there was a second, minor peak of fruit feeding in the afternoon, but during the last hour there was little fruit feeding (Fig. 11).

h.- Fruit feeding bouts.- Feeding bouts for individual tamarins varied from short visits of less than a minute long when tamarins appeared to be tasting the state of fruits (see fruit monitoring below) to visits lasting up to 29 minutes (Table 24). Most of the time feeding bouts were short, lasting between 1-3 minutes, with many visits 3-5 minutes long (Table 24). There was considerable seasonal variation in bout length. Long to very long feeding bouts (8-29 minutes long) were observed almost exclusively in dry season months (33 out of 36 records in this category for the study). Due to their length they constitued from 20-88% of total feeding minutes in a dry season day. This phenomenon was more obvious towards the end of the dry season when the few fruit tree visits were very long. Specimens of *Ficus* sp., *Cissampelos* sp., and *Parkia* sp. received very long visits, which were combined with periods of rest around the fruit trees. It is notheworthy that *Cissampelos* sp. and *Parkia* sp. had big crowns, 10 and 15 m respectively, and the resting periods around them lasted up to 3 hours at a time. *Ficus* sp. had a small crown (5 m), and the rest periods around it were shorter.

i.- Frequency of visits to individual trees.- During each sample period the pool of fruit trees used varied from 11-29. Moustached tamarins fed on an average of seven fruit trees per day (range= 1-12). Fewer trees per day were visited in the dry season (x= 6) than in the wet season (x= 8, range= 5-12) (Fig 13). Significantly more fruit trees and fruit species were visited during wet season days than during dry season days (W: p< .01, n= 57,and p< .05, n=57) (Table 13).

During any sample period (5-day period) more than 60% of the fruit trees were visited only once, about 20% were visited twice and usually only one tree was visited four or five times, usually on consecutive days. Interval between visits to most trees was two days. On very few occasions a tree was visited twice in a day.

j.- Characteristics of preferred fruit trees.- During each sample period the four highest ranking fruit trees accounted for between 45-97% of feeding minutes (Table 25). The most exploited fruit trees fell into one of two groups (Fig.14). Members of the first group comprised one to several selected specimens of a synchronously-fruiting species, whose trees had a restricted fruiting season (4-6 weeks), and were characterized by small crowns (less than 6 meters in diameter). Examples of trees with these characteristics included *Pourouma cecropiaefolia*(20 m tall), *Pourouma ulei*(23 m tall), *Byrsonema* sp.(18 m tall), *Maripa axilliflora* (20 m tall), and *Leonia glycicarpa* (18 m tall) (Table 23). Even though moustached tamarins consumed fruits of several trees (3-11 trees) belonging to one such species within a sample period, there was usually one tree that was preferred over the others. The second group of preferred trees seemed to belong to species that come into fruit one at a time, asynchronously (two species of *Parkia* sp.), or appeared to be rare (species of *Strychnos*, *Ficus* sp.); these species shared a medium to large crown size (>6- 15 meters in diameter) and a restricted fruiting season (4-8 weeks). In the case of Parkia sp. the mature pods remained on the tree for several months.

4.- Exudate feeding

The exudates from 17 trees and two vines, and at least eight species (Table 20) were consumed by the moustached tamarins. Although exudate as a resource is available year around most exudate feeding occurred at the height of the dry season, coincidental with a decrease in the number of fruits available.

a.- Exudate collection techniques.-In most cases (15 out of the 19 trees) the exudate trees being utilized by resident Cebuella pygmaea were parasitized. Over 90% exudate feeding minutes were accumulated while feeding on trees currently being used by Cebuella pygmaea Wind-broken trees showing signs of attack by wood-boring insects were also utilized, as well as non-Cebuella-utilized trees with open wounds of unknown origin.

Most of the time exudates were licked from the surface of trees and lianas and no attempt was made to dig holes. However, in two cases of trees with large holes the moustached tamarins were observed digging with their claws and tearing pieces of bark with their incisor teeth. In both cases bark soaked in exudate was ingested. This behavior most probably elicits further exudate flow.

b.- Exudate feeding bouts.- Visits by individual tamarins to exudate feeding trees lasted from 30 seconds to 7 minutes with an average duration of 3 minutes (n=95). Although all group members visited the exudate trees, not all entered at the same time. At any one time an average of three tamarins were on the exudate tree while the rest were seen sitting on branches leading in or out of the tree (n=57 visits).

c.- Temporal pattern of exudate feeding.- Exudate consumption was markedly seasonal. Most exudate consumption occurred towards the end of the dry season and beginning of the wet season (October- November) (Fig.12). Almost 50% of all exudate feeding observed for the year occurred in October (Fig. 12).

On a daily basis moustached tamarins visited more exudate trees in the morning than in the afternoon, but visits were longer in the afternoon; which resulted in more time spent feeding on exudates in the afternoon than in the morning (Fig.15).

5.- Flower feeding

Flowers were visited a few times during the study. Although tamarins were observed chewing the flowers they were presumably consuming the nectar.

6.- Invertebrate feeding

a.- Types of prey.- Moustached tamarins fed on a variety of arthropods, including both spiders and insects. Insect orders identified from the food remains (wings, discarded legs) and or from direct observations included: Orthoptera (Acridiidae and

Tettigoniidae), Homoptera(Cicadidae), Hemiptera (winged forms), Diptera, and Lepidoptera. The actual variety consumed was probably greater. My observations are most probably biased in favor of larger prey since on many occasions I could see that a moustached tamarin had captured something but could not tell what it was.

More than 90% of prey were mobile. Adult forms were usually ingested, although larvae of the Lepidoptera and winged forms of the Hemiptera were consumed. A high percentage of captured prey was large katydids (Orthoptera) (3-5 cms in length from head to tip of abdomen).

b.- Invertebrate foraging technique.- Since most invertebrate foraging was insect feeding I will use both terms interchangeably. Insect foraging was a solitary activity, but some activity coordination was obvious at certain times of the day and at certain times of the year (see section on temporal pattern of insect foraging). Moustached tamarins usually foraged for insects by scanning the surface of leaves, twigs and bark. Most insect foraging observed was non-manipulative (91% of foraging sequences, n=184). Manipulation of the substrate, although infrequent, was mostly confined to dry season months from August through October. Also during the dry season moustached tamarins were seen jumping on clumps of leaves as if to flush insects. This behavior was infrequently seen during the rest of the year.

Scanning of the vegetation occurs from a seated position or while walking slowly with the body close to the substrate as if ready to pounce. S.*mystax* appeared primarily to scan the surrounding substrate, and every once in a while would glance further afield for a few seconds. Once the prey was located tamarins moved stealthily and quickly towards it, and grabbed it or pounced on it, grabbing it with one or two hands. The prey was either eaten on the spot, or the tamarin moved to a perch where the insect was consumed. Small prey was consumed whole while in the case of larger insects tamarins bit the head first while holding the body with one or two hands. The wings and legs (patella section) were usually discarded, which many times provided a clue for later identification of prey.

c.- Insect foraging bouts.- Foraging bouts were usually short, from one to two minutes in length (x=80 seconds, range=9-256 seconds, n=184). Foraging bouts became longer during the dry season, from an average of 57 seconds in November to 125 seconds in September (Table 26). More searches per hour were initiated in the dry season, also a larger percentage of them were successful. This might account for the longer duration of the foraging bouts since they included ingestion of prey.

d.- When to look for insects.- Insect foraging occurred between bouts of fruit feeding, while traveling or as an exclusive activity. In the first two cases insects were captured opportunistically or only after a brief (couple of seconds) scan of the vegetation. During intensive bouts of insect foraging moustached tamarins moved at a slower pace than at other times and were usually found spread out over more than one tree, but generally not more than 20 meters apart.

e.- Substrate type and canopy level.- Most insect foraging took place on leafy substrate (86% of observations) in the subcanopy of the forest, with most foraging occurring between 6 and 15 meters (Table 27). Leaf clumps were visually inspected from above and from below. Moustached tamarins only rarely inspected dead leaves.

f.- Support.- Trees were the most frequently utilized life-form for insect foraging (Table 27). Branches (63% of observations) and twigs (30% of observations) were most commonly used when foraging for insects (Table 27). Most scanning, capture and ingestion of prey was made on horizontal or nearly horizontal supports.

g.- Temporal patterns of insect foraging.- Insect feeding showed large seasonal variation. S. mystax spent more time foraging for insects in the dry season than in the wet season (See activity budgets). The tamarins usually started insect foraging after 7:00 and continued throughout the day, with a reduced impetus around noontime (Table 15 and Fig.11). Bouts of midday rest were alternated with insect foraging in the vicinity of the rest area. During the dry season, moustached tamarins began foraging for insects in earnest an hour earlier than in the wet season (Table 15).

D.- Interspecific relations of S. mystax

Moustached tamarins shared their range with at least ten other species of primates. Although the woolly monkey was reported to occur in the general area it was never seen in the main study site. Several marsupials, procyonids, and many birds were also observed at the study site. S. mystax appeared to maintain a range of interactions that varied from parasitic to mutualistic but also included the most common interactions with competitors and predators.

1.- Competitors for food.- At the Blanco site several primates and birds had a diet that included fruits and insects. Although a large component of the fruit portion of the diet was shared with the saddle-back tamarin both species did not appear to behave as typical competitors. This very special kind of interaction will be treated separately in section I.

Cebus albifrons displaced the moustached tamarins from their feeding sites on fruit trees without using overt signals. In the only incident observed, S. mystax waited in neighboring trees until the capuchins left the fruit tree. C. apella was seen in the area visiting a fruit tree not used by the tamarins. Their presence resulted in both tamarins calling and scrambling away. The saddle-backs seemed particularly distressed. Overall, the two capuchins were uncommon in the area (Table 5) and did not seem to be important competitors for the fruit resource.

Callicebus moloch and *Pithecia monachus* were seen feeding in some of the fruit trees used by the tamarins. Upon their arrival, they either stayed for a while, or left right away. No obvious signals were given by either species. The moustached tamarins appeared to follow *Pithecia* on at least three opportunities and both species visited the same fruit tree. *Callicebus* was observed most frequently in the vine forest and in the low forest while *Pithecia* was observed in the high ground forest and in the vicinity of the palm swamp formations. Thus titis and sakis appeared to utilize only some of the habitats available to the tamarins.

Callicebus are potentially important competitors of the tamarins at the Blanco site due to their preference for small-crowned fruit trees (Wright, 1985), and because of their relative abundance (Table 5). If *Callicebus* utilizes small-crowned trees to avoid competition with larger primates as was observed at Cocha Cashu, then the reduced presence of larger primates at the Blanco site could result in the titis using large-crowned trees without running the risk of being expelled from them. Such a situation would tend to reduce competition for access to small-crowned trees and might explain the little overlap in feeding tree use observed for *S. mystax* and *Callicebus*.

Aotus, a nocturnal frugivore is known to utilize large crowned trees (Wright, 1985), and as such probably does not exert an important effect on the availability of fruits utilized by the moustached tamarin.

Toucans (*Ramphastos cuvieri*) was frequently seen feeding on fruit trees used by the moustached tamarins. When approached by them, they either moved to another branch or were chased away by *S. mystax*. Moustached tamarins in the Green group did not seemed detered by the presence of toucans from entering fruit trees. However, the members of the Red group when separated from its co-territorial saddle-backs waited for a long time--all the while calling--before entering a fruit tree where toucans and "locreros" (Icteridae) were feeding.

Locreros also fed on many of the same fruits. *S. mystax* tried to chase them away, but the locreros remained steadfast on several occasions.

At least three species of squirrels, *Sciurus* sp. were observed in the area but were never seen to interact with the tamarins.

Most of the primates at the Blanco site include insects in their diet. *Callicebus* practices a foraging technique similar to the moustached tamarin, but spends only about half an hour per day foraging for insects and displays a very low success rate (Wright, 1985). Thus *Callicebus* probably constitutes little competition for insects. The two species of tamarins utilize different foraging techniques and search for insects on different substrates thus avoiding competition. *Cebuella* also includes insects in its diet (Ramirez et al., 1978) but it is so small that it is probably not an important competitor.

Harpagus bidentalis, the double-toothed kite, was observed to follow the tamarins for several hours at a time, without provoking any reaction from the tamarins. The kites were seen feeding on insects which might have been flushed by the tamarins. *Harpagus* seemed to travel closer to the saddle-back tamarin most of the time, although in the dry season they frequently followed moustached tamarins. In the few occassions when the kite seemed disturbed by the observer and called, *S. mystax* responded immediately by giving an alarm call.

2.- Parasitism of exudate trees.- *S. mystax* robbed exudates from trees that were being activily exploited by resident groups of pygmy marmosets. Three groups of pygmy marmosets resided within the range of the Green group, and they were all visited by the moustached tamarins at the height of the dry season. One grove of trees which housed the largest group of *Cebuella* was preferentially exploited during this period. Pygmy marmosets were observed to display (apparently) against the moustached tamarins. However, due to their small size *Cebuella* were ineffective in driving the moustached tamarins away from their exudate trees.

Pygmy marmosets follow a daily cycle in the exploitation of exudates. Collection of exudates is practiced with intensity in the morning, this is followed by digging of holes, a midday rest, a second concentrated collection of exudates in the afternoon, and intensive digging of holes in the late afternoon

(Ramirez et al., 1978). Moustached tamarins concentrated their visits to exudate trees in the afternoon, roughly coincidental with the second peak of exudate production (Fig. 15) which perhaps made it tolerable on the pygmy marmosets. In addition, the occasional prying of bark to get to exudates, which effectively enlarged holes, may benefit *Cebuella*.

3.- **Predators.**-Due to their small size *Saguinus* are potential prey for a large number of predators that range from snakes and raptors to various carnivorous mammals.

Potential predators of the moustached tamarin at the Blanco site included at least an arboreal boa large enough to prey on tamarins (Table 28). *S. fuscicollis* was observed mobbing a small boa (about 80 cm long), which was subsequently approached by all tamarins in the mixed group. They all seemed to want to take a look at the offending snake. After much observation and calling they abandoned the area and traveled for a long stretch without the customary short stops.

Raptors flying overhead invariably elicited strong alarm responses from the tamarins. Moustached tamarins gave several alarm calls per day that were apparently directed towards birds, thus suggesting that they may be important predators of tamarins. The tamarins' reactions to attacks by raptors was very strong as indicated by the loudness and duration of the calls. *Daptrius americanus* was observed to attack and barely miss a juvenile *S. mystax*. The moustached tamarins reacted by giving very loud screeches at the same time that Daptrius was diving towards the juvenile.

Tayras were discovered by the tamarins climbing a large tree (at 15 m height) adjacent to where the monkeys were engaged in bouts of insect foraging. In both cases the saddle-back tamarins were the first to give the alarm call. S. mystax and S. fuscicollis immediately srambled to very thin branches near ground level. S. mystax dropped at least 6m to get to thin supports. After the alarm call, the tayra (and her cub in one of the two cases) continued climbing and traveling in the direction of the moustached tamarins for a few seconds, after which it came down from the tree and continued on the ground amidst vociferous mobbing.

The saddle-back tamarins appeared vigilant, and did not approach toucans as the moustached tamarins did. Only after the toucans were driven away the saddle-backs appeared at ease.

Coatimundis (Nasua narica) attacked a live decoy that was confined to a holding cage.

C. apella elicited escape behavior in both species of tamarins when it approached the area where they were feeding. Although C. apella visited a tree that the tamarins were not using at the time, the tamarins moved away from the general area. The smaller S. fuscicollis moved further than the moustached tamarin and remained away for a long time after the capuchins retired, while S. mystax resumed feeding.

Cats are known to hunt during the day and night and could potentially ambush the tamarins, particularly at night.

In summary, the peaceful relations between the titi monkey--potentially an important competitor at this site-- and *S. mystax* at feeding trees, and when encountered during their daily ranging, suggests that these two species do not compete in any important manner for the fruit or insect resource. The larger frugivores (e.g. *Cebus* spp.) which at Cocha Cashu (Terborgh, 1983) are known to exclude the tamarins--and other small primates--from large-crowned fruit trees, are uncommon at the Blanco site and thus can be dismissed as competitors for the fruit resource. The only conflicts for access to fruit occurred with birds, which in most cases were forcibly expelled from fruit trees by the moustached tamarins. *S. fuscicollis* appeared less assertive than *S. mystax* in their dealings with birds, particularly toucans.

The frequency of alarm calls to raptors and the strength of reactions to their approach indicate that raptors are perhaps the most important predators of *S. mystax*. From the reactions of tamarins to tayras it appears that they may also be an important predator. Although tamarins are not normally exposed to the aquatic anacondas, they have been reported to prey on them when traveling near a lake edge (Heymann, 1987).

E.- Summary and Discussion of activity budgets and feeding results

1.- Activity budgets.- Moustached tamarins were active for an average of ten hours per day, although a good third of that time was spent at rest. Another third was used to look for and feed on insects, fruits and exudates. Activity usually started immediately after dawn, but rainfall and low temperature delayed onset of activities.

On most days, after an early bout of vocalizations (usually near territorial boundaries), moustached tamarins left their sleep tree to travel in search of their first morsels of the day, fruits. Within the next few hours they made most of their fruit feeding visits for the day, although some fruit feeding ocurred in the afternoon. Fruit feeding alternated with foraging for insects as the day advanced and tamarins continued to visit a few more fruit trees. Foraging activities and travel decreased around noon with a consequent increase in rest and social activities.

It is not surprising that moustached tamarins will feed on fruits first thing in the morning, since ripe, sweet fruits are probably the source of high energy carbohydrates, which are necessary to start the day. It is also likely that the concentration of fruit feeding in the first hours of the morning gives tamarins an edge in the competition with diurnal competitors (both intraspecific and interspecific) for fruit trees by consuming the few fruits available before others do.

Insect feeding, although a more important feeding activity in terms of total time devoted to it, usually starts after the tamarins have garnered some quick energy from sweet fruits. This is not surprising since the search for insects requires advanced investment of energy.

In order to collect fruit and insects, moustached tamarins must travel from one place of their range to another. This takes on average about two and a half hours of their daily budget. An undetermined amount of travel appeared obviously related to the patrolling of the home range.

Compared with *Saguinus imperator* studied at a more seasonal forest and as a member of a very rich primate community, a number of differences emerge (Terborgh, 1983). The most striking difference is in the proportion of time devoted to insect feeding by moustached tamarins. *S. mystax* used almost 19% of its time for insect foraging vs. 34% for *S. imperator*; when added to plant feeding, this resulted in a total of 30% of activity time spent in feeding by the moustached tamarin vs. 51% for the emperor tamarin. In terms of feeding time and amount of time spent inactive *S. mystax* resembled saddle-back tamarins at Manu. Like *Saguinus* spp., moustached tamarins preferentially used small-crowned trees for fruit feeding.

Garber (1988) presenting activity data for the October-December period in 1984, reported moustached tamarins spending similar amounts of time on each of the daily activities as during my study. Although feeding activities for that period were reported around 28% for both studies, the amount of time devoted to fruit feeding and insect feeding was quite different, especially when considering that group size during Garber's study changed from 11 to 8, and during my study remained at five individuals. During this study moustached tamarins used 63% of feeding time to forage for insects (vs. 48% during Garber's study), and 33% (vs. 51% during Garber's study) on fruit feeding. In summary, the members of the Green group when belonging to a smaller group spent the same amount of time feeding, but spent more of that time foraging for insects and less time feeding on fruits than when they were members of a larger group. In both cases the group had one pregnant female which gave birth in November.

It could be argued that when there are fewer individuals in a group, interference competition for fruit patches in small-crowned trees is lower than when more (8-11) individuals are trying to feed in the same crown. It would follow that interference competition would extend the length of visits to a fruit tree and consequently the amount of time spent feeding on fruits, even though the net ingestion rate per individual monkey would remain the same. This is an attractive explanation but must be considered with caution since the amount of time tamarins spend feeding on fruits is complicated by fruit handling time which can make comparisons of this kind of little use.

2.- Temporal variation of feeding patterns and their correlates

Moustached tamarins were found to subsist on a diet of arthropods (mostly insects of the Orthoptera), and sweet, small yellow-orange drupes borne on mostly small-crowned, subcanopy trees and vines. Exudates were only a small fraction of the yearly diet.

The advent of the dry season with its concomitant reduction in the number of fruit bearing trees appeared to affect the moustached tamarin's feeding practices.

A first observation indicates that moustached tamarins were active for fewer hours in the dry season than in the wet season, and although they were inactive for a similar number of hours in the dry season, the fact that they left the sleep tree later and retired to it earlier effectively increased the number of hours that the tamarins spent at their sleep tree (from 13 hrs. 30 mins to 14 hrs. 15 mins), presumably resting. By spending more hours at rest, S. mystax presumably saves energy at the time of fruit scarcity.

Seasonality was evident in the number of fruit trees and fruit species visited each day. Moustached tamarins visited more fruit trees of more species in the wet season than in the dry season. However, the overall species diversity of their diet did not decrease in the dry season, due to the inclusion of such items as flowers and exudates which were eaten at a time when there were few fruit species available for consumption.

Moustached tamarins seemed to prefer fruits at all times of the year as indicated by time spent feeding on them. In the dry season other items were added to the diet, notably exudates, but perhaps only to supplement it, since exudates were not consumed at other times even though they were locally available.

The very long dry season fruit feeding bouts appeared to be designed to preempt the few trees of the available fruits. Length of fruit feeding bouts--assuming that they indicate fruit available--varied a lot from day to day during the dry season. Perhaps the tactic of exhausting the available fruits was an insurance against the unpredictability of fruit availability. Also, the extended rest periods that moustached tamarins took near major dry season fruit trees suggests that moustached tamarins were guarding the few extant resources from competitors. Their presence in the vicinity of the few trees bearing fruit probably detered neighboring tamarins from approaching the area.

Fruit feeding minutes were not a reliable indicator of fruit consumption since fruit handling costs of different types of fruit varied with the species being exploited. High handling costs and lower energetic returns might have influenced length of feeding bouts during the dry season. More feeding minutes were tallied during dry season months, and in particular when feeding on legumes and figs. Fruit handling time was considerable when opening dry pods of *Parkia* sp.. In most cases however, fruit handling was minimal, as in the case of *Ficus* sp. fruits, which nevertheless were consumed for many minutes. If, as reported by Milton (1980:83) for *Ficus* spp. from Panama, the ripe fig fruits are low in ready energy components as compared to other ripe fruits (13% dry weight nonstructural carbohydrates vs over 50% for arils of fruits such as *Tetragastris* sp.), then perhaps moustached tamarins were compensating this deficiency by consuming larger quantities than usual. In addition, figs may be particularly attractive to the tamarins if they are parasitized by insect larvae (Redford et al.,1984).

Preferred fruit trees during each sample period accounted for a large portion of time spent feeding on fruits. Even though moustached tamarins visited from 11-29 fruit trees during a five day period of observation they concentrated on the exploitation of 4 or 5 selected trees. Usually one tree accounted for 20% of all fruit feeding minutes for that period.

Throughout the thirteen months of the study 13 species accounted for over 40% of feeding minutes. In this sense *S. mystax* appeared to have a more varied diet than *Saguinus* spp. at Cocha Cashu-where interference competition from other primates was greater--, which relied on a maximum of six or seven major resource species, accounting for between 51-92% of monthly feeding time (Terborgh, 1986).

During most of the year, *S. mystax* exploited small crowned, synchronously fruiting species, which produced crops for about 4-6 weeks. In some months, large crowned trees which produced a bountiful crop were also utilized. Towards the end of the dry season, moustached tamarins relied on comparatively large crowned tree species.

As reported for other _Saguinus_ species, except _S. geoffroyi_ (Garber,1984), the moustached tamarin consumed exudates only in very small quantities,(Terborgh, 1983; Soini and Coppula, 1981). Even more revealing is that exudates gained any importance in the diet at the time of greatest fruit scarcity, even though they were available year around. This seems to suggest that they are a resource of last recourse for the moustached tamarin. However, in environments with fewer fruit resources than in the Blanco site, moustached tamarins may spend from 41-95% of their feeding time eating exudates (during the dry season), as was reported by Norconk (1986) for moustached tamarins living on an impoverished (compared to the Blanco site) island on the Amazon River.

Since exudate consumption increased almost in parallel with a dramatic increase in insect feeding, at first sight it could be argued that exudates were consumed to promote mineral balance, as suggested by Garber (1980, 1984). However, this would not explain why exudates were not consumed at the critical time of lactation, which occurred from November through February, or at other times of the year when insects were still the most important component of the tamarin's diet (See also Ch.IV B3).

Saguinus mystax obtained the bulk of its exudate by feeding from holes excavated by resident Cebuella pygmaea. Like other Saguinus species and other primates that consume gums (=exudates) the moustached tamarin does not possess the morphological specializations to stimulate the flow of gums (Nash, 1986). The tamarins timed their visits so as to get the most exudate in the least amount of time, thus perhaps reducing their exposure to predators while clinging to vertical supports near the forest floor.

Although arthropod prey is available year around, profound variation in abundance has been reported for populations in the tropics (Janzen and Schoener,1968; Pearson and Derr,1986). Moustached tamarins spent more time foraging for insects and captured more insects per hour in the dry season, specially towards the end of the dry season, coincidental with the first rains. The dramatic increase in insect feeding might be a response to increased insect abundance after the first rains, as reported by Pearson and Derr (1986), for Tambopata, Peru. Although this site is further south from the equator (12° 49'S, 69° 43'W) than the Blanco site, the annual rainfall < 3000 mm, the rainfall pattern (See Gentry and Emmons,1987) as well as the soil type (latosol) are similar to the conditions at the Blanco site.

In summary, during most of the year moustached tamarins relied on relatively abundant ripe fruits which they collected from a few preferred fruit trees. Ripe fruits which presumably are low in toxic compounds but rich in nonstructural carbohydrates, must have provided ready energy for the tamarins. Proteins were obtained from orthopterans and other arthropods. During months of fruit scarcity, moustached tamarins depended on the few fruit trees available, which they exploited intensively: feeding bouts were longer than in wet season months perhaps associated with handling costs and nutritional content of fruits. Site-defense was practiced at this time. Insects were exploited intensively at the time of greatest abundance.

F.- Roosting habits

1.- Roosting behavior.-Moustached tamarins spend from 13 to 14 hours of each day in their sleep tree. As other tamarins (Neyman, 1980; Dawson, 1976a; Terborgh,1983; Goldizen,1987), S. mystax become very secretive when followed by human observers before entering their sleep tree. The moustached tamarins at the Blanco site became very quiet and moved in quick spurts, stopping to look around every few meters. On several occasions, they left their sleep tree when apparently bothered by my presence. Twice, their search for a new sleep tree took them 250m away from the original tree. Once in the sleep tree they huddled together for the night. S. mystax usually exited their sleep tree one by one.

Timing of entrance to and exit from the sleep tree appears to be influenced by changes in daylength at this latitude, and may also be related to general resource availability.

2.- Sleep tree morphology.- Most sleep trees used by moustached tamarins were tall with poor connections to neighboring vegetation, located at habitat transition zones and with dense cover (Table 29). Roosting sites on the sleep tree were usually located behind the fork of the tree or to one side. In many trees the tamarins rested over a mat of lianas and epiphytes, and in some trees there was a root mat overhead. In other cases, the precise location of the tamarin in the tree was not detected.

3.- Frequency of use.-Most sleep trees were used only once for sleeping (54%). However, two trees were used five times each, three trees were used four times each and two trees were used three times each. The large number of sleeping trees may be related to predation pressure. The habitual early morning calling of the moustached tamarin could possibly cue in predators. If this is the case it would be advantageous to change sleep sites so as to discourage predators from learning roosting sites.

4.- Habitat type and sleep trees.- Although there were more sleep trees in the high ground forest and low forest (and less in other habitats) than expected by the proportion of those habitats, the differences were not statistically significant ($x= 7.47$, $p< .1$, $df=3$). Perhaps even more relevant to the moustached tamarins was the micro-location of the sleep trees, usually overlooking habitat transition zones of lower vegetation. Two trees used several times during the study illustrate this observation: one was located 5 meters from the southern boundary, overlooking both the palm-swamp to the south and a vine forest to the east. Another such tree was located in the northeast sector of the home range in the low forest, and although it was located 112 meters from known boundaries, it had a good view of the forest up to 80 meters beyond, in the northeast and towards the west. Its location, bordering a supay chacra and near a tree fall, provided a good view of the surrounding terrain.

5.- Distribution of sleep trees.-Sleep trees did not appear to be distributed randomly within the home range. When the distance to the nearest range boundary was estimated, it was apparent that only one sleep tree was located near the center of the home range (at 200 meters from the nearest boundary) (Fig. 16). Over 40% of the trees were found between 12 and 50 meters from the boundary,in an area equivalent to 34% of the range ($x=1.81$, $p< .25$, $df=1$). Moustached tamarins utilized significantly more trees close to the boundaries for sleeping than non-boundary trees in the wet season ($x=4.15$, $p< .05$, $df=1$); while in the dry season sleep trees were equally distributed over the range (Fig. 16). This seasonal difference could be related to the scarcity of fruit trees in the dry season and a change in territorial defense tactics.

6.- Sleep tree location and food resources.- To investigate the relationship between the location of sleep trees and major food resources I measured the distance from the sleep tree to the four highest ranking food trees for each month. On most nigths (59%) the sleep trees were <150m away from at least one of the four highest ranking food trees. On 24% of the nights the sleep trees were further away (151-250m) from the four highest ranking food trees. On 10 nights (17%) the sleep trees were located at considerable distance (251-490m) from the four highest ranking food trees.

Overall differences between seasons were not detected. However, during the month of maximum scarcity (September) all sleep trees were located less than 150m away from the boundaries, observation that adds to the finding that moustached tamarins spent many hours around fruit trees in the daytime.

That sleep trees were most frequently found in the general vicinity of major food trees during the wet season, may suggest that sleep tree location tends to maximize detection of possible intruders at territorial boundaries. However,it is not clear whether trees within a 150m radius from the sleep tree could be defended from the intrusion of neighboring tamarins. Although tamarins approaching feeding trees call softly to each other (Norconk, 1986), it is dubious that these calls could be heard for more than 80m. In addition, when the Green group intruded into a neighbor's range, they were very quiet, even upon finding a food tree.

G.- The use of Space by S. mystax

Moustached tamarin's utilization of patchily distributed fruit resources required that they travel widely through the forest to locate their food. Also, the vocal and physical confrontations at the boundaries of the Green group home range suggested that moustached tamarins were defending the use of their home range. In this section I will present data on use of space and how this relates to habitat type, predation risks, use of plant resources, and presence of other groups of tamarins.

1.- Home range

a.- Size.- The Green group of moustached tamarins utilized 31.5 ha in thirteen months of observations. Fig.17 shows the number of times that the Green group entered each 0.25 ha quadrat. Over the year, about 75% of their range was entered at least once during each five day sample period (Table 30). Most of the range (96%) was visited in the first 12 days of observations and a few new quadrats were added much later (Fig. 18). The index of defendability [which is average daily path length divided by the diameter of a circle with an area equal to the observed home range Mitani and Rodman (1979)] was calculated at 3.9, which means that moustached tamarins could cross the diameter of their home range almost four times every day.

b.- Use of space.- It was apparent that throughout the year moustached tamarins did not use their home range in a random fashion. About half of their range was used less than expected--

if use were distributed equally--, while 34% was used more than expected and only 16% was used according to expectations (Fig. 17). These differences in spatial utilization appeared to be affected by location of the different quadrats relative to: (1) boundary vs. non-boundary; (2) predation risks; (3) distribution of preferred fruit trees; and, (4) presence of neighboring groups.

The Green group exclusively used 26.8 ha (85%) of its range (= territory, sensu Brown and Orians, 1970), while 4.7 ha (15%) was periodically invaded by neighboring groups, or was infrequently used by the Green group (=overlap zone).

Range use and habitat type.- The Green group used most habitat types a little less than expected based on the proportion of each habitat in the home range; only the low forest was entered more often than expected ($x=143, p< .0001$ $df=4$) (Table 31). Since food trees were distributed according to the proportion of the different habitat types (Table 16), it would seem that other factors in addition to presence of food trees influenced quadrat use. It could be argued that distribution of insects might be influencing the preferential use of low forest, since moustached tamarins used this habitat more frequently than expected when foraging for insects; however, the differences observed in habitat use for this activity were not statistically significant ($x= 7.22$, $p=.1$, $df=4$).

Why did the tamarins use some areas less than expected? In the case of the purmas and swamp forest, it was obvious from the travel routes taken by the tamarins that they avoided these habitat types whenever possible. In particular the purma was avoided and a circuitous route was taken to avoid crossing it. The moustached tamarins only entered it during the dry season to feed on _Inga_ sp. and domesticated _Pourouma_ trees. On a few occasions the mixed group split up with _S. fuscicollis_ going across the purma, while the moustached tamarins took the long route around, all the while calling for the saddle-back tamarins. The palm-swamp habitat, which is distributed in strips through the forest, was utilized for fruit trees and little else; if there were travel routes near them, the tamarins rarely included the palm swamp in their forays. The vine forest was used only a little less than expected and the moustached tamarins used it for all kinds of activities. The high ground forest might have been used less than expected due to predation concerns. The trees in this habitat type are more spaced than in the low forest or vine forest, although less spaced than in the swamp forest. _S. mystax_ were more easily detected by the observer in this habitat type--and presumably by predators--than in any of the other habitats. In fact, two of the predator attacks suffered by the tamarins occurred in this habitat.

Range use and distribution of food trees.- Although food trees utilized by moustached tamarins were not evenly distributed in relation to quadrats (Fig. 19), they were distributed in proportion to habitats within the range (See section C1d). Distribution within habitats however, was clumped (Fig. 20).

Overall, more than 60% of the quadrats were either not used for plant feeding or were used less than expected (Table 32). A small percentage (13%) were used as/or a little over what was expected, while only 20% were used intensively: from twice to eight times the amount expected if plant feeding was equally distributed (Table 32). This pattern is not surprising given the habits of moustached tamarins described in the previous section. Moustached tamarins used some individual food trees preferentially over others of the same species, or relied on one or two individuals of a few fruiting species at times of fruit scarcity.

The striking fact is that most feeding minutes were tallied while moustached tamarins were feeding on trees distributed at or near the boundaries of the home range. This pattern was evident when the shortest distance from the ten highest ranking trees to the nearest home range boundary was estimated (Table 33). A significantly greater number ($x=27.46$, $p< .0001$, $df=1$) of the ten highest ranking trees for each month of the study were found within 50 meters of the home range perimeter (from 38% of all second ranking trees to 77% of all first ranking trees). Moreover, 10 out of the 13 first ranking individual trees were located within a 50 meter strip around the range boundaries (Fig. 20).

Food trees within the boundary strip were as numerous as expected. The number of food trees in the 50 meter strip, was proportional to the area (10.6 ha) included by the strip. The next step was to establish whether or not preferred food species were more numerous around the boundaries. The known distribution of two high ranking species with numerous individual trees (Pourouma cecropiaefolia, and Naucoleopsis imitans) did not suggest a clumped distribution around the range boundaries. Both species were distributed randomly over the whole range. This might be interpreted as suggesting that moustached tamarins chose the individual trees closest to the range boundaries over more centrally located trees. In fact, when looking at the four highest ranking fruit trees--which contributed from 45% to 97% of plant feeding-- two observations can be made: (a) the variety of species consumed at the top, and (b) when several individuals of one species were fed on in the same sample, most feeding minutes were tallied on the tree closest to the boundary (Table 23). Pourouma cecropiaefolia, Strychnos spp., Byrsonema sp., Maripa axilliflora and an unidentified Aralaceae were preferred species utilized by the moustached tamarins. In all cases except Pourouma, of the several individual trees used, the preferred tree was the one closest to the boundary (4 of 5 months) (Table 25). These observations suggest that proximity to boundary might be a factor when selecting fruit trees to feed on.

That availability of fruit trees influenced choice is indicated by the fact that a significantly greater percentage of the four highest ranking trees were closer to the boundary in the wet season ($x=30.86$, $p< .0001$, $df=1$) than in the period of maximum scarcity when fruit trees were randomly distributed (Fig. 21).

Since information on the nutritional characteristics of preferred trees is lacking, I will not comment on it, but it was probably an important factor when selecting a preferred tree.

Use of the range perimeter.- Whether boundary quadrats were entered more frequently than non-boundary quadrats was determined by looking at a 50 meter strip of approximately 11 ha (henceforth referred to as "boundary quadrats") around the perimeter of the range. Boundary quadrats were entered as expected by chance (x=.066, p> df=1). However, if little entered quadrats ("trespassing" quadrats, see below) were excluded from the calculations, then boundary quadrats were entered significantly more than non-boundary quadrats (x=54.71, p<.0001, df=1).

About 15% of the range (approximately 5 ha) was used following a double pattern: (a) most boundary quadrats were entered frequently by the Green group and sporadically invaded by neighboring groups of tamarins: the case of the quadrats in the northern, southeast and southwest sections of the range; and, (b) a few quadrats were seldom entered; as was the case with boundary quadrats in the southeastern and southwestern portions of the range. When the moustached tamarins entered these areas they characteristically displayed one of two "trespassing behaviors": they either advanced slowly through the area while vocalizing or traveled stealthily through it. Brief feeding bouts occurred during these periods. In both cases the group reentered known terrain within the hour of entering the little used area. On a few occasions during such excursions the Green group encountered resident neighbors, which caused their rapid retreat. Only twice (2/10 times) did a physical confrontation (fight) ensue when the Green group was trespassing; on five instances they were not discovered by the resident tamarins, and on two a vocal battle resulted, ending with the withdrawal of the Green group.

When moustached tamarins detected the presence of intruders, they rapidly approached the area, vocalizing; once they were close enough to establish eye contact with the invading tamarins, they either physically expelled the intruders (fight) or, if the intruders were on the other side of the invisible boundary, they moved parallel to the boundary while calling (vocal confrontation).

Range use and territorial encounters.- A total of 25, or 3.3 confrontations/week were observed during the study (Table 34). The confrontations were almost equally divided between fights and vocal interactions. Although there were more territorial confrontations in wet season months than in the dry season, the majority of these encounters were vocal. In contrast, in the dry season there were fewer confrontations, but most of them ended in fights.

Range use and seasonality.- Moustached tamarins not only spent more time traveling in the wet season but they covered a greater area of their home range than in the dry season (W:p<.05, n=49), as indicated by the number of quadrats visited (Table 30). Correspondingly, path length was considerably longer in wet season months (x= 2733 + 554) than during the dry season (x= 1987+ 55) (W: p< .0001, n=57), and was positively correlated with number of fruit trees visited (rs= .589, p< .0001, n=57).

During wet season months there was little month to month variation in the number of quadrats entered, and on average nearly 80% of the home range was visited during a sample period (Table 30). In the dry season, there was a reduction in the number of quadrats visited, reaching an all time low in the month of September, when less than 60% of the range was visited.

Figure 22 illustrates the seasonal differences in use of space by the moustached tamarins, by comparing the paths followed during two wet season months (December and April) and two dry season months (August and September). During wet season months all boundary quadrats were entered at least once during a five day period, while during the dry season up to 25% of boundary quadrats (See September map) were not visited during a five day period.

H.- Summary and Discussion of use of space by the moustached tamarin

1.- Least used and most used areas of the home range .- The Green group occupied a range of 31.5 ha, of which 15% was determined to be an overlap zone. Half of the range was visited less than expected: some of those areas included the purma, palm-swamp, and segments of boundary quadrats.

The purmas included open, low forest habitat, where predation risks were probably high. Increased costs of travel associated with avoidance of open areas, and their use only at the time of greatest fruit scarcity suggests that the risks associated with its utilization were probably high. It would seem that moustached tamarins would be vulnerable to both terrestrial (because of low forest height) and avian predators (due to the openness) in this kind of habitat. Little use of open habitats by the Panamanian tamarin was attributed to predator avoidance and decreased fruit resources (Dawson, 1976a).

The little use of swamp forest might have to do with the relative scarcity of preferred fruit trees in this habitat, although high predation exposure can not be ruled out due to the openness of this habitat.

Little used areas also included portions of boundary quadrats which were entered only in the course of trespassing. Thus, some quadrats of the range were avoided due to high predation risks, or were minimally used due to their location.

Moustached tamarins, as other tamarins, utilized different habitats within their range. In terms of total use there was a preference for low forest over other types of habitats; this could be related to insect foraging, which occurred more frequently in this habitat. On the other hand, moustached tamarins did not show preference for edge forest (vine forest in this study) as has been reported for the Panamanian tamarin (Dawson, 1976a).

Use of space was more concentrated around the perimeter than in the center of the home range. In fact, moustached tamarins used boundary quadrats within a 50 meter strip around the range perimeter more than non-boundary quadrats. The number of times they entered this area, the number of feeding minutes tallied on boundary food trees, added to the number of nights they spent on trees located at the boundary quadrats, strongly indicate a preference for areas around the perimeter of the range.

Boundary zone in this study is equivalent in size to the overlap zone of Norconk's(1986) study (=10 ha), although the shared portion of the range (overlap) during this study was only 5 ha, and was included within the boundary. Norconk (1986) found equal use of overlap and nonoverlap area--as reflected in the number of times that respective quadrats were entered-- however, she did not analyze separately for plant feeding time. Nevertheless, Norconk (1986) found more sleep trees in the overlap zone than in the non-overlap zone as in this study. Thus it appears that the Green group followed a similar pattern of range use during the second year of observations. Dawson(1979) found that the outer half and inner half of the range were used equally by the Panamanian tamarins. On the other hand, Terborgh (1983) found that Saguinus spp. used the centers of the territory intensively, and the margins lightly, and distribution of major food trees seemed to parallel quadrat use, at least for the month of April (Terborgh,1983:149). Thus, as in the moustached tamarin, spatial utilization of fruit resources influenced range use, although the patterns of use differed.

2.- Use of space, seasonality and territorial defense.- Within the home range two areas could be distinguished according to the pattern of use. The boundary zone: 15 ha around the periphery of the home range was used proportionally more than the rest of the home range. High use was related to intensive plant feeding in peripheral fruit trees during most of the year, territorial patrolling and confrontations, and location of sleep trees. The overlap zone, which covered aproximately 5 ha within the boundary zone, was used intensively by the resident group, and was periodically invaded by neighboring groups. The non-boundary zone was used less than expected and included most of the traditionally defined territory, an area of exclusive use, defended against conspecifics. My observations indicate that most of the overlap zone was intensively used, and very little passive sharing with neighboring groups was detected.

Thus, moustached tamarins were at the same time residents and trespassers when using the home range; overall, however, I observed more instances of defense of the home range against intruders than apparent trespassing into other groups' home ranges.

When fruit was abundant tamarins ranged widely--visiting most of their range and all boundary quadrats at least every five days--, most used trees were found less than 50 meters from the boundary, and although there were more encounters with neighboring groups, proportionally fewer ended in fights. Fruit scarcity in the dry season resulted in limited ranging--absolutely fewer quadrats, and a smaller percentage of boundary quadrats were visited--, most used trees were found further from the boundary than in the wet season, and even though there were fewer territorial encounters, a larger percentage ended in fights. Also, tamarins practiced resource site defense by remaining for long periods of time around feeding trees. This last is not unlike the behavior displayed in a very seasonal forest by Panamanian tamarin groups, which became nomadic and practiced site defense during the period of maximum scarcity (Dawson, 1979).

Norconk (1986) found a greater rate of territorial encounters during May, June and October (excluded from her sample were July-September) than during the rest of the year, which was correlated with fewer food trees in overlap zones. Terborgh (1983) concluded that _Saguinus_ spp., although fiercely defending their territory at Cocha Cashu, did not show seasonality in the pattern of territory use in any important fashion; he related this to their reliance on common, continuously available major plant food resources. Although the Blanco stream site receives more rain than the forest at Cocha Cashu, and as such less seasonal variation should be expected, it is surprising that this is not so. The forest at Cocha Cashu shows a mosaic of habitats, with great floristic richness and apparently enough resources that there was no need for the tamarins to change their tactics of resource exploitation. Alternatively, any seasonality displayed by Saguinus spp. at Cocha Cashu might have been obscured by the changes of territory and group composition between each pair of samples (Terborgh, 1983:147). On the other hand, the Blanco site, although supporting fewer primate competitors, required that the tamarins change their tactics of resource exploitation during the dry season.

3.- Temporal variation of range use.- Year to year .- During this study the Green group had 5 members, they occupied a range of 31.5 ha; 15%(= 5 ha) of which overlapped with at least four other mixed-species groups of tamarins. Norconk (1986) studied the Green group when they had from 7-9 members, she found them occupying a home range of 29 ha, and observed 35%(= 10 ha) overlap with four mixed-species groups of neighbors. Garber (1988) observed the group when it had 11-13 individuals, occupied 40 ha of home range, and shared 23%(=9.2 ha) of it with seven mixed-groups. Home range calculation methods employed by Norconk (1986) are comparable to mine; however, it is not clear what method was employed by Garber (1988).

Between the end of 1982 and the end of 1984 the Green group increased in size, while at the same time it expanded its home range when the group grew from 11 to 13 individuals. Reports for 1983 also indicated that neighboring groups grew in size, although the number of groups remained the same (Norconk, 1986). During my study and Norconk's the neighboring groups were not marked and thus our figures could be an understimate of real number of groups; alternatively, the number of groups might have increased between Norconk's and Garber's study.

Thus, with increasing density the degree of overlap doubled from 5 ha to 10 ha between 1982 and 1983. In 1984, although density was even higher, the number of shared hectares was similar to the previous year, since the size of the home range had apparently increased.

In summary, home range size and degree of overlap fluctuated with changes in size of the group and presumably with size of neighboring groups. In contrast, Terborgh (1983) did not observe changes in territory size during a four year period although the number and composition of resident tamarins changed.

4.- Distribution of preferred fruit trees and habits of moustached tamarins .- Although food trees utilized by S. mystax were distributed in proportion to habitats, their distribution within habitats was clumped. Most plant feeding occurred on fruit trees in the periphery of the home range. Most of the highest ranking trees were located within 50 meters from known boundaries. Food trees were not more numerous in this area, and at least two of the preferred species with numerous individuals were well distributed within the range. Similarly, Norconk (1986) found feeding trees distributed proportionally between overlap and non-overlap zones during her eight month study.

Proximity to boundaries was associated with intensive use of individual trees. This was evident when the use of several individual trees of a preferred species was compared. The tree closest to the boundary was preferred for feeding in 4 out of 5 months compared. This suggests that location near boundaries might be an important criterion when selecting fruit trees.

Given a widely distributed species bearing fruit, the tamarins might choose boundary individuals if in this way they also reaffirm their presence to neighboring groups. Thus visits to boundaries would not only serve to patrol them but to discourage trespassers by feeding on fruit trees. It may not be coincidental that moustached tamarins increased calling rate while approaching food trees (Norconk, 1986), thus perhaps warning possible interlopers.

In the previous discussion I have not excluded the possibility that preferred trees might produce better quality fruits. In the cases of P. cecropiaefolia and N. imitans, where boundary individuals of the second species were preferred, all individual trees throughout the range produced fruit that was equally tasteless. Moreover, all Pourouma used produced sweet fruits, but at least two individual trees which bore much sweeter fruits were not high ranking trees, thus supporting the suggestion that at least in these two cases fruits trees were selected for reasons other than nutrient content.

It is tempting to speculate that preferred species grow in boundaries due to the dispersion activities of moustached tamarins. The seeds of Pourouma and N. imitans are ingested by moustached tamarins and it has been suggested that they might be their dispersal agents (Garber,1986). Garber (1986) suggested a possible correlation between the actual distribution of fruit trees and the seed shadow left by moustached tamarins. Since the tamarins have a high passage rate of seeds, they void them every few hours, thus resulting in more or less random distribution of seeds. Going one step further, if moustached tamarins are in part responsible for the peripheral distribution of preferred food trees, their selection of sleeping sites might help provide an explanation. The tendency to select sleep trees near range boundaries would result in accumulation at the boundaries of seeds that were voided during the night or in the morning. In many instances, preferred fruit trees were last visited before entering the sleep tree. These practices would promote the development of tree-marked boundaries which would remain permanently stable. Only long-term observations of the same group can provide evidence of such a phenomenon. Terborgh (1983) noted that tamarin territories maintained their integrity through several years, even though the tenants changed in some cases. Maintenance of territorial integrity could be facilitated if there existed territorial markers, such as preferred fruit trees.

Discriminant use of boundary vs. non-boundary quadrats has only been reported for S. mystax and S. fuscicollis (this study). Dawson (1976) did not find differences in the use of the inner half vs the outer half of the range in S. geoffroyi. Terborgh (1983) found that Saguinus spp. used the center of the range more than the boundar. His observations however, were admitedly confused by changes in territory and group composition of the subjects. On the other hand, Easley (1982) in his study of Callicebus torquatus noted that this territorial species spent most of its time feeding on Jessenia fruits on palms very close to the boundary.

5.- Sleep tree location, predation risks, and territorial behavior.- Most sleep trees were located within 75 meters of the boundaries and only one was located 200 meters away. Norconk (1986) similarly found that 50% of the sleep trees were in the overlap zone which only occupied 33% of the range. Perhaps more importantly the majority of sleep trees were bordering habitat transition zones which provided both an open platform from which to broadcast calls, and a panoramic view of the forest below and beyond. Moustached tamarins called every morning from their sleep tree or soon after leaving it, and calling rate was highest in the first hours of the morning (Norconk, 1986; this study). I will argue that selection of sleep tree morphology is related to predator protection while the location of sleep trees and selection of preferred fruit trees is related to the economics of territorial defense.

Long-distance calls (LDC) in moustached tamarins are high pitched vocalizations (8-12khz) composed by a series of short, repeated syllables, that allow recognition of individuals (Snowdon and Hodun, 1985; Norconk, 1986). LDC, of which at least two variants can be recognized, carry for short distances, 100-150 meters, and seem to be designed to maximize localization rather than long-distance transmission (Norconk,1986; Snowdon and Hodun, 1985; Waser and Waser, 1977; this study). Two main functions have been suggested for long distance calls: (a) cohesion-maintenance among group members and with co-territorial saddle-back group, and (b) advertisement of territorial residency (Norconk, 1986; Snowdon and Hodun, 1985).

It would seem that by vocalizing from a tall tree with little interference from foliage, moustached tamarins will increase the distance traveled by the call. Kloss gibbons also vocalized from forest types with the tallest trees and above the break of slope on Siberut Island (Whitten, 1982). If early morning calls are used to advertise presence, then it makes sense for tamarins to select tall sleep trees located at the border of forest openings, and less than 200 meters away from boundaries. Furthermore, since visits to fruit trees usually take moustached tamarins to boundary quadrats, and fruit trees are usually approached while calling, the incursion into boundary quadrats serves a dual purpose: (a) feeding, and (b) advertisement of presence when the probabilities of being heard are greater, thus minimizing costs of territorial maintenance. That most territorial confrontations occurred within the hour of leaving the sleep tree (Norconk, 1986; this study) indicate that early morning long-distance calls while visiting boundary quadrats act to attract groups moving in the vicinity of range boundaries.

Thus, one of the criteria for selection of sleep trees was closeness to range boundaries so as to maximize the likelihood that early morning calls could be heard by neighboring groups. Selection of trees near forest openings might also be related to reduction of foliage interference to call transmission, although the importance of a visual component to the call has not been excluded.

That a greater percentage of sleep trees were closer to boundaries in the wet season than in the dry season might be related to monitoring and defense of abundant fruit resources. In the dry season may not be as important to be close to boundaries to claim ownership of a range that contains few fruit trees. Moustached tamarins engaged in fewer territorial encounters (although more ended up in fights) and practiced site defense in the dry season.

Selection of sleep trees on the basis of proximity to territorial boundaries and/or safety from predators is probably not unique to *S. mystax*. Soini and Coppula (1981) found that *S. fuscicollis* also selected most of its sleep trees near the water (range boundary) or near a forest opening, while Dawson (1979) found that *S. geoffroyi* sleep trees were much taller than the surrounding vegetation and were located all over the range. Long-distance calls in *S. geoffroyi* are low pitched (1-2 khz) and appear better designed for long-distance transmission (Snowdon, 1988) than the calls of the moustached tamarin. If, as I hypothesize, location of sleep trees is related to territorial defense then it may not be as important for *S. geoffroyi* to select sleep trees close to boundaries since their LDC travels further in the forest.

Sleep tree morphology seems related to avoidance of predation risks. Tall trees, with few connections to neighboring vegetation may provide safety from arboreal- terrestrial predators with crepuscular/nocturnal habits such as snakes, felids and maybe mustelids. However, they make tamarins particularly vulnerable to avian predators. The moustached tamarins seem to have adopted tactics that minimize this exposure. It would appear that entrance to and exit from the sleep tree would be the most vulnerable times; but the stealthy behavior displayed by moustached tamarins upon entering the sleep tree tended to reduce predation risks at this time. Tamarins left their sleep tree one by one and in silence which might reduce the likelihood of being detected by raptors.

Stealthy behavior when entering the sleep tree and selection of sleep trees with few connections to neighboring vegetation has been reported for other tamarins (*S*. *geoffroyi*, *S*. *fuscicollis*, *S*. *imperator*) (Dawson, 1976a; Soini and Coppula, 1981; Terborgh, 1983) and are likely part of a general tamarin strategy to deal with high predation pressure from nocturnal-crepuscular predators. Since tamarins have not been observed at night, this is a difficult point to substantiate. However, mobbing responses of tamarins to mostly nocturnal predators (margays, ocelots) provide indirect evidence of predation risks (Caine, 1988; Izawa, 1978; Norconk, 1986).

I.- Association with *S. fuscicollis*

Moustached tamarins at the Blanco site lived in semi-permanent associations with the saddle-back tamarin (Table 35). Group composition of the Green group changed little during the study. The Green group had ten members at the beginning of the study in 1981 (5 *S. mystax* and 5 *S. fuscicollis*). After the death of a *S. fuscicollis* there were 9 individuals left for the rest of the study.

1.- Interspecific attraction.-Both species of tamarins displayed strong attraction for each other. This was particularly obvious upon leaving the sleep trees, and when the tamarins were separated during the day.

On 30% of the mornings both tamarins exited from the same sleep tree. *S. fuscicollis* was observed to sleep on a different branch or at a lower level in the tree. On most days *S. fuscicollis* selected a sleep tree in the vicinity of the moustached tamarins (25-75 m). On a few occasions, *S. mystax* entered its sleep tree while the saddle-backs continued traveling. After a few minutes the saddle-backs would call, and if there was no response from the *S. mystax* they were observed to retrace their steps presumably in search of their associates. Once located, they settled in the vicinity.

On some mornings when it was apparent that the saddle-backs were not close by, the moustached tamarins called for a long time and only stopped once they were joined by the saddle-backs. Both species gave contact calls throughout the day (Norconk, 1986; this study). Rain and thunderstorms seemed to affect vocal contact between the tamarins, which invariably tried to re-establish contact with their associates after rain or thunder ceased.

S. fuscicollis spent--in the daytime--79% of the time within 20m of the moustached tamarin. They responded to each other's alarm calls by becoming alert, running for cover or mobbing the object of their distress.

2.- Dietary overlap.- *S. fuscicollis* visited 73% of the fruit trees visited by the moustached tamarin [82% during Norconk's study (1986)]. In addition, they fed on small trees that were never used by *S. mystax*. The saddle-backs fed on exudates in every month while the moustached tamarin confined its exudate feeding to the height of the dry season. *S. fuscicollis* foraged for insects on tree trunks in the lower levels of the forest (Garber, 1988; Norconk, 1986; this study), while *S. mystax* gleaned insects from leaves in the periphery of the subcanopy.

On many occasions the moustached tamarin entered fruit trees ahead of the saddle-backs. There is a chance however that this might have been an artifact of the observer concentrating on *S. mystax*. Once in a fruit tree, *S. mystax* was always observed to supplant the saddle-backs at feeding sites, without using overt aggression. *S. mystax* also chased *S. fuscicollis* from exudate trees inthe dry season. Inter-specific grooming or other affiliative behaviors were absent from this association.

3.- Vertical stratification.- The tamarins generally used different heights in the forest during most activities (Norconk, 1986). In general *S. fuscicollis* used the lower 8m of the forest while *S. mystax* was most often observed above 8m (Norconk, 1986).

4.- Territorial behavior.- Both tamarins engaged in confrontations with conspecifics at territorial boundaries. *S. fuscicollis* was perceived as the more vocal of the two and also more frequently engaged in physical contact.

J.- Demographic variables of _S. mystax_ at the Yarapa river site.-

1.- Population density.- After the initial cropping of 66% of the _S. mystax_ population in 1978 (Table 36), three groups of moustached tamarins remained within the study area, plus eight individuals that did not enter the traps (Table 37) shows the composition of trapped groups in 1978 and 1981). All individuals trapped in 1978 were removed from the population. The census of 1981 revealed an active recovery of the population, which had increased by 124% (Table 36) in the three years following the cropping. Even so, it had not reached the pre-cropping density of 32.1 ind/sq km (Table 36). The 1982 census indicated a slight decrease in the number of _S. mystax_ when compared with 1981 (Table 36).

The _S. fuscicollis_ population, although minimally affected at the time of the cropping of 1978 -since only 9.5% of the population was cropped- (Table 36), had, in fact, decreased by 12% between 1978 (after the cropping) and 1981. Between 1981 and 1982 the population of _S. fuscicollis_ increased by 18% (Table 36). In spite of this, they had not recovered to pre-cropping levels in four years.

2.- Group size.- Group size for _S. mystax_ varied from 3-9 for reproductive groups (Table 35 and 36). Although previous to the cropping most groups were average-sized (mode= 5), in 1981 there were more larger groups (mode= 7), while in 1982 groups of 4 and 5 individuals were more common. Not only were there fewer S. mystax in 1981 and 1982, but there were also fewer groups than in 1978.

Saguinus fuscicollis groups ranged in size from 4-14 for reproductive groups. Groups of 4 and 5 were common in 1981 and 1982. At least one very large group was reported in both years of observations and also in 1978 (Tables 37 and 38).

3.- **Group structure** .-The census of 1981 revealed a high proportion of immatures to adults (0.86:1) in the population (Table 39). All the groups except one had juveniles, and one of them had three, most probably the survivors of two successive litters born in one year period. This is in contrast to the widespread occurrence of only one birth per year and the fact that usually only one infant survives into the juvenile stage (Soini and Soini,1982). Also the moustached tamarin population in 1981 had a higher proportion of young adults 2-3 years of age (65-85%) than other non-cropped populations, which averaged 50% young adults (Soini and Soini, 1982).

With regards to sex ratio, the 1981 census indicated an excess of males per female as occurs in all the other areas censused. This is in contrast with the pre-cropping findings of a sex ratio where females were more abundant than males (Table 39).

All the groups captured in 1981 had at least one male and one female of reproductive age (Table 37). Group 5 had the appearance of an incipient group but included a small juvenile. Even though they were trapped at the same capture site of another group, they appeared to be an independent unit. The fact that no adult male was observed in this group does not rule out the possibility of the subadult's siring the juvenile.

When comparing the census data of 1981 with the pre-cropping data for 1978, it is apparent that a larger percentage of the female population (71%) bred in 1981, while only 50% did so in 1978 (Table 40). Furthermore, at least one of every adult resident female in a reproductive group appeared to have bred in or around 1981, as evidenced by the presence of juveniles. In contrast, only 50% of the females of breeding status bred in 1978. In other words, of all the females that had a chance to breed by being the dominant or mature female in a group, only 50% of them did so in 1978, while all reproduced in 1981. Not surprisingly, juvenile productivity was much higher in 1981. There were 5.2 juveniles /sq km/year vs 3.15 juveniles/sq km/year for 1978 before the cropping. In other words , there were 0.25 juvenile per adult female before the cropping vs 1.0 juvenile per adult female three years after the cropping.

K.- Summary and Discussion of Demographic findings at both study sites

1.- Population growth.- At the beginning of the study Saguinus mystax were moderately abundant at both study sites (Table 41).

a.- Population growth at the Blanco stream site.- At the Blanco Stream, although deaths occurred, the population increased due to births. Groups were initially average in size,increased their membership, and continued to do so for the next two years following the end of my study. Two females were observed to give birth within the same group. Observations on a focal group provided evidence that females can became pregnant every 6.5 months. Births occurred within the period reported for other areas of Amazonia.

Between 1981 and 1984, a base population of 22 ind/sq km, organized in a few groups, increased in size until it reached a density of 33 ind/sq km. Groups grew for several years, without breaking up into smaller units. During the almost four years when the moustached tamarins were monitored continuously, survivorship appeared high as evidenced by group membership and infant survival of monitored groups (Garber, 1988; Norconk, 1986; this study).

Demographic and environmental conditions appeared favorable for population increase in 1981. The availability of food is a prime factor affecting population growth, since it determines the condition of the animals, which has been shown to affect fertility in many mammals (Dunbar, 1987) including primates (Strum and Western, 1982). The tamarins at the Blanco site appeared in excellent physical condition [body weights were high (Garber and Teaford, 1986) and they did not show any signs of disease] which might be related to the apparent abundance of food resources and/or reduced interspecific competition. In addition inter-specific competition appeared unimportant as indicated by the very low level of interference competition observed. Demographic parameters such as age structure, sex ratio, and social factors (e.g. rank,competition) are also known to affect fertility (Altmann, 1980; Dittus, 1975; Dunbar and Sharman, 1983; van Schaik, 1983). Females in the trapped groups appeared young, aproximately 4-5 years old (age scale follows Soini and Soini, 1982), the age at which female tamarins show the highest fecundity rate (Soini and Soini, 1982).

b.- Mechanisms of population recovery at the Yarapa river site.- Censuses at the Yarapa river site in 1981 (including trapping) and 1982 when compared with the initial census and cropping of 1978 provided evidence of population recovery, as well as insights into its mechanisms, and the dynamics of population recovery in mixed species associations of tamarins.

My findings at the Yarapa River site can be summarized as follows: The S. mystax population, cropped of 66% of its members, showed recovery three years after the cropping. In that period of time it had increased by 124%. The initial high tamarin density for the area had not been reached in three years post-cropping. Analysis of group structure in 1981 revealed a population significantly different from the population before the cropping. Its profile was that of an actively growing population: most adults were young, there was evidence of high birth rate and high infant survivorship.

Immigration at the Yarapa river.- Although it is not possible to assess with certainty the relative importance of immigration and natality on the population recovery, there are indications that immigration played a minor role, since birth rate and juvenile productivity were high.

Birth rate and age of breeding females at the Yarapa river.- In 1981 there was a very high proportion of immatures in the population. Pre-cropping ratios indicate about two thirds fewer immatures per adult in the population (Table 39), a figure similar to that found in other areas (Soini and Soini, 1982) of Amazonia.

The large proportion of young adults in 1981 indicates a vigorous population, which, in spite of the young age of its members, showed higher breeding success than populations with a greater proportion of older individuals. All captured females in 1981 appeared younger than four years of age, and most of them were successful breeders. Usually only 25% of young females (up to five years) breed, whereas middle-aged females are the most active breeders (Soini and Soini,1982). This indicates that given the appropriate circumstances young females are able to show a better breeding performance than similarly aged females in other population.

The effect of habitat loss on the incomplete recovery of S. mystax at the Yarapa appears unimportant due to the very low rate of forest clearing between 1978 and 1981 (1.5 ha, according to reports from the inhabitants). Three years might not have been enough for the population to recover its pre-cropping density. At the Blanco stream, a denser basal population (22 ind/sq km) reached a density of 33 ind/sq km in three years, thus it might take longer to recover from an initially much lower (11 ind/sq km) density. S. fuscicollis on the other hand seems to be well on its way to full recovery.

In summary, although immigration might have played an initial role in the population recovery, it seems that increased reproduction in situ and reduced infant mortality carried the population recovery in the Yarapa population.

2.- Dispersion.- From 53 groups of moustached tamarins captured in the Tapiche and Maniti rivers (data from Soini, 1982b), only 13% were large groups (over 8 independently locomoting individuals) which suggests that large groups are either unstable and consequently short-lived, or that groups do not grow to be large because of yearly departure of individuals as they mature.

Fluctuation in group size as a result of yearly departure of individuals from natal groups has been reported as a seasonal phenomenon by Soini and Soini (1982). These researchers report changes in group size preceding the birth peak for the area. In September and early October modal group size was 5 for a large population of tamarins (n=72 groups) at the Maniti river. From late October-February modal group size dropped to 3, coincidental with the start of the birth season for the area. Small groups were usually composed of two adult males and one female (most of which were young adults).

In summary, dispersal has been reported to occur by splitting of large groups into smaller units (Garber, 1988) every few years, or by the yearly departure of maturing individuals from natal groups (Soini and Soini, 1982). Local conditions such as population density, food resources, competitors and predators will most likely influence whether one strategy or the other is employed at any one time.

There is little indication of the proximate factors involved in group fission. Time budget data for the Green group inmediately preceding and following group fission in November 1984 (Garber,1988) did not show a decrease in time spent either feeding or traveling as a result of decreased group size. From the data presented by Garber (1988)it is not possible to exclude factors such as increased within-group competition for food resources, which can burden some members of the group more than others (e.g. Janson, 1986), thus resulting in e migration of subordinate individuals. At the Blanco site, the reduced intraspecific competition and the benefits of increased group size favored the steady increase in group size.

At the Maniti river (reported by Soini and Soini, 1982) we know much less about the possible factors at work. Population density was around 25 ind per sq km, inter-specific competition from other primates, was reportedly low, and tamarins were lower in body weight than at other sites. This last might indicate that food resources were not as abundant as at the Blanco Stream site, and that an increase in group size--which might intensify within-group competition-- might conceivably burden certain individuals (young, subordinate adults) remaining in larger groups.

Perhaps one of the factors favoring departure of young adults is the harrassment they suffer from maturing subadults. During the dry season, when the subadult in Green group was about 10 months old, he was observed begging food from the two males on several occasions. Both, fruits with tough exocarp (<u>Parkia oppositifolia</u> pods, and other large fruit) and captured Orthoptera were relinquished to the subadult after much vocalizing on its part. Alternatively or concomitantly the behavior of the pregnant female/and or male(s) during the last stages of pregnancy might trigger departure of young adults. Thus, the seasonal emigrations of young adults could be related to high intraspecific competition and/or good probabilities of successful dispersion into sparsely populated--albeit suboptimal--habitats. Similarly, Dawson (1977) found higher rates of migration in a group living in a more unstable habitat when compared with the group living in a more stable habitat.

I suspect that the consequences for the individual migrants of either one of the strategies are markedly different. Individuals that emigrate as members of a group are better able to compete with established groups, since it is likely that they include older, more experienced adults and also are exposed to decreased predation risks; while young adults in "incipient" groups probably suffer higher mortality due to predation and interference competition.

The following observations lend some support to the previous suggestion. Two young adult females that I intermittently observed at the study site were trapped once and utilized as decoys. The reaction from the resident tamarins (the Green group), particularly the adult males, was the strongest that I have ever seen against conspecifics. They attacked each one of the females (one of them appeared to be in estrus as indicated by the tumescent condition of the vulva) trying to grab and bite at them through the wire cage.

It is noteworthy that dispersion episodes coincide with the period of greatest fruit abundance, thus presumably increasing the chances of survival for the emigrating tamarins.

3.- Consequences of dispersion: population fluctuation.- Fluctuation in density of local populations of moustached tamarins could be part of a regular cycle of local population expansion followed by shrinking of the population as a result of emigration of either individual maturing tamarins or sub groups of tamarins. Depending on local environmental conditions, one or the other will be practiced and the consequences for individual migrant tamarins, and for the population as a whole, will differ.

Outwardly, Maniti-like populations will vary little in size from year to year due to yearly departure of young maturing individuals which might suffer high mortality due to predation and marginal access to food resources. Blanco-like populations will go through noticeable periods of expansion followed every few years by reduction of the population. Census data for the Blanco Stream population in 1975 (32 ind/sq/km) and 1981 (22 ind/sq/km) may be evidence of these fluctuations (Table 41). Departing tamarins, protected in the midst of a group probably will not suffer as high mortality due to predation as individual migrants. However, in Blanco-like conditions with a large tamarin population, competition for access to food resources by tamarins not holding a territory will be particularly strong. This in turn might prevent breeding such as at the Yarapa river in 1978 where a high population density was associated with a high proportion of non-breeding units (Moya et al., 1979).

Thus, the Maniti population was associated with an environment with a lower carrying capacity for tamarins and yearly dispersion episodes, while the Blanco population, apparently in an environment with a higher carrying capacity displayed less frequent dispersal episodes.

4.- Dynamics of population growth and recovery of mixed species groups.- At the Blanco Stream *Saguinus fuscicollis* were not as abundant as moustached tamarins but their abundance was within the range for the area. Saddle-back tamarins, paralleled the population growth of moustached tamarins.

Given the reported strong association among the saddle-back and moustached tamarins it is not surprising that the removal of one species affects the remaining population. The fact that *S. fuscicollis* did poorly in absence of moustached tamarins with which to associate, prompts a number of questions about the mechanisms of this phenomenon and about the ultimate causes for the mixed species association.

The reduction in numbers of one species of tamarin as a consequence of cropping at the Yarapa river resulted in outcomes that suggested a mutualistic relationship (sensu May, 1976) between both tamarins (Ramirez, 1984b).

Some of the outcomes included:

(a) Change in density: the reduction in density of *S.mystax* resulted in depression of the growth rate of *S. fuscicollis*. At the Yarapa site more than 60% of the local moustached tamarins were cropped in 1978. Even though less than 10% of the *S. fuscicollis* population was cropped in 1978, by 1981 the population had decreased by about 12% following the cropping. Between 1981 and 1982, however, they increased by 18%. Glander et al., (1984) reported similar observations for a mixed population of tamarins where S. fuscicollis had not recovered its precropping density in five years even though proportionally fewer saddleback tamarins were initially cropped from the population. At Los Angeles site 67% of an average-sized population of moustached tamarins was cropped, while few saddlebacks were taken. Five years later, there were 37% more moustached tamarins than before the cropping, but the saddlebacks had not fully recovered.

Other evidence hinting at a mutualistic relationship is suggested by population density estimates of the tamarins. Where mixed-species associations can be formed, tamarins seem to thrive. The highest densities of tamarins have been reported for Upper Amazonia (Garber, 1988; Moya et al., 1979; Norconk, 1986; Soini and Soini, 1982) where tamarins live in mixed associations pointing perhaps to the success of this arrangement (Table 42). Furthermore, S. fuscicollis which associates with all species in the hairy-faced group occurs at lower densities when not in sympatry. At the Pacaya River, in northeastern Peru, S. fuscicollis lives in single-species groups (S. mystax, being absent) and population density is lower (18 ind/sq km) than at other locations (as the Maniti River) where they join in mixed groups with S. mystax (Table 42). However, conclusions are clouded by factors such as the presence of competitors and predators. At Pacaya, the forest is protected, and both Saimiri (a competitor for insects according to Soini and Coppula [1981]), and Cebus apella (a probable predator), are both abundant, while at the Maniti, larger primates--including _C. apella_--are absent.

(b) Change in some rate that could affect density, such as emigration, mortality, fecundity, growth, etc.: although the mechanisms of population decline acting on _S. fuscicollis_ at the Yarapa River are not known, it is likely that saddle-back groups left behind could have emigrated from the area--perhaps in search of moustached tamarin groups to join--, or suffered high mortality resulting from their decreased power to detect predators; and/or were outcompeted by conspecifics in mixed-species groups, which resulted in loss of territory.

A small single species group of _S. imperator_ was driven from its territory by a mixed-species group where the conspecifics were more numerous (Terborgh, 1983). Territory loss in turn might have resulted in depression or more likely suppression of breeding. Lack of territory has always been associated with lack of breeding. All transient groups of tamarins observed to date have been non-reproductive (Norconk, 1986; Soini and Soini, 1983; this study).

At the Yarapa River, the recovery of the moustached tamarin population has been tied to increased reproductive rate, early breeding and a somewhat reduced infant mortality of _S. mystax_ when compared with the pre-cropping condition (Ramirez, 1984b). The availability of _S. fuscicollis_ groups after the cropping can not be underplayed. Their presence probably favored the emigration of young adults from natal groups earlier than normally occurs,thus making possible for both species to hold a territory and sucessfully compete with conspecifics in mixed-species groups. It is also likely that adult female mortality was reduced, since presumably, the period spent in transient status was eliminated or drastically reduced. I suspect that adult female mortality is highest (and higher than the male's) during dispersal. Demographic and behavioral observations support this contention. Sex ratio at birth and during the juvenile phase is 1:1, but favors males in the adult class (Soini and Soini, 1982). Transient adult females suffer severe attacks from resident tamarins. It is likely that tolerance for adult males is greater if they can be recruited into the group and eventually help raise infants.

CHAPTER IV.- GENERAL DISCUSSION

In section A the tactics employed by S. mystax in food resource exploitation will be related to resource availability. The use of range for multiple purposes will be examined, and the population findings will be related to aspects of tamarin physiology, local environmental/demographic conditions and the proposed mutualistic relationship with S. fuscicollis.

A.- The moustached tamarin modus vivendi

Small body size, tendency to twin, claw-like nails on all digits except the hallux, and tritubercular upper molars, are all characteristics of the Callitrichidae (Sussman and Kinzey, 1984). Within the group, the morphology of the incisor-canine battery separates two adaptively different groups: the marmosets, equipped with a dental anatomy appropriate for tree gouging, more readily include exudates in their diet; while the tamarins, not so equipped, use exudates only opportunistically (Dawson, 1976a; Norconk, 1986; Soini and Coppula, 1981; Terborgh,1983; this study). S. geoffroyi may be an exception, since it does consume a high proportion of exudates (Garber, 1980). All callitrichids are highly insectivorous, and all seem to include large orthopterans in their diet (Sussman and Kinzey, 1984). Fruits are an staple in all tamarins studied to date, while marmosets vary a lot in their exploitation of fruits (Rylands, 1988). In this study, S. mystax, like other tamarins, relied on a diet of insects and fruits; exudates and nectar were consumed opportunistically.

1.- Insect feeding.- At the Blanco Stream insect feeding by S. mystax occupied over 60% of feeding minutes or roughly three hours each day. Although insects were available year around, their abundance presumably increased several-fold coincidental with the first rains. At the Blanco site rainfall increased in September and this was paralleled by a highly significant increase in insect foraging. By looking for insects when they were most abundant, S. mystax maximized ingestion rate of animal protein at a time when other resources were scant. Increased search and capture rates in the late dry and early wet seasons were also observed in the five primates of Cocha Cashu studied by Terborgh (1983).

2.- Plant feeding.- Fruit was the most important plant food of the moustached tamarin. Fruit availability decreased in the dry season, while insects were presumably more abundant towards the end of the dry season and beginning of the wet season. Tamarins responded to reduced fruit availability by maximizing ingestion rate of animal protein, and by making opportunistic use of exudates and nectar.

The moustached tamarin exploited small-crowned, relatively common, synchronously fruiting species for most of the year, thus assuring itself of a more or less steady supply of fruits. Even though moustached tamarins fed on plant products of 72 species, in 25 families, almost a quarter of plant feeding was tallied on members of the Moraceae. Leguminosae (sensu lata) were also important components of the tamarin diet. Members of the Moraceae are commonly included in the diet of frugivores (Fleming et al., 1987) and primates in general. The five primates studied by Terborgh (1983), as well as the eight species surveyed by Mittermeier and van Roosmalen (1981), intensively exploited Moraceae. A clear "preference" for Moraceae was demonstrated for howler monkeys by Milton (1980). Over 50% of howler feeding time was spent eating Moraceae, although the relative density of species in this family was below 9% (Milton, 1980).

Terborgh (1983) has suggested that the abundance and production of readily digestible fruits perhaps make the members of the family Moraceae so popular amongst monkeys. More importantly perhaps, from the point of view of the tamarins, is the phenology of the Moraceae consumed. Most of the Moraceae exploited included synchronously ripening, relatively common species (_Pourouma_, _Naucoleopsis_, _Nausteopsis_, _Brosimum_), but also asynchronously ripening, relatively common, and not so common species (_Cecropia_, _Ogcodeia_, _Ficus_).

Thus, during most of the year--namely the rainy season--moustached tamarins utilized common, synchronously ripening fruit species that bore fruit for several weeks at a time; they also made use of asynchronously ripening--unpredictable--food sources when available (Fig.14). By utilizing common species most of the time they probably reduced search costs while the opportunistic use of unpredictable crops helped to tide them over the period of scarcity.

3.- Use of space.- Range use in the moustached tamarin seems to be shaped by economic constraints on territorial defense, use of widely dispersed resources (fruits), and, anti-predator concerns (as in the selection of sleep tree morphology and cover types). Distribution of food trees heavily influenced the patterns of movement of the tamarins, while selection of preferred individual fruit trees appeared constrained by their proximity to the boundaries of the range. Thus, moustached tamarins showed a marked preference for fruit trees located close to the boundaries. Their exploitation contributed to a pattern of heavy use of boundary quadrats vs. central quadrats. Visits to boundary quadrats thus served at least two purposes: to feed on preferred fruits, and to advertise presence (ownership) to neighboring groups of tamarins, reducing costs of territorial maintenance. The selection of sleep trees near range boundaries--from which the tamarins vocalized first thing in the morning--would appear related to territorial defense/deterrence.

During the dry season, coincidental with a decrease in fruit availability, range use and its defense changed, and became more similar to site defense. When compared with the wet season, a smaller area of the range was visited and fewer boundary quadrats were monitored. Also, territorial confrontations, although fewer in number, ended more frequently in fights than when resources were abundant. That moustached tamarins could range over a smaller area when resources were scant was due to the presumed higher density of insects at this time, and the intensive exploitation of the few food trees that provided enough fruits. They combined this pattern of ranging with extended periods of inactivity near the main fruit sources. Thus, when fruit resources decreased, presumably it was more cost efficient to guard the few resources available and to discourage trespassing of neighboring groups by engaging in fights when trespassers were discovered.

4.- **Demography** .- The populational aspects of this study suggest that moustached tamarins (a) are able to turn estrus on and off in close coordination with environmental cues, (b) show different dispersion tactics depending on demographic/environmental conditions, (c) correlate their density with that of _S_. _fuscicollis_; i.e., when their numbers are reduced, as after the artificial cropping, _S_. _fuscicollis_ density does not increase disproportionately, thus suggesting a possible mutualistic relationship for the two species (see Chapter III.K).

All field studies on tamarins and marmosets have reported that although there is usually more than one adult individual of each sex per group, only one female appears to breed (Goldizen, 1987). Only two exceptions have been reported: one for _S_. _fuscicollis_ (Goldizen,1987), and one for _S_. _mystax_ (this study), where two females were observed to breed within the same group. Laboratory observations have also indicated reproductive inhibition of subordinate adult females living in family groups, and have provided evidence for the mechanisms controlling suppression of breeding (Abbott, 1984). Breeding in adult subordinate females is supressed either physiologically (supressed ovulation in Callitrix jacchus, S. fuscicollis, and S. oedipus), or behaviorally (ovarian cyclicity without mating in Leontopithecus). Physiological supression appears to be accomplished via scent (e.g. S. oedipus [Savage et al., 1988]) while social stress might be responsible in the second case. Tamarins and marmosets once removed from the family situation and paired with an adult male quickly start cycling and can became pregnant (Abbott, 1984; Epple and Katz, 1980; French et al., 1984; Savage et al., 1988).

Although the mechanisms of reproductive inhibition in moustached tamarins are unknown, the demographic variables indicate that only one adult female per group breeds (Moya et al., 1979; Ramirez, 1984b; Soini and Coppula,1981; Soini and Soini, 1982). It appears that the cropping at the Yarapa River favored the early breeding of young adult females. The percentage of young female breeders in the population after the cropping was considerably higher than the observed proportion in non-cropped populations. It is suggested that with the cropping, territories were vacant and young adult females (and males) which would have normally remained in their natal(?) group, or would have emigrated to form a non-territory holding "incipient unit", had the opportunity to take possesion of a territory and breed. These territories probably had the extra added attraction of a resident S. fuscicollis group (See Chapter IV A6).

5.- **Dispersal.**- Two different dispersal patterns were displayed by the moustached tamarins at two locations that differed in population density, the Blanco Stream (33 ind/sq km) and the Maniti River (23 ind/sq km). At a saturated habitat such as the Blanco Stream, perhaps dispersal is better delayed until a breeding vacancy is located without leaving home. As group size increases, home range might increase thus increasing the number of groups abutting the home range, which in turn exposes the tamarins to more neighbors and to possible vacancies. In fact, the increase in group size of the Green group, apparently resulted in a larger home range (40 ha vs. 31.5 ha) and a greater number of neighboring groups (7 vs. a maximum of 5) at the boundaries than when the group was smaller [Garber(1987), this study]. Similarly, Woolfenden and Fitzpatrick (1984) found that Florida Scrub Jays dispersing from larger territories were more likely to encounter a breeding vacancy without leaving home (Woolfenden and Fitzpatrick, 1984).

On the other hand, in habitats not completely saturated, such as the Maniti, the probability of sucessful dispersal may be higher, such that they balance out the risks involved in dispersal forays.

6.- Mixed-species associations .- Moustached tamarins formed semi-permanent associations with saddle-back tamarins: they shared most of the fruit portion of the diet, were in close contact most of the time, responded to alarm calls of each other, slept in the same or neighboring trees, and jointly defended their territory. Differences in resource use included: the preference of *S. fuscicollis* for the lower stratum of the forest for traveling and insect foraging, their use of fruits growing on low bushes, and the use of a distinct foraging technique. *S. mystax* was dominant over *S. fuscicollis* at feeding sites. Both species activily sought each other's company when separated. The strong attraction shown by both species suggests that they probably derive some advantages from the association.

The reduction in numbers of one species of tamarins as a consequence of cropping at the Yarapa river resulted in outcomes that suggested a mutualistic relationship (sensu May, 1976) between both tamarins (Ramirez, 1984b). The reduction in density of *S. mystax* was coincident with a depressed density of *S. fuscicollis*. It is suggested that the absence of the moustached tamarin left saddle-back tamarins at a competitive disadvantage in relation to resident conspecifics associated in mixed species groups. Decreased competitive ability might have manifested in: reduced capability to detect predators, and perhaps loss of territory which might have resulted in more time spent in vigilant behavior and use of marginal habitats or emigration from the area (See Chapter III J3).

B.- Predation and the moustached tamarin

Hawks and eagles are the major predators of primates worldwide (Struhsaker, 1975; Rettig, 1978; Terborgh, 1983). In the Neotropics, moustached tamarins are constantly faced with the threat of predation. Due to their small size and diurnal habits tamarins are potential prey to numerous raptors.

Primates have evolved two major types of predator protection. Among the small primates (< 1 kg), avoidance of predators by means of concealment, vigilance and flight seems to be more common than confrontation (reviewed in Cheney and Wrangham, 1987). Among Saguinus spp., observed anti-predator behavior includes: silent approach of the sleeping tree (moustached tamarin; this study; geofroyii tamarin, Dawson,1976a) and surveillance (moustached tamarin, this study; saddle-back tamarin [Bartecki, 1987; Goldizen, 1987;Soini and Coppula, 1981; Terborgh, 1983]; white-lipped tamarin [Caine,1984, 1986, 1987]). Mobbing of snakes and small arboreal predators (such as tayra) has also been reported for most species (Soini and Coppula, 1981; Norconk, 1986; Sussman and Kinzey, 1984; Izawa, 1978; this study).

Evidence gathered during this study indicate that S. mystax avoids predation by minimizing risky situations and by maximizing early detection of predators. Anti-predator concerns are the governing factors in food resource exploitation and are probably an important factor in the maintenance of mixed species associations.

Some activities are more predator-risky than others and the moustached tamarin seems to have developed tactics that minimize the risks or increase probabilities of detecting predators. The well-covered sleep trees with few connections to neighboring vegetation, and the large proportion of time spent resting in the daytime in well-protected areas seem to afford anti-predator protection. On the other hand, subcanopy traveling and feeding, which take up about 60% of the tamarin's day, expose them to greater risks.

1.- **The risks of insect foraging** .- All food gathering activities exposed _S mystax_ to the dangers of predation, from feeding on fruits in the subcanopy and canopy, to exudate feeding while clinging to vertical supports, to concentrated insect foraging. I suspect that during insect foraging moustached tamarins are particularly vulnerable to avian predators, since during this activity they are concentrating on looking down at leaf clumps close to them and thus their ability to detect approaching avian predators might be impaired. A predator attack by _Daptrius americanus_ (tatatahu) occurred when most group members were engaged in insect foraging. On that occasion the juvenile of the group barely escaped the attack.

That insect foraging is risky, is further supported by their behavior when doing so. During foraging episodes tamarins are constantly surveying ahead of them and turning their heads, perhaps to increase their field of vision. Exposure to predation during insect foraging in *S. mystax*, is probably countered by the greater use of habitat types with dense cover, such as the low forest, which might afford some protection from raptors. Alternatively, it has been suggested that low forest might harbor a greater density of arthropods than other habitat types.

2.- Use of small-crowned trees: Feeding competition or anti-predator strategy? .- *S. mystax*, like other species of tamarins, intensively exploited small-crowned trees for the fruit resource. Over 70% of fruit feeding minutes were tallied on trees with crowns 5 meters or less in diameter. Moraceae and Leguminosae--whose trees have crowns of varying sizes--figured prominently in their diet. Although medium and large-crowned trees were available within their range (e.g. several *Parkia* sp. bore fruit from February through October), the tamarins exploited them only marginally. Again, only in the dry season, when choices were few due to general scarcity, large crowned trees were important in the tamarin's diet. This was particularly evident in the month of maximum scarcity, September, when large crowned trees contributed to over 80% of plant feeding.

At Manu, Terborgh (1983) found that *Saguinus* spp, although potentially capable of exploiting both large and small food patches--due to their small body size--, concentrated in small patches that went unnoticed by the larger primates. Saguinus spp. were excluded from large crowned trees by larger monkeys and as a result fed on them only infrequently (Terborgh, 1986). Terborgh (1983) suggested that interference competition was the main force behind the preferential use of small trees by tamarins at the Manu.

If interference competition from larger species were the major factor favoring the use of small trees in tamarins, it would follow that (a) in the **presence** of competition tamarins would exploit small trees, and (b) in the **absence** of competition tamarins would exploit larger trees. At the Blanco site, the notable sparseness of larger primate competitors excludes competition as an explanation for the marked use of small crowned trees by the moustached tamarin. It is more likely that tamarins avoided using large-crowned trees due to predation risks. In general, small-crowned trees only reach the subcanopy, and as such are less exposed to aerial predators. This was certainly the case of most trees used by S. mystax (e.g. Pourouma spp., Naucoleopsis sp.). Large-crowned trees, on the other hand, were more exposed to predators due to their height, and scant leaf cover (e.g. Parkia sp.). Thus, fruit feeding in small crowned subcanopy trees, which generally posses a leafy cover, provided relative safety from predators--especially if visits were short--, it was certainly less risky than feeding on taller, more exposed trees.

The end result, extensive use of small-crowned trees, is the same at both study sites. Some characteristics of the environment, however, vary, and suggest different selective pressures acting on the tamarins. The tamarin environment at the Blanco site differs in at least one aspect from the environment at Cocha Cashu. At Cocha Cashu density of medium size and large primates is greater, resulting in stronger competition; predation pressure however, is very high. Goldizen (1987) reports attacks on tamarins once every 1 or 2 weeks. In such an environment tamarins compete with an array of larger primates for access to fruit trees. Due to their small body size, tamarins are excluded from large-crowned trees by the larger species, as was observed by Wright (1985). This might have resulted in tamarins preferentially using small crowned trees (seldom used by larger primates, and with the added advantage of being less exposed to raptors). The concentrated use of central areas of the range by Cocha Cashu Saguinus spp., is perhaps also related to the avoidance of interference competition. At the Blanco site, relaxed competition as a result of the reduced density of large primates, would potentially free large trees for exploitation by the tamarins. However, high predator pressure might have resulted in tamarins avoiding--as much as possible--to exploit large-crowned trees due to predation risks. The preferential use of small-crowned trees by the Blanco tamarins in the absence of larger primates seems to agree with this suggestion.

3.- Predation risks vs. starvation: a delicate balance.- For S. mystax, fruits were the preferred plant food in every month; exudates and nectar were only exploited in the dry season. Since exudates were available year around it was surprising that S. mystax would not utilize them more than they did. It is argued that moustached tamarins avoided the exploitation of exudates during most of the year because of predation risks and limited nutritional rewards of this resource. Nectar as a seasonal resource in the tropics, was exploited opportunistically. It is argued that although nectar is energy-rich, it may expose tamarins to raptors. The scarcity of fruit resources in the lean season confronted the tamarins with two options: to avoid predation risks of exploiting exudates and nectar, and subsist on the few fruits available (starve), or exploit the less desirable resources while incurring added predation risks. The moustached tamarins at the Blanco site choose the second option.

Exudates were consumed during brief visits to exudate trees while clinging to large vertical surfaces. My observations indicate that exudates were a resource of last recourse, which was probably largely due to the predation risks involved in their exploitation. While feeding on exudate trees, moustached tamarins are vulnerable to all kinds of predators, mainly because their ability to detect them is impaired. Behavioral clues further suggest that the tamarin is uneasy when visiting exudate trees. Vigilant behavior before entering exudate trees is obvious in the moustached tamarin. Tamarins, typically waited on branches leading to an exudate tree before entering it. Exudate feeding is also risky for infant-carrying _S_. _fuscicollis_, who wait until being relieved of the infant before entering an exudate tree (Soini and Coppula, 1981). It may be more than just coincidence that the most exudativorous of the callitrichids: _Cebuella_ and _S_. _geoffroyi_ show the most cryptic pelage coloration. Both species are very difficult to detect--by humans and probably predators--while feeding on exudate trees.

Moustached tamarins countered the risks of predation by reducing the time spent searching for and collecting exudates. This was accomplished by parasitizing _Cebuella_-dug exudate trees, which constitued the major source of exudates. There are two possible advantages to the use of _Cebuella_-dug trees over beetle-attacked trees for the exploitation of exudates. First, _Cebuella_ exudate trees, well covered with piths, are easier to locate than beetle-attacked trees. Second, since pygmy marmosets follow a daily pattern of harvesting exudates followed by intensive digging of holes, accumulation of exudate is predictable (Ramirez et al., 1978). It seems that moustached tamarins take advantage of this habit by timing their visits to exudate trees to coincide with the time when exudate has accumulated in the holes dug by _Cebuella_,thus effectively reducing the time exposed to predators while clinging to exudate trees.

Garber (1980) found that exudates from _Anacardium_ _excelsum_ consumed by Panamanian tamarins showed high ratios of calcium to phosphate. He suggested that callitrichids eat exudates to complement a high phosphorous/low calcium ratio (P/Ca) in the digestible parts of the insects they eat, and the low calcium content in their fruit diet. It was also suggested that calcium may be particularly important to lactating females (Garber, 1984). Although in moustached tamarins increase in insect foraging coincided with consumption of exudates (albeit in small quantities), the lack of exudate consumption during the rest of the year, when insects were also consumed--is difficult to account for in light of Garber's suggestion. If exudates were consumed to balance the P/Ca ratio then they should be eaten throughout the year. In addition, exudate consumption did not occur when females were lactating. The same pattern of exudate consumption was observed by Terborgh (1983) in _Saguinus_ spp., and in _S_. _fuscicollis_ by Soini and Coppula (1981). Thus the available evidence seems to indicate that exudates are consumed seasonally, coincidental with a decrease in fruit availability.

A good example of opportunistic utilization of resources, was the nectar feeding on trees of _Symphonia_ sp.. Only two individual _Symphonia_ sp. flowered during my study and they were used by the tamarins at that time; however, in July-August 1984 (Garber, 1987), it appears that the whole population flowered in unison during a 12-day period. Moustached tamarins seemingly took advantage of this resource by spending a third (31%) of total feeding time on this species during those 12 days.

Symphonia flowers are borne all over the crown of trees that grow at or near forest gaps. The exploitation of this resource thus exposes the tamarins to aerial predators. The availability of nectar--which usually has a high content of sugars and aminoacids--at a time when fruits were scant, probably balanced against the risk of exposure to predators.

4.- The benefits of mutualism: increased predator detection.- Behavioral attraction between species has been interpreted as evidence that selection has favored associating (Waser, 1987). But associations incur both costs and benefits for the participants; thus some associations can be commensal, others parasitic and others mutualistic (reviewed in Waser, 1987). A number of benefits have been suggested to account for the existence of mixed groups, and these include: (a) access to otherwise unavailable food, when one species guide other species to locate food resources [e.g., *C. albifrons* joins *C. apella* when traveling through its range, Terborgh(1983)]; or when the smaller species gains access to well protected foods due to the activities of the larger species [*Saimiri* feeds on palm fruits opened and discarded by *C. apella*, Terborgh (1983)]; (b) increased feeding efficiency, when overexploitation of fruit or insect resources is reduced, or dietary diversity is increased [proposed for *Cercopithecus* spp in Gabon, Gautier-Hion et al., (1983)]; (c) increased intraspecific competitive ability, when the species in mixed species association increase home range or maintain home range over monospecific group [S. imperator group lost territory to bispecific group, Terborgh (1983)]; (d) increased safety from predators, for example if species complement each other's abilities to detect predators [Cercopithecus spp. in Gabon, Gautier-Hion et al., (1983)]; (e) social benefits, if few conspecifics are available for play or grooming [Colobus badius, Waser (1987)], and (f) a potential reproductive benefit via interspecific reproduction (Waser, 1987).

In the case of mixed species of tamarins, Terborgh (1983) concluded that cooperative competition resulted in increased feeding efficiency, and secondarily in reduction to predator exposure for the mixed groups of S. fuscicollis and S.imperator at Manu. More recently, Goldizen (1987) has suggested that predator detection benefits may be more important than feeding efficiency for mixed groups at Manu. Norconk (1986) suggested that the major benefit of mixed groups of S. fuscicollis and S.mystax was territorial maintenance (which would result in c above), while Garber (1987) reached the same conclusion and added increased feeding efficiency as a benefit to the association. Evidence obtained in this study indicates that the association of S. mystax with S. fuscicollis affords both tamarins increased predator protection and possible access to otherwise unavailable food for one of the species. At this point it can only be inferred that tamarins living in sympatry will have an advantage (in access to food resources: via joint territoriality and/or feeding efficiency) when forming mixed-species associations over single-species groups.

The association of the moustached tamarin with S. fuscicollis, by increasing eyes and ears most likely diminishes overall predation risks for both species, especially due to the close spatial association that they maintain. Both tamarins spent close to 80% of their time within 20 m of each other and used over 70% of the same food trees in close coordination, thus effectively maximizing predator detection at times when risk from aerial predators is greatest. Moustached tamarins appear less vulnerable to terrestrial predators--which are probably important predators of these tamarins--because of their association with S. fuscicollis. The saddle-back tamarin prefers the lower levels of the forest, and as such probably provides early warning of terrestrial predators, as it did during attacks by tayra.

Up to now, predators that most frequently travel on the ground but that are good climbers (=terrestrial-arboreal predators such as tayras, felids and snakes) have been regarded as unimportant predators of tamarins (Terborgh, 1983). The report by Heymann (1987) of a successful attack on S. mystax by an anaconda (an inhabitant of lake edge and lower levels of the forest near water) indicates that predators other than raptors do prey on moustached tamarins. These observations, added to the surreptitious roosting behavior of the moustached tamarin, suggest that moustached tamarins are vulnerable to terrestrial-arboreal predators not only during the day, but also at their roosting sites at night.

Thus, moustached tamarins seem to minimize daytime predation by associating with *S. fuscicollis* who can better detect terrestrial-arboreal predators. Furthermore, the danger of nighttime predation is perhaps minimized by selecting trees with few connections to nearby vegetation, maybe in an effort to discover/deter scansorial/reptant predators. *Aotus*, sleeping in daytime, selects similar trees to avoid diurnal predators (Wright, 1985). Kloss's gibbons in Siberut, where human predation is accomplished by climbing lianas at night to shoot primates, appear to suffer low mortality from human predation due to their choice of vine-free emergent trees (Tenaza and Tilson, 1985).

Similarly, *S. mystax* are more likely to detect raptors--thus warning the saddle-back tamarins--due to their preference for higher levels of the forest. Another possible advantage for the saddle-back tamarin associated with *S. mystax* might be related to the fact that moustached tamarins were always observed to approach and even chase toucans (*Ramphastos* sp.) at feeding trees. In doing so they may make it possible for *S. fuscicollis* to gain access to this resource. There might be a further advantage to the saddle-backs if, as Dawson (1976a) reported, toucans prey on tamarins. He observed *R. sulfuratus* trying to dislodge an infant from the back of *S. geofroyii*. Toucans have been reported to attack *Saimiri oerstedii* infants (Caine, 1988), so it is plausible that they could prey on tamarins. Due to its smaller size, the saddle-back tamarin might be at greater risk to predation by toucans.

Terborgh (1983) suggested improved predator detection with increased group size as one of the advantages of mixed-species troops of tamarins, but did not think it was important for the maintenance of the association since tamarins were separated more than half the time, thus reducing the benefits of reciprocal warning. At his site, although the emperor tamarin moved at higher levels of the forest, the saddle-backs used all levels, and thus complimentarity of detection was more difficult to argue. On the other hand, complementary skills for the detection of predators has been demonstrated for three species of Cercopithecus sp. which occur in mixed-species associations and utilize different forest strata in Makokou, Gabon (Gautier-Hion et al., 1983).

In this study both tamarins derived slightly different benefits from the association: S. mystax benefited by primarily increased detection of terrestrial-arboreal predators while the saddle-back tamarin derived both: increased protection from raptors, and access to food resources from which they would otherwise have been excluded by avian competitors, and (possibly) predators. Both species would seem to benefit from joint range defense, in particular during the dry season when fruit resources are at a premium. Benefits could be gained because both species of tamarins spent much time in close proximity.

5.- What happens when one species of tamarin is missing? .- If, as I am suggesting, mixed-species associations of the saddle-back and moustached tamarin confer increased anti-predator protection, a number of outcomes can be predicted for the remaining species in the absence of the other: (a) higher mortality due to predation, (b) increased vigilant behavior to compensate for the loss of extra eyes and ears, and (c) increased group size as a tactic to increase predator detection, since predation pressure in tamarins--as opposed to marmosets--seems to have placed a premium on detection.

Since predation incidents are very rare and are seldom observed (Cheney and Wrangham, 1987) prediction "a" (above) would be difficult to test unless the predators were followed as suggested by Waser (1987). Suitable candidates for study would include:tayras, margays, raptors, and large toucans. A behavioral clue to increased predation risk would be an increase in time spent in vigilant behavior (prediction "b"). Although the methods of observation are not exactly comparable, it is noteworthy that vigilant behavior in _S. fuscicollis_ progressively decreased along a gradient, from single-species groups, to mixed groups with little time in association to groups with increasing time spent in association. Single-species groups of _S. fuscicollis_, spent 2% of their activity budget in vigilant behavior (Soini and Coppula, 1981). Vigilance was particularly obvious when entering the crown of tall trees, or food trees occupied by fruit competitors. Saddle-backs in mixed groups that spent over 50% of the time apart engaged in obvious vigilant behavior, although this was not reported as a separate activity (Goldizen, 1987, Terborgh, 1983), and thus it is assumed to have been low. S. fuscicollis in a mixed group that spent about 80% of the time in association was only occasionally vigilant (this study). Thus, a single species group devoted more time to vigilance than either of two species associated in mixed groups. Moreover, it seems that the tighter the association the lesser the need to engage in vigilant behavior.

Single-species groups of tamarins range in size from 1-13, but more commonly have 5-6 individuals (Sussman and Kinzey, 1984). Traditionally, it had been suggested that one of the benefits of mixed-species groups was to double group size without incurring the costs of increased intra-specific competition. More recently, the observations by Garber (1988), that feeding competition within a group of moustached tamarins did not increase with a change in group size from 11 to 6 individuals, suggest that intra-specific feeding competition might not be as strong as suspected. If this is the case, then it would be advantageous for groups of tamarins to join conspecifics, even if only while feeding on fruit. After all, fruit feeding is the most risky activity as it exposes tamarins to raptors, the most pervasive predators of tamarins.

Aggregations of this kind (prediction "c") have been reported for allopatric species of tamarins: S.geoffroyi (Dawson, 1976a), *S. nigricollis* (Izawa, 1978), and *S. fuscicollis* (cited in Sussman and Kinzey, 1984).

C.- SYNTHESIS AND PERSPECTIVE

Due to their small body size and diurnal habits, *S. mystax* (and other tamarins) are an ideal prey for numerous raptors and maybe for some mustelids. It is proposed that predation exerts a strong selective pressure on tamarins. Predator pressure has placed a premium on the adoption of anti-predator tactics, mainly through early detection of predators. Predator avoidance in *S. mystax* includes the adoption of feeding tactics that decrease exposure to predators. Predator concerns also appear to be a factor in the selection of roosting trees and ranging patterns. In addition, *S. mystax* and *S. fuscicollis* maintain a mutualistic relationship the main advantage of which is to avoid predation pressure by maximizing predator detection.

Anti-predator behavior that relies on vigilance requires coordinated effort. The prevalence of semi-permanent asociations of Hylean tamarins which compliment each other in predator detection is an outstanding example of cooperation. Moreover, several aspects of cooperative behavior are common in the lives of tamarins. Some of them include: shared infant carrying (done mostly by males), high degree of tolerance between adult males, and mechanisms of fertility suppression through scent (Cain, 1988).

Tamarins regularly give birth to twins. Since back-carried infants are particularly vulnerable to raptors, adult males usually share the burden of carrying the infants (Terborgh and Goldizen, 1985). Since carriers go without food while carrying infants, the need arises for more than one carrier. Terborgh and Goldizen (1985) have suggested that polyandry--and male male tolerance--will evolve if infant survival is maximized by males sharing carrying duties.

Although aggression in captive mother-daughter tamarins has been observed in some species, it has not been reported in the wild. This is particularly puzzling considering the degree of intra-sexual competition amongst females, since as a rule, only one female per group breeds. But it makes sense if reproductive suppression by endocrinological means avoids disruptive behavior.

Thus it appears that tamarins have placed a premium on cooperation. Small size, twinning and the need for multiple infant carriers seem to favor a social system which may ultimately have evolved due to high predator pressure on these small primates.

CHAPTER V.- SUMMARY

1.- At the Blanco stream, moustached tamarins increased in density from 22-26 ind/sq km in thirteen months of observation. The saddle-back population also increased in size. The two marked groups of moustached tamarins grew in size by virtue of births; migrations were not observed; either into or out of the groups. Demographic and environmental conditions appeared favorable to population increase at the Blanco site. Both tamarins were the commonest primates at the Blanco site. Group size at the Blanco site ranged from 4-8 (n=9, mode=4-5).

2.- Successful breeding was seasonal. All infants were born between September and December at the Blanco site. One marked female had three pregnancies in 19.5 months, only two of them were full term. In November, most groups had newborns.

3.- Three years after the cropping of 66% of the moustached tamarin population and 9.5% of the saddle-backs at the Yarapa River, S. mystax had **increased** by 124% while S. fuscicollis had **decreased** by 12%. Between the third and fourth year after the cropping moustached tamarins slightly decreased in density (24.7 vs 23.7 ind/sq km respectively) while the saddle-backs increased in density (26 vs 31 ind/sq km respectively).

4.- In spite of the active recovery of the moustached tamarins, and the initial minimal cropping of the saddle-backs, they had not reached pre-cropping densities. *S. mystax* may need more than four years to recover their initial high density, while *S. fuscicollis* seem to be on their way to full recovery.

5.- It is suggested that the tamarins maintain a mutualistic relationship. Thus, the reduction in density of *S. mystax* coincided with a depression of the growth rate of *S. fuscicollis*. This effect probably resulted from a combination of emigration, increased mortality due to predation, and reduced fecundity due to decreased competitive ability with conspecifics in mixed groups.

6.- Group structure of *S. mystax* at the Yarapa three years after cropping revealed a high proportion of immatures to adults (0.86:1) quite in contrast with the pre-cropping figure (0.30:1). Also, compared with non-cropped populations, a higher proportion of adults were young. A larger percentage of the potential female breeders bred in 1981 (71%), than before the cropping (50%). Juvenile productivity was much higher in 1981 (5.2 vs. 3.15 juv/sq km/year)than previous to the cropping.

7. - Rapid population recovery of the moustached tamarin at the Yarapa was the result of early breeding of females, and high infant survivorship.

8 .- Moustached tamarins were active on average ten hours per day (x=10:10, n=52). Activity cycles were significantly shorter in the dry season (x=9:42 hours), than in the wet season (x=10:37 hours). Exit and entrance to the sleep tree, occurred later and earlier (respectively) in the dry season, than in the wet season. These activity differences were probably due to the fact that the average day length was longer in the wet season.

9 .- S. mystax spent over a third of their time inactive (35%), another third looking for and ingesting food (19% in insect feeding, 11% in plant feeding), a fourth in travel (28%), and 7% in various activities (vocalizing, grooming, unknown).

10.- Two seasons were identified on the basis of rainfall pattern and fruit abundance. At the Blanco site it rained every month, with the least amount of rain falling in June, July and August. The first heavy rains in September marked the beginning of the wet season which extended until May. Fruits were abundant from November through June, and scarce from July through October. Exudates were available year around. Insects were presumed to increase with the first rains of September.

11.- Plant feeding, resting, and miscellaneous activities occupied the same amount of time during both seasons. Insect feeding significantly increased in the dry season, resulting in more time spent in feeding activities in the dry season (32.8%), than in the wet season (28.4%). Moustached tamarins spent significantly more time traveling, and traveled longer paths in the wet season, than during the dry season.

12.- Moustached tamarins did most of their plant feeding in the early morning; insect feeding started an hour after leaving the sleep tree, and was a sustained activity for the entire day. Travel was more intense in the early morning and late afternoon. Tamarins were inactive for short periods throughout the day; a major bout of resting was observed around midday. Vocalizations peaked in the early morning.

13.- Insect feeding occupied 63% of feeding minutes, while fruit feeding used 34% of feeding minutes; 3% of feeding minutes were used for exudates, and nectar and leaf buds occupied only a minute fraction of feeding minutes (0.4%).

14.- S. mystax utilized 223 trees of 72 species for feeding. Fruits of the Moraceae contributed to 25% of the yearly diet. Legumes were second in importance, specially in the dry season. The phenology of the Moraceae exploited might be the key to their extensive use, not only by tamarins, but by other primates as well.

15.- Tamarins fed on an average of six plant species per day (range=1-11, n=57) by visiting 8 trees on average (range=3-12, n=57). The five highest ranking **species** contributed between 54% and 96% of feeding minutes to the monthly diet.

16.- Tamarins characteristically fed on small, sweet, meaty, yellow or purple drupes. The fleshy mesocarp or aril was always ingested, seeds were sometimes swallowed.

17.- Longer paths were positively correlated with number of fruit trees visited. Significantly more fruit trees were visited in the wet season. However, fewer feeding minutes were tallied in the wet season than in the dry season (difference non significant), which might be related to increased handling costs, and low energetic returns of dry season fruits.

18.- During each five day sample period, the four highest ranking **individual** fruit trees accounted for between 45-97% of feeding minutes per month. Exploited **individual** trees were usually:(a) one of several synchronously-fruiting species, with restricted fruiting season and small crowns; (b) asynchronously fruiting species, or (c) rare species with restricted fruiting periods and medium to large crowns. Relatively common, synchronously ripening species provided a more or less steady supply of fruits throughout the year.

19.- Over 70% of fruit feeding minutes were tallied on small-crowned trees (up to 5 meters in diameter). Only in the dry season, when fruit trees were scarce, large crowned trees were used by the tamarins. It is suggested that the preferential use of small-crowned trees by the Blanco stream tamarins, in the absence of larger primate competitors, is due to avoidance of predation risks in tall, large-crowned trees.

20.- Exudates from at least 8 species were exploited while robbing *Cebuella*-dug exudate holes. Exploitation of exudates was coincidental with maximum scarcity of fruits, and avoided at other times of the year,due to predation risks, and limited nutritional rewards. Nectar, as a seasonal resource, was exploited opportunistically.

21.- Mobile prey (mostly Orthoptera) was captured with the technique of scan and pounce, while foraging on leafy substrates in the subcanopy of the forest. Insect feeding intensified in the dry season, foraging bouts became longer, the number of searches increased , and a larger percentage of them ended with the capture of prey.

22.- The tamarins utilized a range of 31.5 ha., of which 27 ha (85%) was used exclusively (=territory) . 5 ha (15%) around the perimeter of the range was periodically invaded by neighboring groups (=overlap zone), which were evicted when detected. This zone also included seldom entered areas of the range.

23.- Home range use was uneven in terms of the number of times that 0.25 ha quadrats were entered. 50% of the range was underused, 16% was used as expected, and 34% was overused. Use of space was affected by its location in relation to home range boundaries, distribution of preferred fruit trees, presence of neighboring groups, or by predation risks.

24.- The low forest habitat was entered significantly more than expected, associated with insect feeding activities. An open, low habitat was avoided, presumably due to predation risks. Moustached tamarins used edge forest (=vine forest) less than expected by chance.

25.- Food trees used by the tamarins were distributed in proportion to the area occupied by each habitat, but were clumped within habitats. Most feeding minutes were tallied on feeding trees located within 50 meters of the range boundaries. 10 out of the 13 first ranking **individual** trees were found in this area. The majority of the ten highest ranking trees for each month were found within 50 meters of the range boundaries. It is suggested that proximity to boundaries might be an important criterion when selecting preferred fruit trees, selection that might be related to economics of territorial defense.

26.- On 61 nights tamarins used 40 different sleep trees. Most sleep trees were tall, densely covered, located in high ground forest, usually overlooking habitat transition zones of lower vegetation. Over 50% of the trees were located less than 75 meters from the boundary. Only one tree was located 200 meters away. It is argued that sleep tree morphology is related to protection from predators, while sleep tree location appears related to the economics of territorial defense.

27.- 3.3 territorial confrontations per week were observed during the study. Confrontations were more frequent in the wet season (3.6/week) than in the dry season (2.8/week). More dry season confrontations ended in fights (2.1/week) than in the wet season (1.3/week). Most wet season confrontations ended in vocal confrontations (2.3/ week vs. 0.7/week for the dry season).

28.- During the wet season, nearly 80% of the range was visited per sample period, and all boundary quadrats were entered at least once. In the dry season fewer quadrats were visited per period, and up to 25% of boundary quadrats were not visited during a five day period.

29.- A set of 44 boundary quadrats (=11 ha) around the perimeter of the home range was entered significantly more than non-boundary quadrats. High use was related to intensive plant feeding in peripheral fruit trees, territorial patrolling and confrontations, and location of sleep trees.

30.- *S. mystax* as a small, arboreal mammal is constantly threatened by predation. It is proposed that the moustached tamarin avoids predation by (a)minimizing predator-risky situations as when it selects small-crowned, subcanopy fruit trees, which presumably are less exposed to predators; and when avoids feeding on exudates while clinging to vertical surfaces that expose the tamarin to predation, or when foraging for insects in habitats with dense cover, or when selecting sleep trees with few connections to nearby vegetation; and (b) maximizing early detection of predators by associating with the saddle-back tamarin which, due to its vertical range, can better detect terrestrial-arboreal predators. Similarly, *S. fuscicollis* benefits from increased protection from raptors.

This study has shown that for *S. mystax*, anti-predator concerns are the governing factors in food resource exploitation, and are a major factor in the maintenance of mixed species associations with *S. fuscicollis*.

TABLE 1

Species in the genus Saguinus. Follows Hershkovitz (1977) and Mittermeier and Coimbra-Filho (1981).

Group/Species	Common name
Hairy-faced tamarins	
S. nigricollis group	
S. nigricollis	"black-mantle tamarin"
S. fuscicollis	"saddle-back tamarin"
S. mystax group	
S. mystax	"moustached tamarin"
S. labiatus	"red-chested tamarin"
S. imperator	"emperor tamarin"
S. midas group	
S. midas	"golden-handed tamarin"
Mottled-faced tamarins	
S. inustus group	
S. inustus	"mottle-face tamarin"
Bare-face tamarin	
S. bicolor group	
S. bicolor	"bare-face tamarin"
S. oedipus group	
S. oedipus	"cotton-top tamarin"
S. geoffroyi	"rufuous-naped tamarin"
S. leucopus	"silvery-brown bare-face tamarin"

TABLE 2
Field studies* of *Saguinus* spp.

Species	Study site	Reference
S. nigricollis	Peneya River, Colombia	Izawa,1978
S. fuscicollis	Cocha Cashu, Peru	Terborgh,1983; Goldizen & Terborgh 1986
	Tambopata, Peru	Crandlemire-Sacco, 1986
	Pacaya River, Peru	Soini & Coppula, 1981
S. mystax	Blanco Stream, Peru	Garber, 1986, 1987, 1988; Norconk, 1986; Ramirez, 1984a
	Upper Amazonia, Peru	Soini & Soini, 1982
S. labiatus	Pando, Bolivia	Pook & Pook, 1982; Yoneda, 1981
S. imperator	Cocha Cashu, Peru	Terborgh, 1983
S. midas	Raleigh-vallen-Voltzberg, Surinam	Mittermeier & van Roosmalen,1981
S. oedipus	Sincelejo, Colombia	Neyman, 1980
S. geoffroyi	Rodman, Panama	Dawson, 1976a
	Rodman, Panama	Garber, 1980

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*includes studies that provide data on habitat, diet and demography. Most studies lasted for at least 6 months.

TABLE 3

Monthly* records of temperature and rainfall at the Blanco Stream site from September 1981 through October 1982.

	Temperature ^{o}C			Rainfall
Month	Mean max	Mean min	Monthly mean	mm
September	31.6	23.8	27.7	189
October	31.3	23.8	27.7	167
November	30.3	23.5	26.9	187
December	31.4	24.5	27.9	209
January	31.3	22.7	26.9	138
February	31.3	22.8	27.1	139
March	31.9	22.4	26.7	142
April	31.1	22.7	26.9	172
May	29.5	23.5	26.5	160
June	31.5	22.3	26.8	104
July	31.1	21.1	25.6	120
August	31.5	21.0	26.3	79
September	31.3	21.1	26.2	141
October	31.3	22.3	26.8	142

*based on 15 days of continuous records for each month (see Methods section for details)

TABLE 4

Timetable of behavioral sampling for the study groups at the Blanco Stream site.

Group	Dates of samples	# of days
Red	October 29-November 2 1981	5
	December 1-5 1981	5
Green	November 6-10 1981	5
	December 9-13 1981	5
	January 27-31 1982	5
	February 27-28 1982	2
	March 25-28 1982	4
	April 21-25 1982	5
	May 6-7 1982	2
	June 17-20 1982	4
	July 14-18, 20-21	7
	August 17-21 1982	5
	September 18-22 1982	5
	October 12-16 1982	5
	October 30- November 3 1982	5
	Total	69

Dates include only full-day follows.

TABLE 5

Population density of primate fauna at the Blanco Stream site in 1982

Species	group size*	groups/ sq km*	individuals/ sq km**	kg/ sq km
Cebuella pygmaea	5	6	30	2.8
Saguinus mystax	5.8	4	26	11.0
Saguinus fuscicollis	4.3	4	20	6.5
Calicebus moloch	4.5	4	18	12.6
Pithecia monachus	4	3	11	11.0
Aotus sp.	4	2.2	9	6.3
Saimiri sciureus	one group of 20 seen once			
Cacajao calvus rubicundus	20-25 individuals seen several times			
Cebus albifrons	one group ranged through site			
Cebus apella	seen only once			
Ateles sp.	two individuals seen once			
Lagothrix lagothricha	reported further inland			

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* estimates based on groups observed within the main study area;

* *includes carried infants. *Saguinus* spp. represent accurate (maximum) values, including corrections for range overlap; other figures are far less accurate and are probably underestimates.

TABLE 6
Tamarin population density at the Blanco Stream site, 1981-1984.

Date	*S. mystax* ind/sq km (total numbers)	*S. fuscicollis* ind/sq km (total numbers)
October 1981	22(19)	18(14)
Oct-Nov 1982	26(23)	20(17)
November 1983a	30(c)	26(c)
November 1984b	33(c)	28(c)

a= data from Norconck,1986.
b= data from Garber,1988.
c= total numbers not available.

TABLE 7

Size of tamarin groups, including infants, at the Blanco Stream site, 1981-1982.

	1981		1982	
Group	Saguinus mystax	Saguinus fuscicollis	Saguinus mystax	Saguinus fuscicollis
Red	6	4	7	6
Green	6	5	7	4
Alta D	5	6	6	7
Bajial	4	5	6	5
Tunche	6	7	8	8
Vecinos	5	4	6	6
Purple	5	4	7	5
Yellow	8	5	7	8
Otra	4	3	5	4
Rosadas*	2	-	2**	-
		2***		2***

*=Non-reproductive group; two adult females.

**= last seen in April.

***= seen several times; adult size, one female.

TABLE 8

Changes in group size and composition for the Green and Red groups at the Blanco Stream site.

	Date	Group size	Group composition						
			Am	Af	SA	J	If	Im	Ii
G	10/81	6	2	2	-	-	1	1	-
R	10/81	5	2	2	-	-	1	-	-
E	03/82	5	2	2	-	1	-	-	-
E	11/82	5	2	2	1f	-	-	-	-
N	11/82b	7	2	2	1f	-	-	-	2
	11/83b	9	4	2	1	2	-	-	-
	11/84c	13	4	3	2	2	-	-	2
	12/84c	8	2	2	-	2	-	-	2
R	10/81	6	1	2	1f	1d	1	-	-
E	10/81	8	1	2	1f	1	1		2
D	01/82	5	1	1	1f	1	1	-	-
	05/82	7	1	2	1	1	-	-	2
	10/82	7	1	2	1	1	-	-	2

Af=adult female, Am=adult male; SA=subadult; J=juvenile; I=infant,m=male,f=female,i=sex unknown.

a=died during trapping; b= data from Norconk,1986; c= data from Garber,1988.

TABLE 9

Time of exit from and entrance to sleep tree by _S_. _mystax_, and length of active day.

Month	Mean time of exit	Mean time of entrance	Active hours
N	6:00	16:41	10:40
D	6:07	16:32	10:41
J	6:10	17:01	10:49
F	6:11	16:59	10:47
M	6:30	17:01	10:46
A	6:45	17:04	10:07
M	6:25	16:50	10:23
J	6:06	16:43	10:40
J	6:24	16:13	9:54
A	6:24	16:18	9:55
S	6:25	15:55	9:31
O	6:21	15:47	9:26
N	6:16	16:00	9:48
YEARLY MEAN	6:20	16:29	10:10
MAX	7:10	17:35	11:30
MIN	5:55	15:30	8:59

TABLE 10
Yearly activity budget of _S. mystax_ at the Blanco Stream site. Figures in percentage of time.

Activity	Mean	S.D.	Maximum	Minimum	CV
Plant feeding*	11.2	3.4	23.1	3.3	30.9
Insect feeding	18.8	6.2	33.8	5.9	30.1
Travel	27.9	5.7	44.7	17.2	24.3
Inactive/ resting	34.9	4.7	45.4	23.1	15.3
Miscellaneous**	7.0	5.4	29.6	0	79.0

*includes 0.6 % of exudate feeding.
**includes: about 1% of unknown activities, and 2.7% of the time spent vocalizing.

TABLE 11
Monthly activity budget of *S. mystax* at the Blanco Stream site. Figures in percentage of time.

Month	Activity state				
	Plant feeding	Insect feeding	Travel	Inactive	Mis/unk
Nov	9.5	15.8	29.3	36.6	8.5
Dec	9.9	11.6	33.5	37.1	7.6
Jan	9.6	14.8	32.6	34.6	8.1
Feb	10.5	15.2	31.0	36.8	6.5
Mar	11.3	16.7	31.6	33.2	6.9
Apr	13.6	15.5	29.3	35.4	5.9
May	14.0	16.1	31.5	36.5	5.2
Jun	18.1	18.4	29.6	28.4	5.4
Jul	13.5	13.8	28.7	33.2	10.5
Aug	8.8	20.7	26.1	37.3	7.0
Sep	10.1	28.0	19.7	35.2	6.7
Oct	10.2	26.4	20.7	37.1	5.5
Nov	9.6	26.9	24.1	32.6	6.6
Wet season mean	11.55	16.85	30.27	34.58	6.73
Dry season mean	10.65	22.15	23.90	35.75	7.52

TABLE 12

Daily mean plant feeding minutes (PF), total number of food trees visited (TT), mean number of trees visited (XT), total number of species visited (TS), index of fruit abundance (IFA), and path length in meters (PL).

MONTH (sample days)	PF	TT	XT	TS	IFA	PL
N (5)	72	20	6.6	10	17	2679
D (5)	82	25	7.2	8	22	3029
J (5)	70	24	7.8	15	37	2980
F (2)	100	12	8.5	11	34	3009
M (4)	131	21	8.0	17	36	3071
A (5)	91	21	7.2	20	22	2645
M (2)	83	11	6.5	7	30	2706
J (4)	155	24	9.5	11	29	3101
J (5)	133	29	8.2	11	14	2661
A (5)	101	24	6.6	15	10	2083
S (5)	101	14	5.0	9	3	1599
O (5)	111	26	8.6	14	9	1607
N (5)	101	27	7.4	20	15	1666

TABLE 13

Daily fruit feeding minutes (FF), total number of fruit trees (TFT), mean number of fruit trees per day (FT), and mean number of fruit species per day (FS).

Month	FF	TFT	FT	FS
N	68	20	6.4	4.2
D	82	25	7.2	2.3
J	70	24	7.8	6.4
F	100	12	8.5	7.5
M	130	21	7.7	7.5
A	90	21	7.2	6.4
M	83	11	6.5	4.5
J	155	23	9.5	5.7
J	133	29	8.2	4.8
A	96	19	6.2	4.8
S	94	11	3.8	3.4
O	64	11	3.4	2.8
N	65	16	5.0	4.8

TABLE 14
Daily activity budget of S. mystax at the Blanco Stream site. All data combined. Figures in percentage of time.

Hour	Plant feeding	Insect feeding	Travel	Inactive	Miscellaneous
6 - 7	13.7	2.4	26.8	41.1	15.0
7 - 8	16.8	15.9	34.5	27.0	5.6
8 - 9	17.5	20.4	29.5	25.3	7.0
9 -10	15.4	24.5	25.0	28.1	6.8
10-11	12.5	24.7	23.2	32.8	6.6
11-12	7.1	19.0	17.5	49.0	7.3
12-13	5.9	18.8	19.0	50.3	5.8
13-14	7.6	21.4	22.0	42.6	5.1
14-15	10.7	24.3	27.5	35.0	2.2
15-16	12.6	21.0	29.9	29.4	6.9
16-17	3.1	10.2	41.2	30.1	15.2
17-18	0	0	37.1	51.3	11.5

TABLE 15
Activity records in each of several periods during the day, seasonally and over the whole year.

Activity/ Season		% of records during time period*				Chi square	significance
Plant/fruit feeding							
		6-10:59	11-13:59	14-17			
Wet	O	61	20	19		47	p< .001
	E	45	27	27			
Dry	O	58	21	21		19	p< .05
	E	45	27	27			
Yr	O	60	17	22		65	p< .001
	E	45	27	27			
Insect feeding							
		6-7:59	8-15:59	16-17			
Wet	O	6	90	4		90	p< .0001
	E	18	73	9			
		6-6:59	7-15:59	16-17			
Dry	O	1	98	1		116	p< .0001
	E	9	82	9			
Yr	O	1	97	2		190	p< .0001
	E	9	73	18			
Travel							
		6-10:59	11-13:59	14-16:59	17-18		
Wet	O	51	19	29	1	110	p< .0001
	E	42	25	25	8		
			11-11:59	12-17			
Dry	O	45	6	49		7	N.S.
	E	45	9	45			
			11-13:59	14-16:59	17-18		
Yr	O	48	22	29	1	166	p< .0001
	E	42	25	25	8		
Inactive							
		6-10:59	11-13:59	14-16:59	17-18		
Wet	O	32	41	26	1	265	p< .0001
	E	42	25	25	8		
		6-9:59	10-14:59	15-17			
Dry	O	29	60	11		98	p< .0001
	E	36	46	18			
Yr	O	27	58	14	1	354	p< .0001
	E	33	42	17	8		

* time periods reflect the natural emphasis(or lack of it) of the tamarin's activities;
O=observed, E=expected.

TABLE 16
Index of fruit abundance (IFA)*

Month	# of fruit trees	# species	IFA
November	5	5	17
December	8	4	22
January	11	8	37
February	12	8	34
March	9	8	36
April	6	6	22
May	7	7	30
June	6	6	29
July	11	6	14
August	6	5	10
September	1	1	3
October	6	4	9
November	5	5	15

IFA= Crown size (values from 1-3) X Crop size (values from 1-3). See processing of data in methods section for scale of values.

TABLE 17

Fruit production of monitored species of feeding trees.

TREE	N	D	J	F	M	A	M	J	J	A	S	O	N
Strychnos sp.		x											
Strychnos spp.		x											
Inga sp.					x	x							
Inga spp.								x	x				
Eugenia sp.	x												
Hyppocrateaceae					x								x
Ogcodeia tamamuri		x											
Annona sp.					x	x							
Pourouma ulei			x										
Pourouma cecropiaefolia												x	x
Pourouma sp.				x									
Tapirira guianensis					x	x							
Spondias mombin			x	x									
Cecropia sp.	did not produce fruit												
Sideroxylon ulei	x	x											
Hymenaea palustris						x							
Leonia glycicarpa						x							
Maripa sp.						x	x	x	x				
Maripa sp.								x					
#30						x							
#43B Araliaceae											x	x	
Parkia oppositifolia										x	x	x	
Ficus sp.					x	x							
FP1		x											
FP1A			x										
FP1G													x
FP1C			x										
FP1R						x							
Quararibea sp.			x										

TABLE 18

Distribution of food trees utilized by S. *mystax* Green group per habitat type.

Month	#trees	HGF	LF	PS	VF	Purma
N	19	13	4	2	0	0
D	24	20	3	0	1	0
J	24	13	7	2	2	0
F	12	5	6	1	0	0
M	19	12	5	2	0	0
A	21	12	8	1	0	0
M	11	8	2	1	0	0
J	23	17	3	1	2	0
J	30	15	11	4	0	0
A	24	12	9	3	0	0
S	14	11	2	1	0	0
O	27	17	9	1	0	0
N	27	12	11	0	1	3
% food trees per habitat		61	29	7	2	1
% area covered by habitat		58	26	8	5	3

months with less than five sample days: February and May= 2 days; March and June= 4 days.

HGF= High ground forest;
LF= Low forest;
PS= Palm swamp;
VF= Vine forest;
Purma= Cultivated fields.

TABLE 19
Life-forms of food-bearing plants eaten by *S. mystax*.

PLANT FOOD SPECIES n=74				
Fruit species n=68			Exudate species n=6	
Tree	Palm	Vine	Tree	Vine
66%	1%	24%	7%	1%

TABLE 20

List of the plant feeding species utilized by S. mystax at the Blanco Stream site, listed by plant family. In each case fruit was the plant part consumed except in the case of those with an *, in which case exudate was consumed.

Anacardiaceae
   Spondias mombin
   Tapirira guianensis
   Tapirira sp.
Annonaceae
   Annona sp.
   Duguetia quitarensis
Araliaceae
   #43B
   #64
Bombacaceae
  * Quararibea sp.
Convolvulaceae
   Maripa sp.
Clusiaceae
   Symphonia sp.
   Symphonia spp.
Flacourtiaceae
   Maina odorata
Hyppocrataceae
   #11b
   #31
   #25
   Salacia sp.
Leguminosae
  *Cassia sp.
   Hymenaea palustris
   Hymenaea oblongifolia
   Inga edulis
   Inga ingoides
  *Inga sp.
   Inga spp.
   Inga sppp.
  *Mimosa sp.
   Parkia oppositifolia
Loganiaceae
   Strychnos pitscherlichi
   Strychnos sp.
   Strychnos spp.
   Strychnos sppp.
   #54
Marcgraviaceae
   #69
Malpighiaceae
   Byrsonema sp.
Meliaceae

- Guarea sp.

Menispermaceae
- #37
- Abuta rufescens
- Cissampelos sp.
- Orthomene schomburgkii

Myrtaceae
- Eugenia sp.
- Eugenia spp.

Moraceae
- Nausteopsis imitans
- Ogcodeia tamamuri
- Pourouma sp.
- Pourouma ulei
- Pourouma cecropiaefolia
- Pourouma "domestica"
- Naucoleopsis sp.
- Brosimum sp.
- Ficus sp.
- Cecropia sciadophylla
- Cecropia sp.

Melastomataceae
- Mouriri sp.

Palmae
- #47

Rubiaceae
- Botryarrhena venezuelensis
- Genipa americana
- *#A46A

Sapindaceae
- #35

Sapotaceae
- Manilkara sp.
- Manilkara spp.
- Sideroxylon quinilla
- #16,#13,#30,#59

Simaroubaceae
- Simarouba sp.

Sterculiaceae
- #63
- *#63A

Tiliaceae
- Mallia sp.
- Luehea sp.

Violaceae
- Leonia cymnolosa
- Leonia glycycarpa

Vitaceae
- Cissus sp.

Vochysiaceae
- *Vochysia sp.
- *Vochysia lomatophylla

TABLE 21

Rank order of five highest ranking plant species consumed by <u>Saguinus</u> <u>mystax</u>. Percentage of feeding time in parentheses.

Month (*)	Rank First	 Second	 Third	 Fourth	 Fifth
N (87)	Naucoleopsis (28)	Strychnos 1 (20)	Strychnos 2 (14)	Pouroumal (13)	Eugenia (12)
D (93)	Pourouma 1 (71)	Pourouma 2 (11)	Duguetia (5)	Strychnos 2 (4)	Manilkara (2)
J (70	Pourouma 2 (20)	Spondias (15)	Hyppocrataceae (12)	Pourouma 1 (12)	Anona (11)
F (67)	Manilkara (23)	Tapiria (18)	Inga (12)	Sapindaceae (10)	Loganiaceae (4)
M (66)	Leonia (22)	Eugenia (21)	Hymenaea (10)	Hyppocrataceae (7)	Hymenaea (6)
A (54)	Parkia (17)	Hymenaea (12)	Unknown 1 (9)	Unknown 2 (8)	Rubiaceae (8)
M (74)	Byrsonema (48)	Inga (10)	Maripa (10)	Violacea (4)	Menispermaceae (2)
J (90)	Maripa (71)	Guarea (10)	Abuta (4)	Araliaceae (3)	Unknown 3 (2)
J (93)	Araliaceae (47)	Cassia (21)	Maripa (15)	Rubiaceae (9)	Tapiria (1)
A (78)	Parkia (39)	Maina (12)	Strychnos 3 (11)	Araliaceae (9)	Cissampelos (7)
S (96)	Cissampelos (35)	Parkia (35)	Menispermaceae (12)	Loganiaceae (8)	Quararibea (6)
O (70)	Ficus (29)	Quararibea (17)	Vochysia (13)	Menispermaceae (8)	Maripa (3)
N (62)	Pourouma 3 (22)	Luehea (13)	Cecropia (11)	Quararibea (10)	Vochysia (6)

*sum for five highest ranking species.

TABLE 22
Characteristics of fruits consumed by the S.mystax Green Group at the Blanco Stream site.

		% of species
Fruit type* n=57	Drupe	51
	Hesperidium	12
	Capsule	11
	Berry	9
	Aggregate	7
	Legume	5
	Aril	4
	Inflorescence	2
Fruit diameter n=59	0.6-1.0 cm	8
	>1.0 - 2.0	63
	>2.1 - 3.0	17
	>3.0 - 8.0	12
Color n=62	Yellow	40
	Purple-black	19
	Green	15
	Red	11
	Orange	10
	White and brown	5
Taste n=62	Sweet	86
	Sweet-sour	7
	Tasteless	5
	Sour	2

*= Fruit type categories follow van Roosmalen (1984) with an added category, Hesperidium [fleshy fruit with leathery epicarp, such as a citrus fruit. Fluid filled trichomes fill the locule of each carpel to form the characteristic segments (Blackmore and Tootill, 1984)].

**= Shortest dimension.

TABLE 23
Dimensions of fruit trees and vines utilized by *S. mystax* at the Blanco Stream site.

	%	% of feeding minutes
Height (m)		
8-14	10.8	17.8
15-20	45.3	40.0
21-25	19.5	23.2
26-30	13.2	11.0
31-40	11.1	8.0
Crown diameter (m)		
1.5-5	68.5	51.0
6-10	25.7	38.0
11-15	5.7	11.0

TABLE 24

Total length of food gathering visits to fruit trees by *S. mystax*.

Length of visit (in minutes)	#visits	% of total	% wet season	% dry season
<1-2	121	33	33	32
2.2-4	122	33	37	23
4.2-6	71	19	20	17
6.2-8	25	7	5	11
8.2-10	13	3	4	5
10.2-12	8	2	1	4
12.2-29	12	3	<1	8

TABLE 25
Characteristics of the four highest ranking individual fruit trees used by the Green group.

Month	Species	Field #	Feeding minutes of use during sample	# trees used during sample	Crown diameter/ distance to boundary (meters)
N	Strychnos sp.	M1	70	1	15 / 23
	Strychnos spp.	M2	50	1	6 / 26
	Eugenia sp.	M3	44	1	4 / 74
	Naucoleopsis sp.	4D	23	7	3 / 60
D	Pourouma cecropiaefolia	U7	77	11	5 / 175
	Pourouma ulei	U6	49	7	4 / 168
	Pourouma cecropiaefolia	U8	31	7	5 / 0
	Pourouma cecropiaefolia	U15	29	11	5 / 12
J	Pourouma sp.	U4	55	3	4 / 32
	Spondias mombin	6	54	1	7 / 75
	Duguetia sp.	8	40	1	4 / 28
	Salacia sp.	11	31	3	3 / 40
F	Manilkara sp.	6A	32	1	6 / 25
	Tapiria guianensis	10	17	1	8 / 70
	Sapindaceae	5A	20	2	3 / 25
	Inga sp.	F1	13	1	4 / 28
M	Eugenia spp.	23	81	2	5 / 45
	Leonia glycicarpa	22	73	3	5 / 20
	Hyppocrateacea	24	38	1	7 / 100
	Hymenaea palustris	17C	37	2	8 / 160
A	Parkia oppositifolia	34	79	1	10 / 35
	Hymenaea palustris	17F	54	2	3 / 37
	Unknown	33B	39	1	6 / 12
	Unknown	3F	35	1	5 / 0
M	Byrsonema sp.	38	30	10	4 / 25
	Byrsonema sp.	38	27	10	4 / 110
	Inga edulis	F1	17	1	6 / 25
	Maripa axilliflora	36	17	2	5 / 35
J	Maripa axilliflora	36E	138	11	8 / 43
	Maripa axilliflora	36A	105	11	5 / 50
	Maripa axilliflora	36	69	11	7 / 50
	Abuta rufescens	41	60	1	10 / 93

J	Araliaceae	43A	107	7	3 / 10
	Araliaceaea	43H	84	7	4 / 84
	Cassia sp.	34B	76	6	5 / 76
	Rubiaceae	46A	57		5 / 57
A	Parkia oppositifolia	34E	80	5	10 / 13
	Maina odorata	58	62	1	4 / 120
	Loganiaceae	54	58	1	5 / 133
	Cissampelos sp.	52	38		10 / 85
S	Parkia oppositifolia	34	178	2	15 / 70
	Cissampelos sp.	52	178	1	10 / 65
	Menispermacea	60	60	1	15 / 0
	Loganiaceae	54	40	1	5 / 125
O	Ficus sp.	65	161	1	5 / 75
	Macgraviaceae	62	47	1	7 / 125
	Cissampelos sp.	52	45	1	10 / 0
	Maripa axilliflora	360	19	2	5 / 38
N	Luehea sp.	74	63	1	3 / 0
	Unknown	U1C	56	1	4 / 32
	Unknown	U2C	54	1	7 / 28
	Strychnos sp.	46	31	1	15 / 45

TABLE 26

Insect foraging.-length of foraging bout, foraging bout rate, success rate and capture rate.

Month	mean length of foraging bout(seconds)	bouts hour*	success rate**	capture/ hour ***
N	57	8	0.11	0.88
D	59	7	0.13	0.91
J	61	9	0.09	0.81
F	68	9	0.13	1.17
M	69	10	0.14	1.4
A	71	10	0.14	1.4
M	58	10	0.16	1.6
J	75	11	0.20	2.2
J	83	8	0.20	1.6
A	96	13	0.28	3.64
S	125	17	0.55	9.35
O	117	16	0.47	7.52
N	104	16	0.33	5.28

*=all foraging bouts /group size

**=#successful foraging bouts/ # of foraging bouts

***=foraging bouts/hr X success rate.

TABLE 27
Insect foraging*: type of support, type of substrate, forest type, forest height.

	# observations**	%
Support use		
Perch		
Bough	102	7
Branch	876	63
Twig	414	30
Life-form		
Tree	331	78
Vine	86	20
Palm	8	2
Substrate		
Leaves	1372	86
Branches	160	10
Palm fronds	44	3
Other	20	10
Forest type		
HGF	702	51
LF	384	27
PS	84	6
VF	192	14
Purma	24	2
Forest height		
0-5	44	5
6-10	372	40
11-15	452	46
16-20	84	9
21-25	4	0.4

*all observations combined
**number of scans during which the tamarins engaged in insect foraging.

TABLE 28
Potential predators of *S. mystax* at the Blanco Stream site. Those with an * were observed to attack the moustached tamarins.

Species		Weight(g)
Snakes: Species of boas and venomous snakes.		
Raptors:		
Accipiter bicolor	bicolored hawk	204-454
Spizaetus ornatus	ornate hawk-eagle	835-1607
**Daptrius americanus*	tatatahu	
Leucopternis shistacea	slate-colored hawk	1000
Toucans		
Ramphastus	pinsha	
Mammals		
**Eyra barbara*	tayra	3000-5000
Felis yagouaroundi	jaguarundi	
Felis pardalis	ocelot	
Felis weidii	margay	
Cebus apella	brown capuchin monkey	2000-5000

TABLE 29
Characteristics of sleeping trees used by *S. mystax* .

Mean tree height	24.0 meters
Range	19-30
Average # of trees used/5-day sample	4.4
Total # used during 61 nights	40
% of trees in High ground forest	69
" " " Low forest	29
" " " Vine forest	2
% of trees at habitat transition	69
% not at habitat transition	31
% of trees with dense cover	73
% of trees without dense cover	27
% of trees between 0-50 m from boundary (corresponds to 34% of range)	43
% of trees between 51 m and the center of the range (corresponds to 66% of the range)	57

TABLE 30

Quadrat use by the Green group.- Comparison of wet and dry season months with similar number of sample days.

Month	# quadrats entered	% of home range visited
November	99	79
December	101	80
January	98	78
June	99	78
Wet season mean		79
July	103	80
August	83	65
September	72	57
October	80	63
Dry season mean		66
Yearly mean		74

Total quadrats= 126

TABLE 31
Quadrat use and habitat type.

	Number of times habitat was entered*	
	Observed frequency	Expected frequency**
High ground forest	1443 (52%)	1599 (58%)
Low forest	975 (36%)	717 (26%)
Swamp forest	188 (7%)	221 (8%)
Vine forest	114 (4%)	138 (5%)
Purma	37 (1%)	83 (3%)

*if tamarins exited quadrat and returned to it the same day it was counted as separate visits.

**expected frequency of visits were divided equally between quadrats.

TABLE 32

Plant feeding time and quadrat use in relation to expected use if feeding trees were distributed randomly.

	# quadrats	Ha	% of home range
Not used for feeding	29.5	7.4	23.4
Used less than expected	50.3	12.6	39.9
Used as expected	2.3	0.6	1.8
Used more than expected	14.0	3.5	11.1
Used twice-three times as expected	21.3	5.3	16.9
Used four-eight times as expected	8.0	2.0	6.3
Totals	126	31.5	100

TABLE 33

Distance from home range boundaries for the ten highest ranking food trees utilized by the Green group from November 1981 to November 1982.

Distance (meters)	Rank % in each rank for the whole period 1*	2	3	4	5	6	7	8	9	10	% ** O	E
0 - 50	77	38	66	57	43	56	66	53	50	40	54	34
51-250	23	62	34	43	57	44	34	47	50	60	46	66

Chi-square= 27.46, p< .0001

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* 62% of all first ranking trees located at < or = to 35 meters from the boundaries.

**percentage of ten highest ranking food trees observed (=O) and expected (=E) to occur in each of two zones of the tamarin's range if their distribution were in proportion to the area occupied by each of the two zones.

TABLE 34
Territorial confrontations of the Green group. Number of confrontations observed and normalized weekly rate (in parentheses) are presented.

Month	# Vocal confrontations	# Fights	Total
N	1 (1.4)	2 (2.8)	3 (4.2)
D	1 (1.4)	0	1 (1.4)
J	3 (4.2)	0	3 (4.2)
M	1 (1.8)	2 (3.5)	3 (5.3)
A	2 (2.8)	0	2 (2.8)
J	1 (1.8)	0	1 (1.8)
J	0	3 (4.2)	3 (4.2)
A	1 (1.4)	1 (1.4)	2 (2.8)
S	0	2 (2.8)	2 (2.8)
O	1 (1.4)	0	1 (1.4)
N	2 (2.8)	2 (2.8)	4 (5.6)
Total	13 (1.7)	12 (1.6)	25 (3.3)
Mean wet season rate	(2.3)	(1.3)	(3.6)
Mean dry season rate	(0.7)	(2.1)	(2.8)

TABLE 35

Characteristics of the association between *S. mystax* and *S. fuscicollis* at the Blanco Stream site

Body weight	*S. mystax* 595 g vs. 412 g for *S. fuscicollis*
Diet	Visited 73% of the same fruit trees Saddle-backs visited exudate trees every month of the year Foraging techniques and substrates exploited differed
Contact	Spent 79% of the time within 20 m of each other Respond to each other's alarm calls *S. mystax* always supplanted *S. fuscicollis* at fruit trees Overt aggression(grabbing, biting) was never observed between the tamarins
Sleep trees	Slept in same sleep tree 30% of the time
Territorial behavior	Both species responded to intruding conspecifics by means of calls, chases, and by grappling and grabbing at each other.

TABLE 36
Change in population density at the Yarapa River
(1978* to 1982).

	S. mystax		*S. fuscicollis*	
	Population size	Change from previous yr (%)	Population size	Change from previous yr (%)
1978 b.c.	61	-	>63	-
1978 a.c.	21	-66	>57	-10
1981	47	+124	50	-12
1982	45	-4	59	+18

	S. mystax			*S. fuscicollis*	
	# Groups	Groups/ sq km	Individuals/ sq km	Groups/ sq km	Individuals/ sq km
1978 b.c.	12	6.3	32.1	>4.7	>33
1978 a.c.**	6	3.1	11.1	>4.2	>30
1981	9	4.7	24.7	4.7	26
1982	9	4.7	23.7	5.8	31

* data adapted from Moya et al.,(1979)

** estimated from difference between located and trapped groups plus individuals from three groups that escaped capture and probably remained as distinct groups

b.c.= before cropping

a.c.= after cropping.

TABLE 37

Group size and composition of the tamarin population at the Yarapa study area in 1978* before the cropping and in 1981.

	S. mystax								*S. fuscicollis*
Group number	Adults M	Adults F	Subadults M	Subadults F	Juveniles M	Juveniles F	Number trapped	Total	Group size
1978									
2	1	-					1	3	7
6,7	2	2	-	1	-	-	5	5	7
4	1	1	1	-	2	1	6	10	5
8	1	3	-	1	-	1	6	6	7
10	2	2b	1	1	-	-	6	6	6
11	1	2b	1	1	-	-	5	5	8
16	2	2	-	-	1	-	5	5	4
9,17	-	2	-	-	-	-	2	4	16
18	1	1	1	-	-	1	4	4	4
c								5,5,3	d
Total									
12	11	15	4	4	3	3	40	61	>63
								x=5.1	x=7.0
1981									
1	2	2	1	-	1	-	5	7	10
2	2	1	1	-	1	2	6	7	4
3	1a	2	-	1	-	1	4	5	4
4	2	1	1	-	-	1	5	5	5
5	-	1	1	-	?		2	3	5
6							0	7	4
7							0	3	6
8							0	4	7
9							0	6	5
Total									
9	7	8	4	1	2	5	22	47	50
								x=5.2	x=5.5

---

*from Moya et al., (1979), group numbers and composition same as original;M=male; F=female; ?=unknown sex.

a= did not enter the trap.

b= at least one young adult.

c= replaces several groups counted more than once.

d= unknown.

TABLE 38
Group size of the tamarin population at the Yarapa River site in 1982.

	S. mystax	*S. fuscicollis*
	5	5
	5	3
	9	14
	6	5
	3	5
	2	3
	4	4
	4	6
	7	5
	-	5
	-	4
Total	45	59
	x=5	x=5.4

TABLE 39

Age and sex ratio of *S. mystax* at the Yarapa River site*

Year	Adult/ immature ratio	Sex ratio	Operational sex ratio
1978**	1:0.30	1:1.40	1:1.33
before cropping			
n=6	76% 24%	42% 58%	43% 57%
1981	1:0.86	1:0.85	1:0.85
n=5	54% 46%	54% 46%	54% 46%

*only reproductive groups from which complete counts were obtained were included in the calculations.

**modified from Moya et al.,(1979).

n= number of groups.

TABLE 40

Reproductive data for S. *mystax* at the Yarapa River site. Based on groups captured complete.

% of Adult females	Yarapa 1978a (n=6)	Yarapa 1981 (n=5)
In sample	12/31 = 38%	7/27 = 25%
Of breeding status b	6/12 = 50%	5/7 = 71%
That bred c	3/6 = 50%	5/5 = 100%

n= number of groups captured complete.

a= adapted from Moya et al., (1979).

b= at least one adult female per group is considered a potential breeder.

c= from the presence of juveniles among females of breeding status.

TABLE 41

Group and individual densities of _S_. _mystax_ in Peru.

Locality	Groups per sq km	Individuals per sq km	Method used to estimate density	Reference
Maniti River				
Los Angeles,	5.0	23	A	Soini and
		25	B	Soini(1982)
Sta. Cecilia 1980	1.5	8	B	" "
Tahuayo River				
Blanco Stream 1975	6.5	32	B	Castro and Soini (1977)
Blanco Stream 1981	4.0	22	C	This study
Blanco Stream 1982	4.0	26	C	" "
Blanco Stream 1983		30	C	Norconk(1986)
Blanco Stream 1984		33	C	Garber(1988)
Yarapa River 1978	6.3	32.1	C	Moya et al., (1979)
Yarapa River 1981	4.7	24.7	C	This study
Yarapa River 1982	4.7	23.7	C	This study
Jenaro Herrera	6.0	30	B	Soini and Soini (1982)

Method used to estimate density: A= excludes carried infants from counts, gives figures close to ecological density; B= excludes carried infants. Modal group size is used in estimates of density. Slightly overestimates density when compared with A or C; C= includes carried infants when present. Produces estimates close to ecological density.

TABLE 42
Population densities of *S. fuscicollis* and *S. mystax* at various locations in Peruvian Amazonia.

Locality	Individuals/ sq km		Source
	S. fuscicollis	*S. mystax*	
Maniti River	28	22	Soini and Coppula (1981)
Blanco Stream 1982	20	26	This study
Blanco Stream 1984	28.3	33.2	Garber (1988)
Yarapa River 1979	33	32	Moya et al.,(1979)
Yarapa River 1981	26	25	Ramirez (1984)
Yarapa River 1982	31	24	Ramirez (1984)
Pacaya River	18	0	Soini and Coppula (1981)

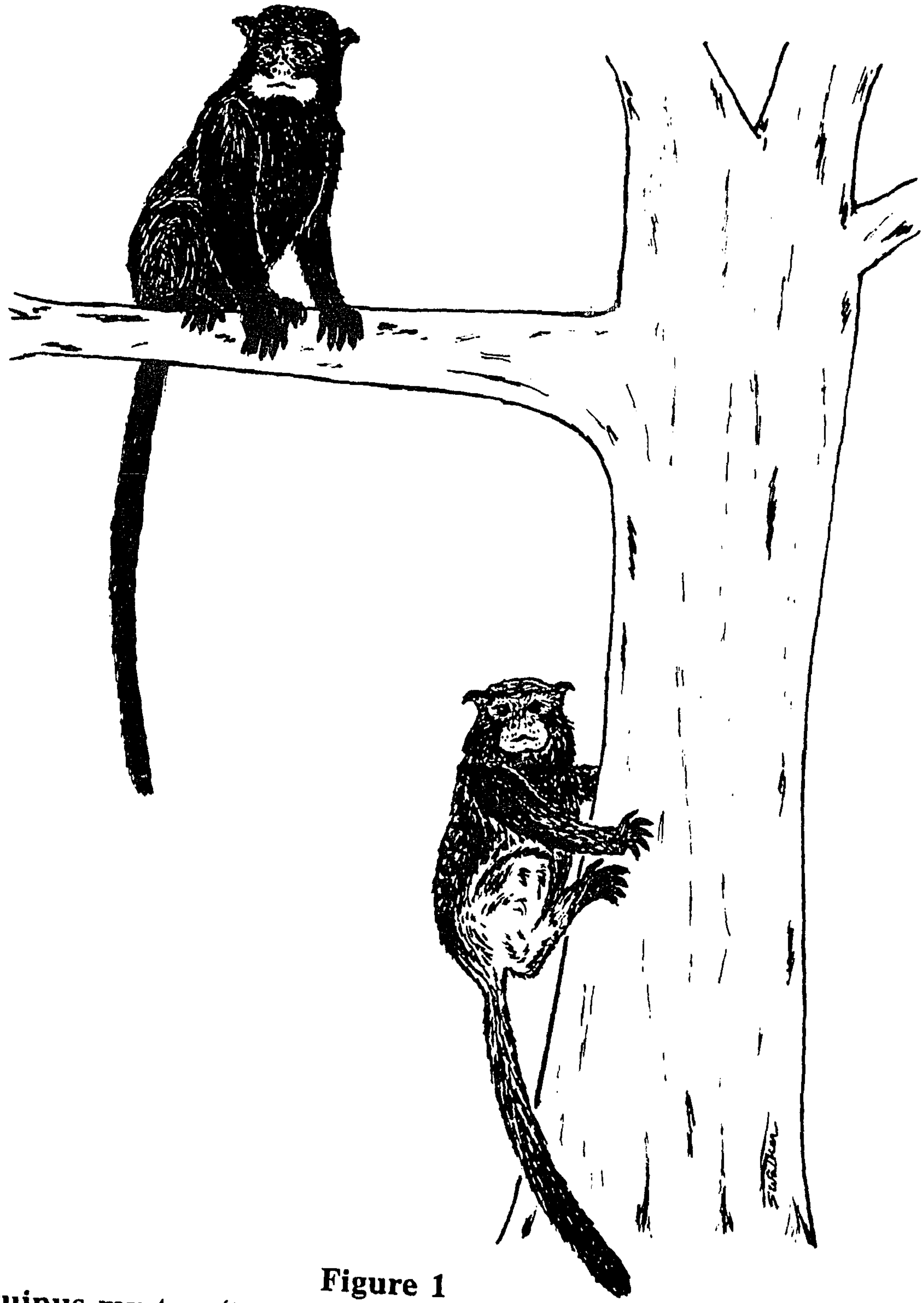


Figure 1
Saguinus mystax (top) and Saguinus fuscicollis (bottom)

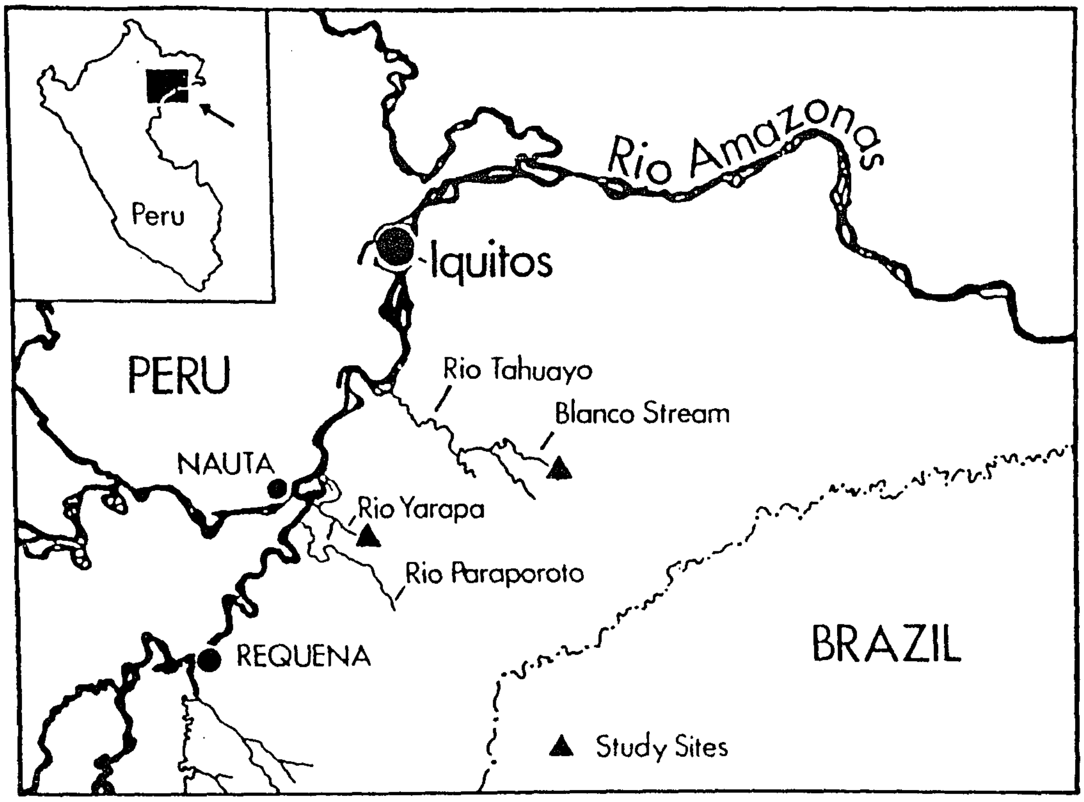


Figure 2
Location of the Blanco Stream and Yarapa River Study Areas in the Loreto District of Peru

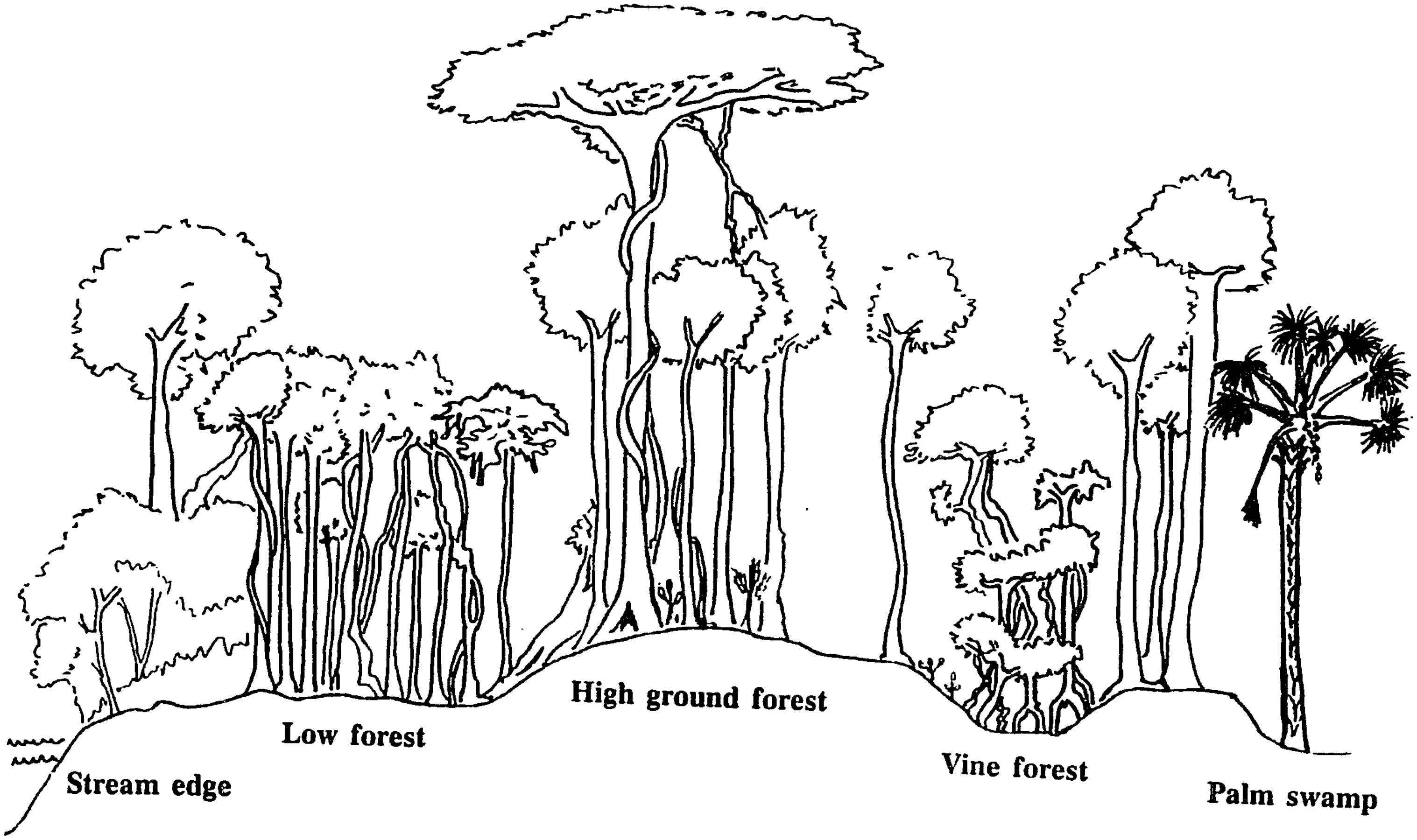


Figure 3
Habitat types at the Blanco stream site

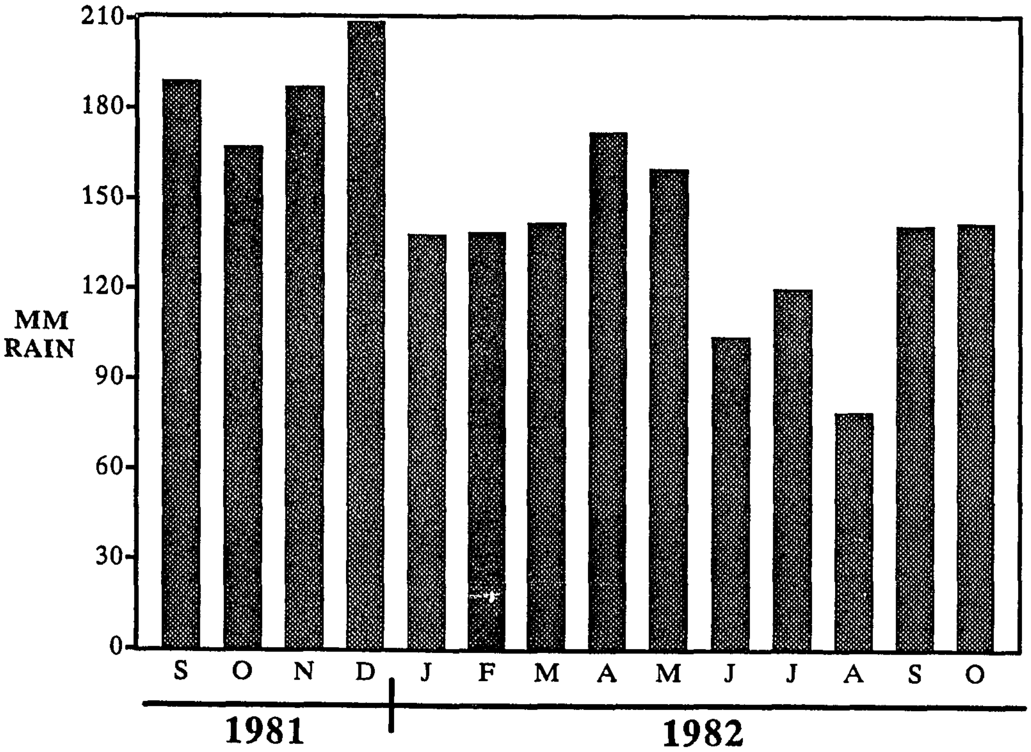


Figure 4
Monthly Pattern of Rainfall at the Blanco Stream Site (September 1981 - October 1982)

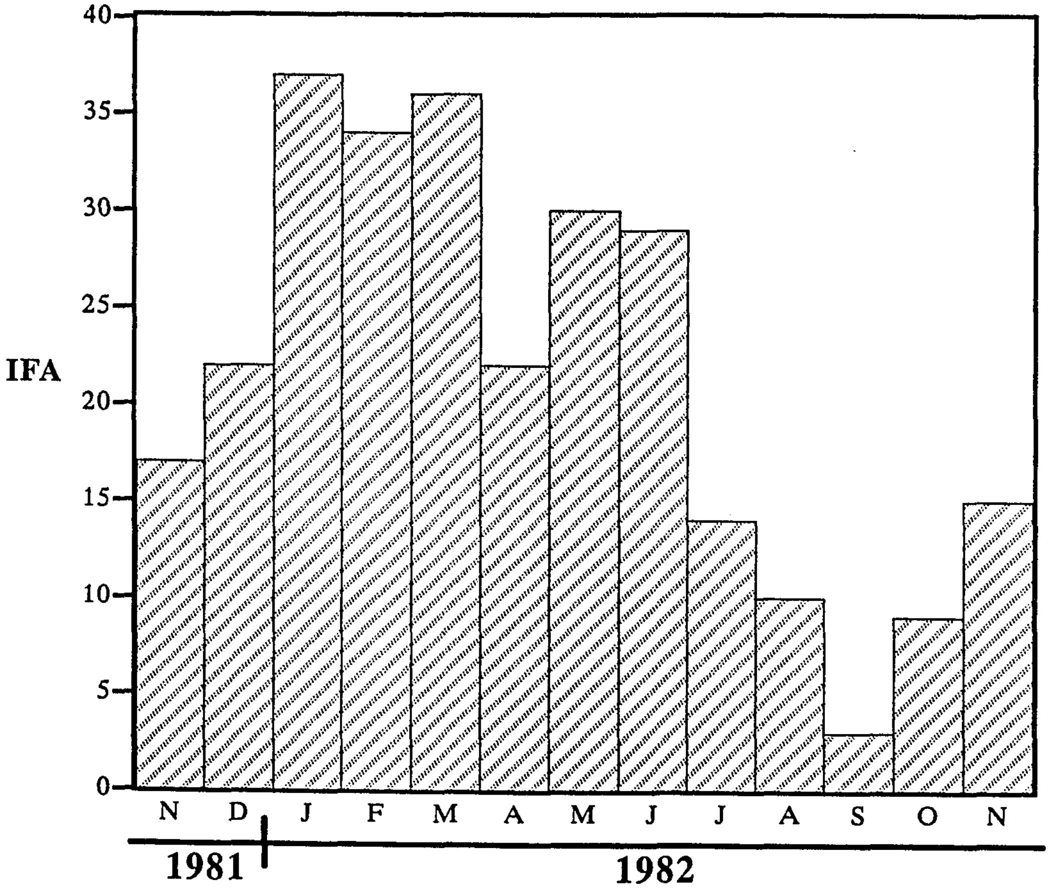


Figure 5
Index of Fruit Abundance (IFA) at the Blanco Stream Site

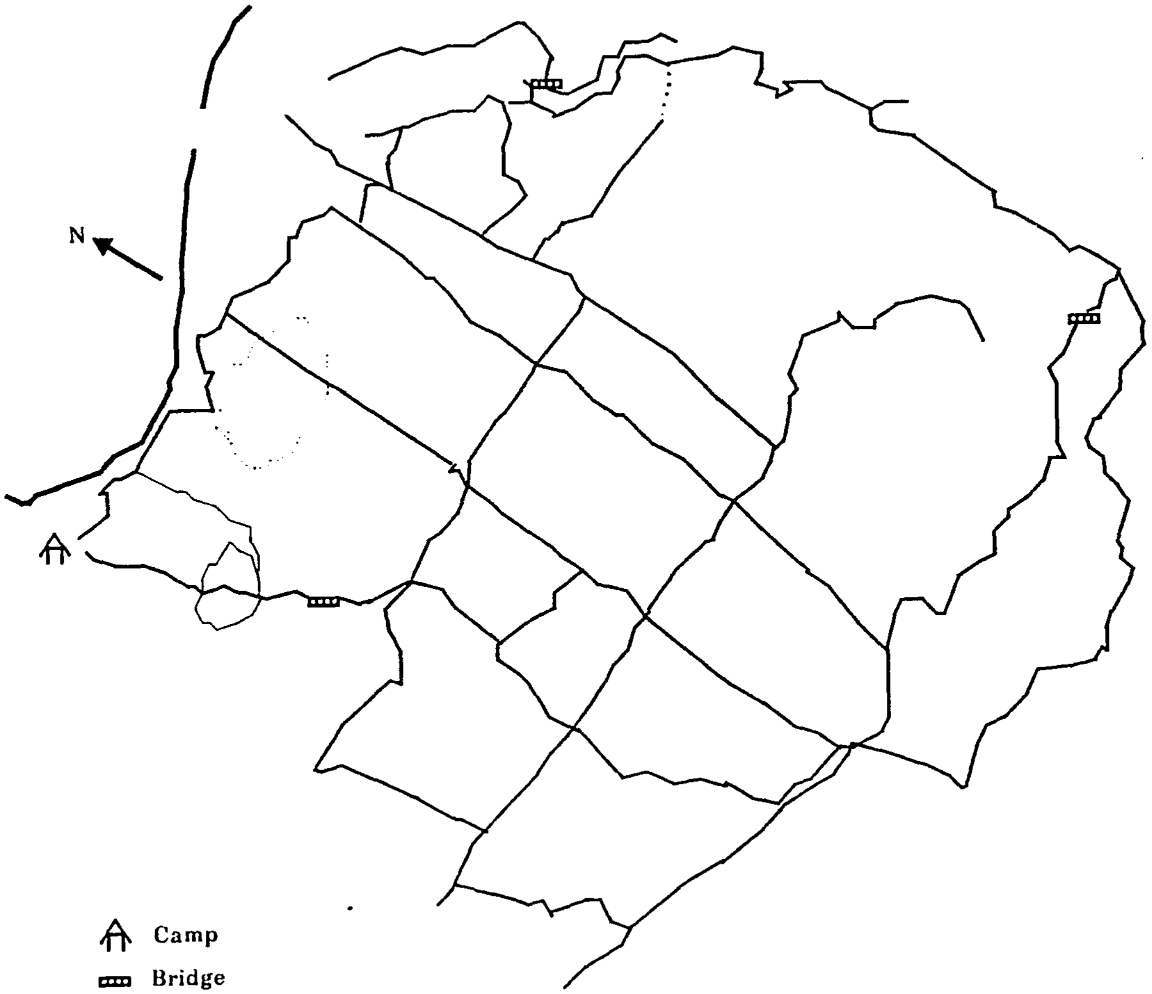


Figure 6
Trail System at the Blanco stream site

Figure 7
Habitat types within the range of the green group

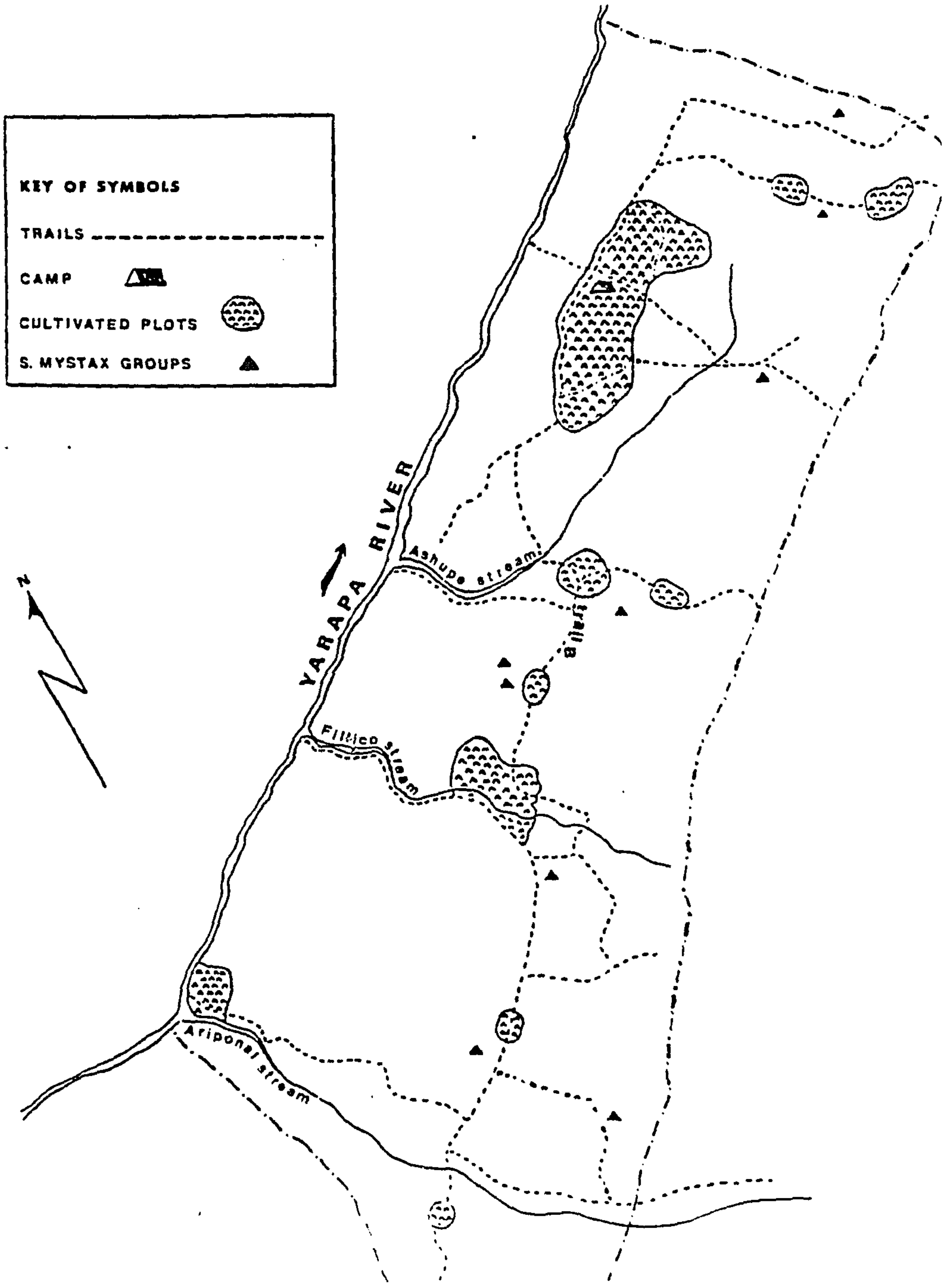


Figure 8
Yarapa River Study Site

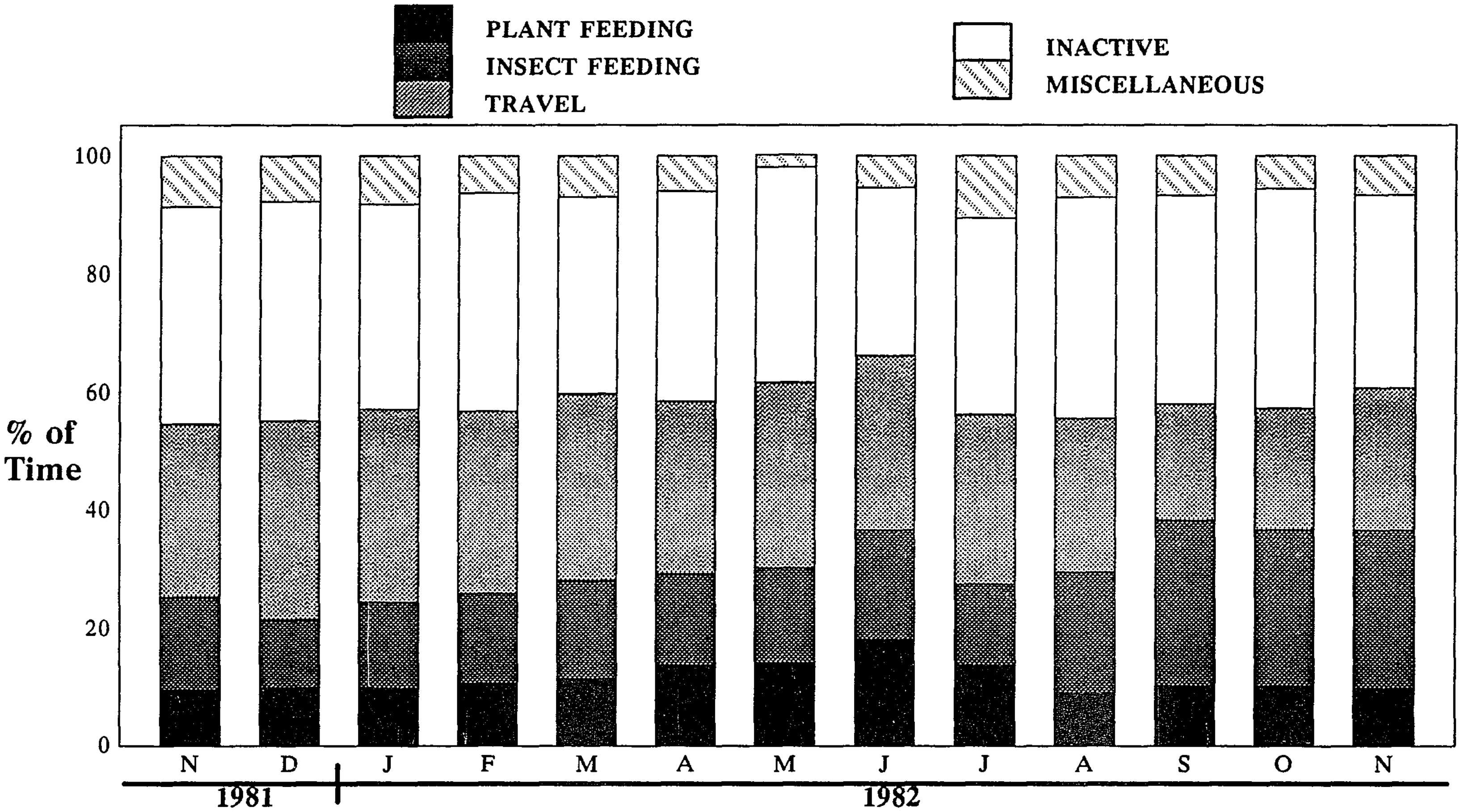


Figure 9
Monthly Activity Budget of Saguinus mystax at the Blanco Stream Site

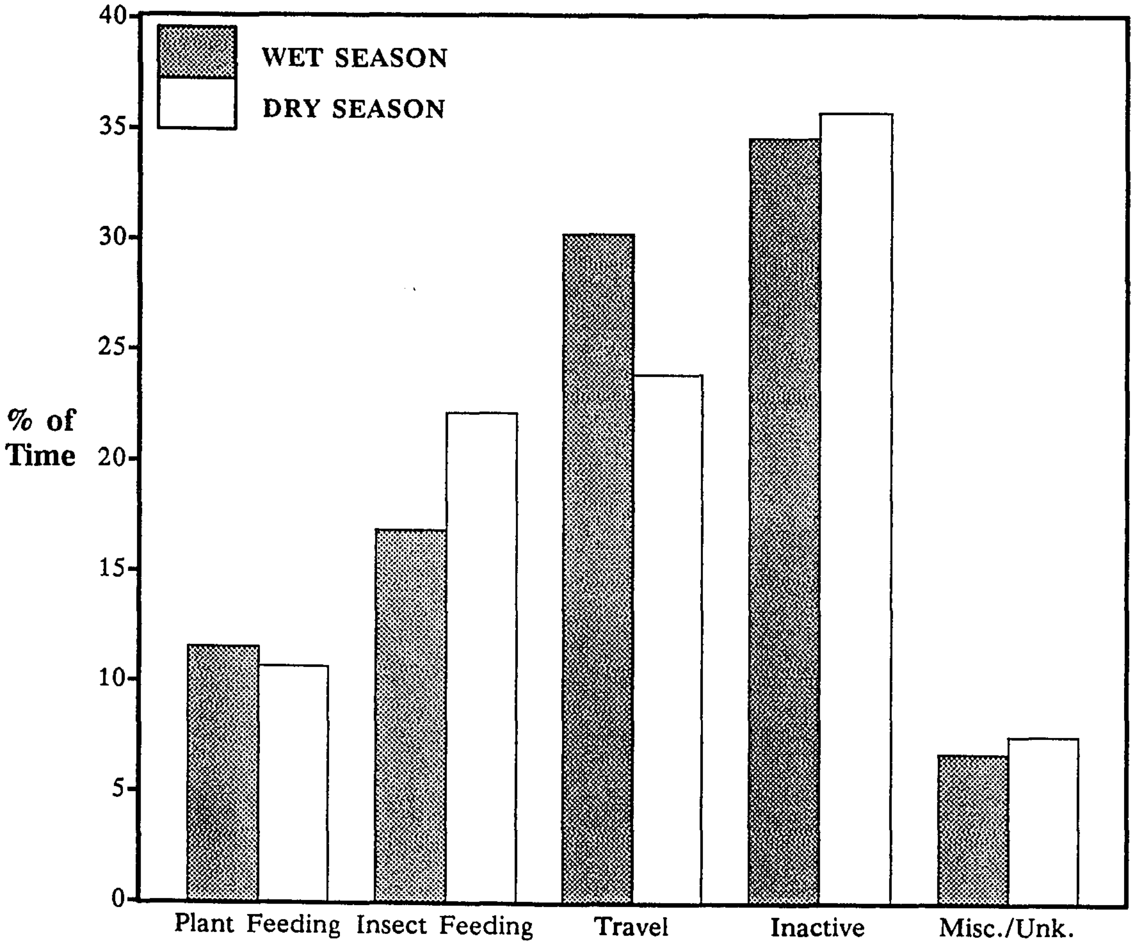


Figure 10
Monthly Activity Budget of *Saguinus mystax* at the Blanco Stream Site. Wet and Dry Season Means

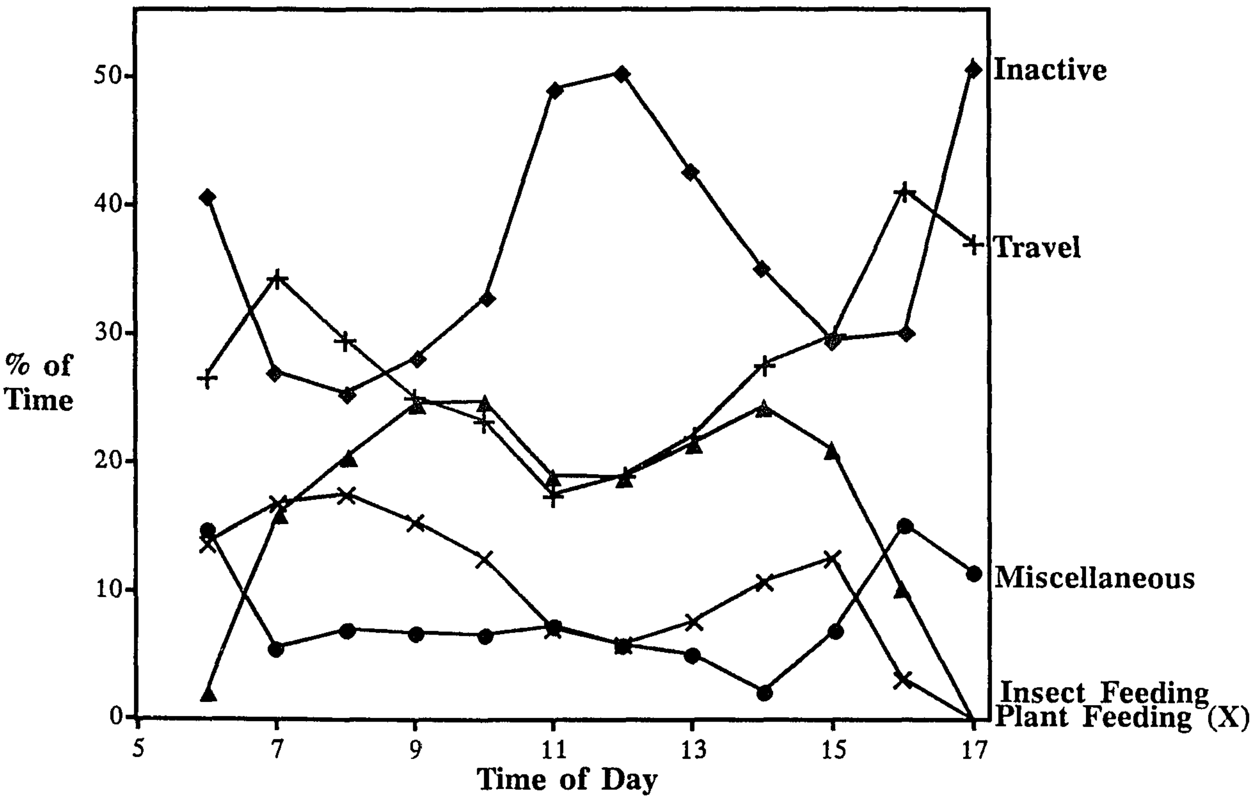
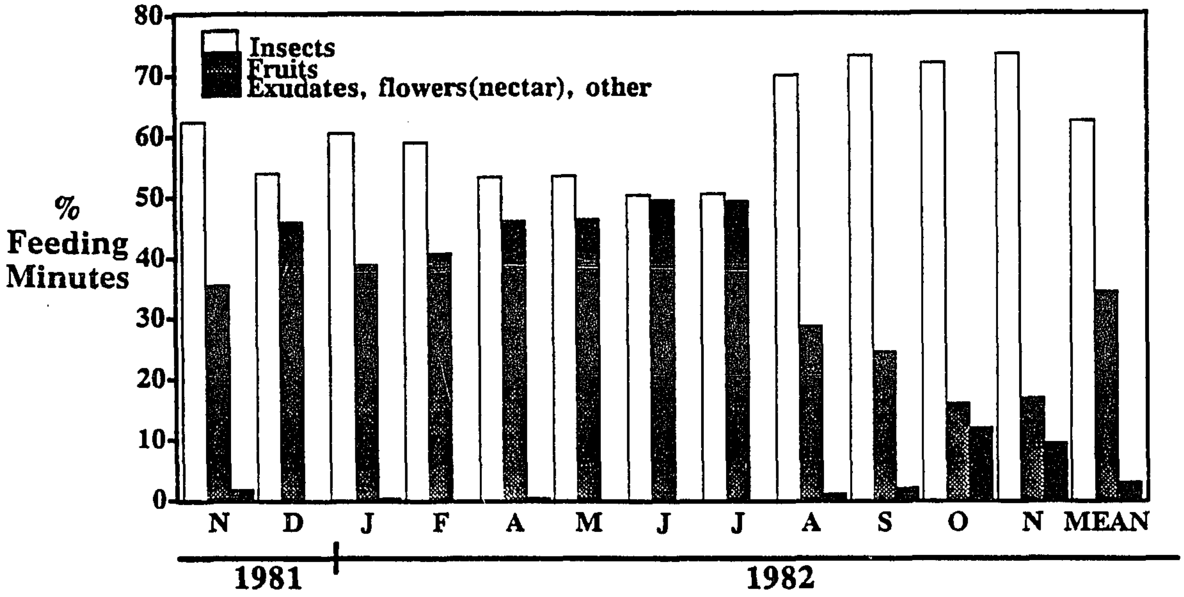


Figure 11
Daily Activity Budget of Saguinus mystax at the Blanco Stream Site



Diet of the Moustached Tamarin (*Saguinus mystax*) at the Blanco Stream Site

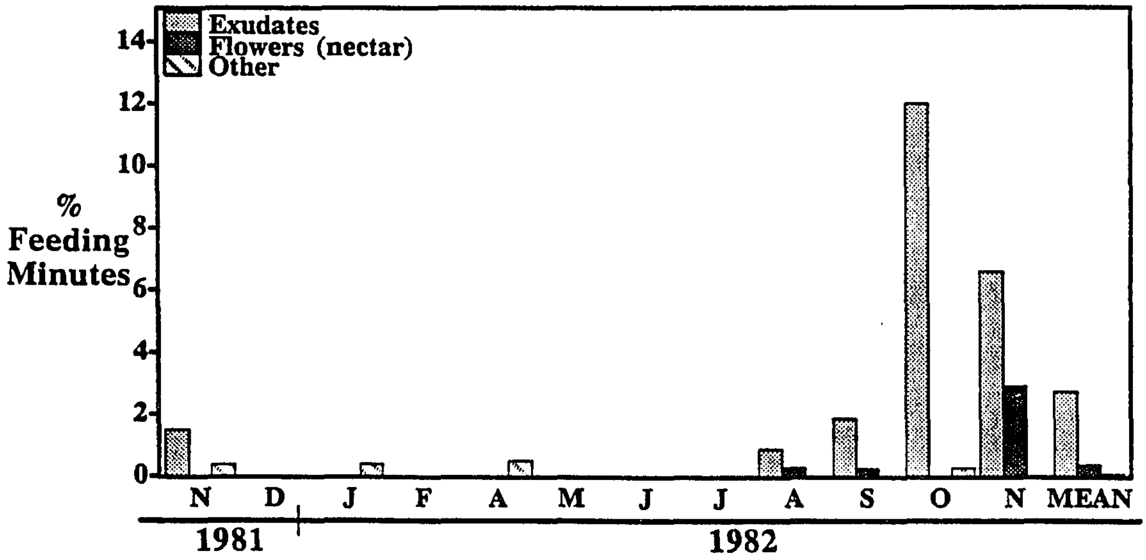


Figure 12
Diet of *Saguinus mystax* (Minor Components) at the Blanco Stream Site

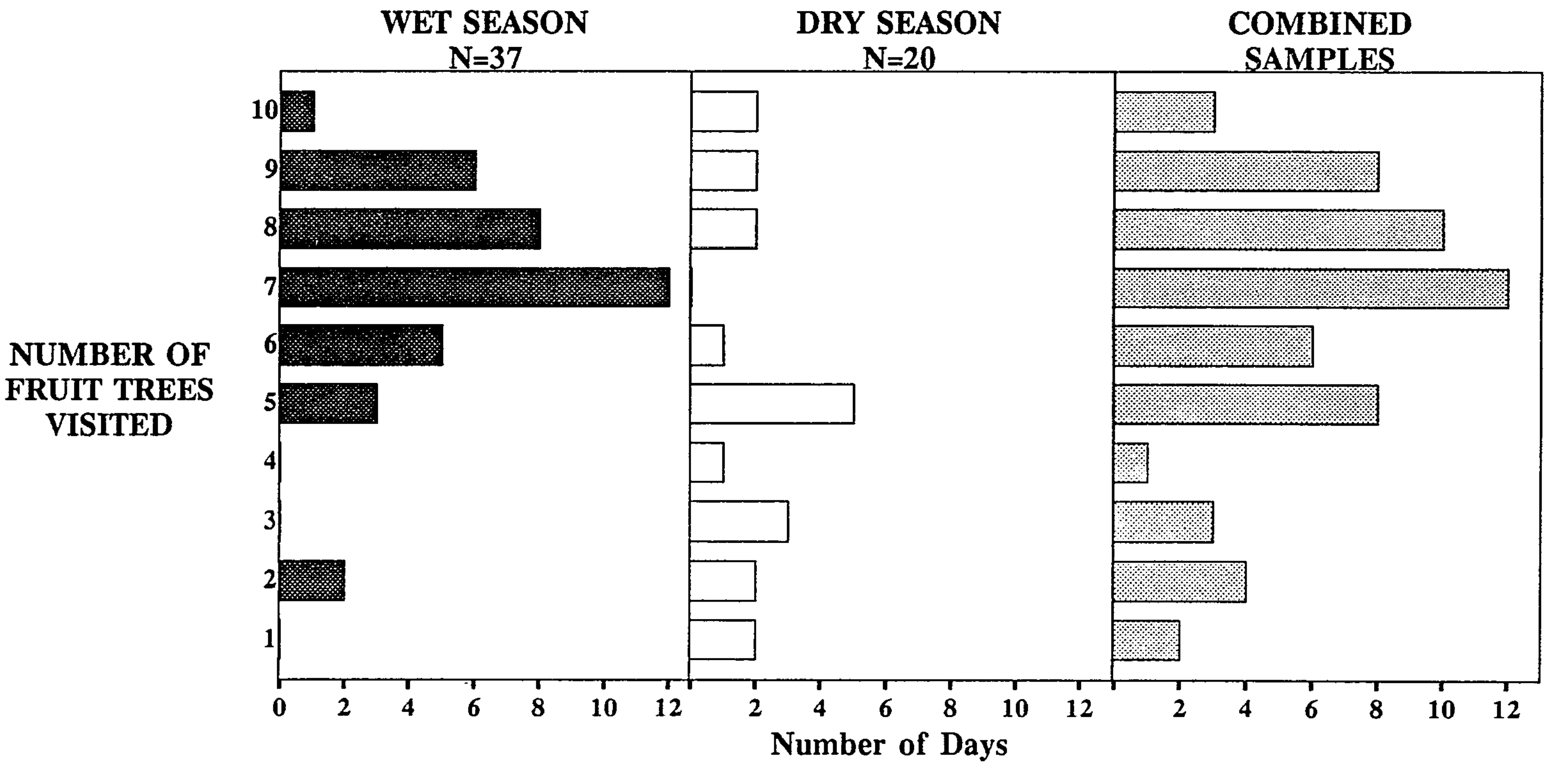


Figure 13
Number of fruit trees visited each day during the wet and dry seasons

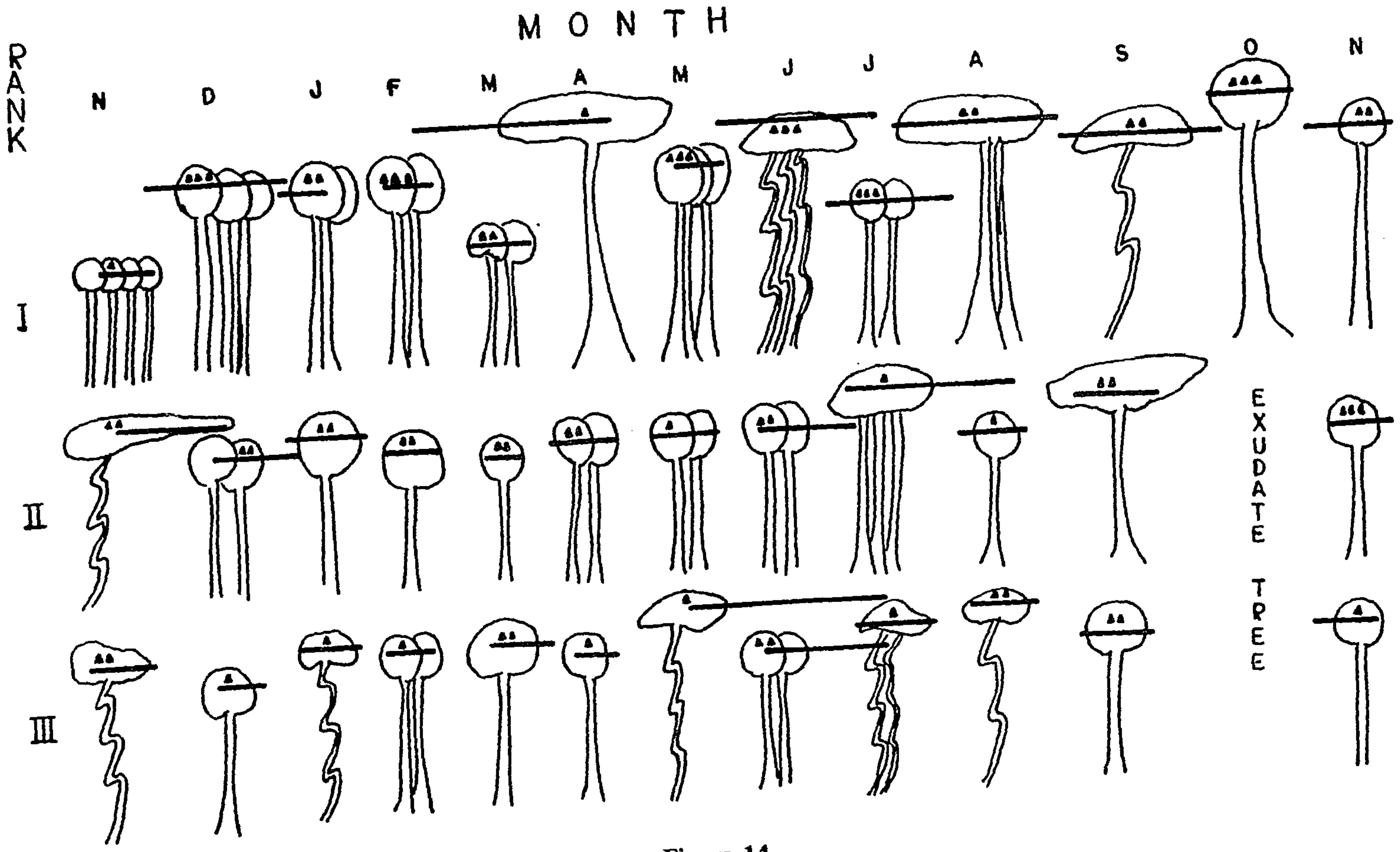


Figure 14
Fruit Phenology of the three highest ranking species utilized by S. mystax at the Blanco Stream. Legend: Columnar trunk= tree; wavy trunk=vine; Fruiting period= ________; Few fruits=▲ ;Half crown covered with fruits=▲▲; many fruits covering the crown=▲▲▲.

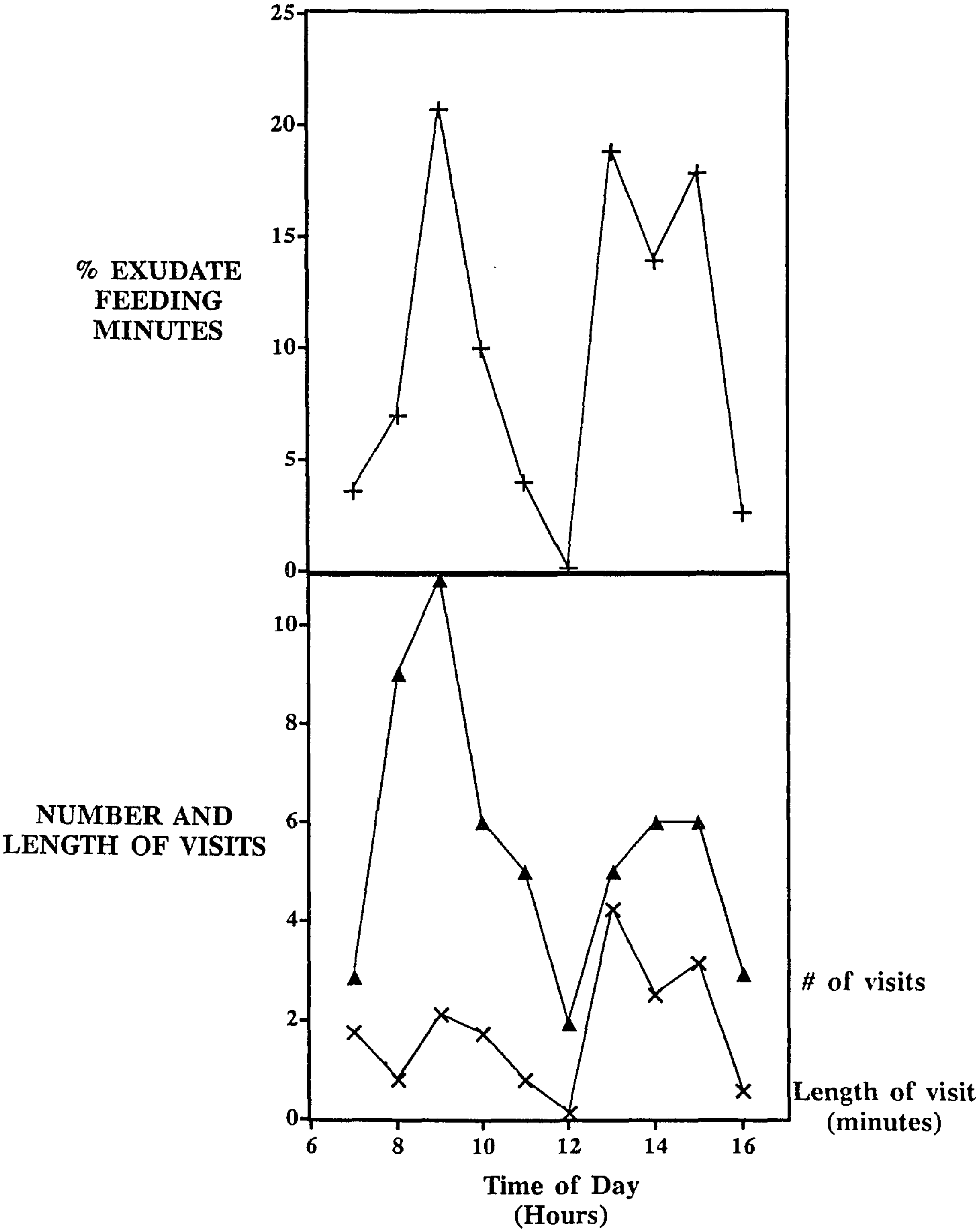


Figure 15
Daily pattern of exudate feeding: Number and length of visit to exudate-producing trees

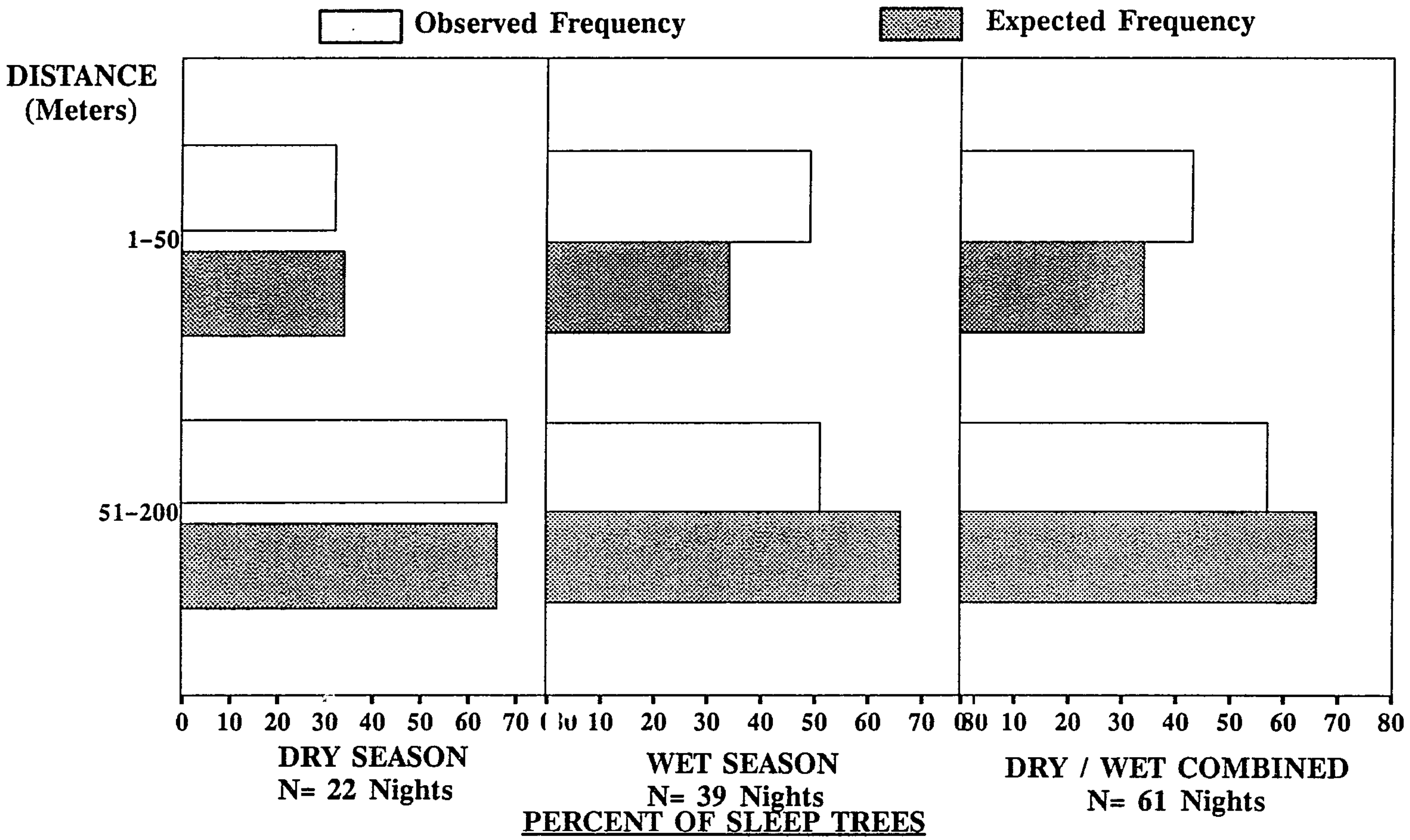


Figure 16

Location of sleep trees. Distance from nearest home range boundary

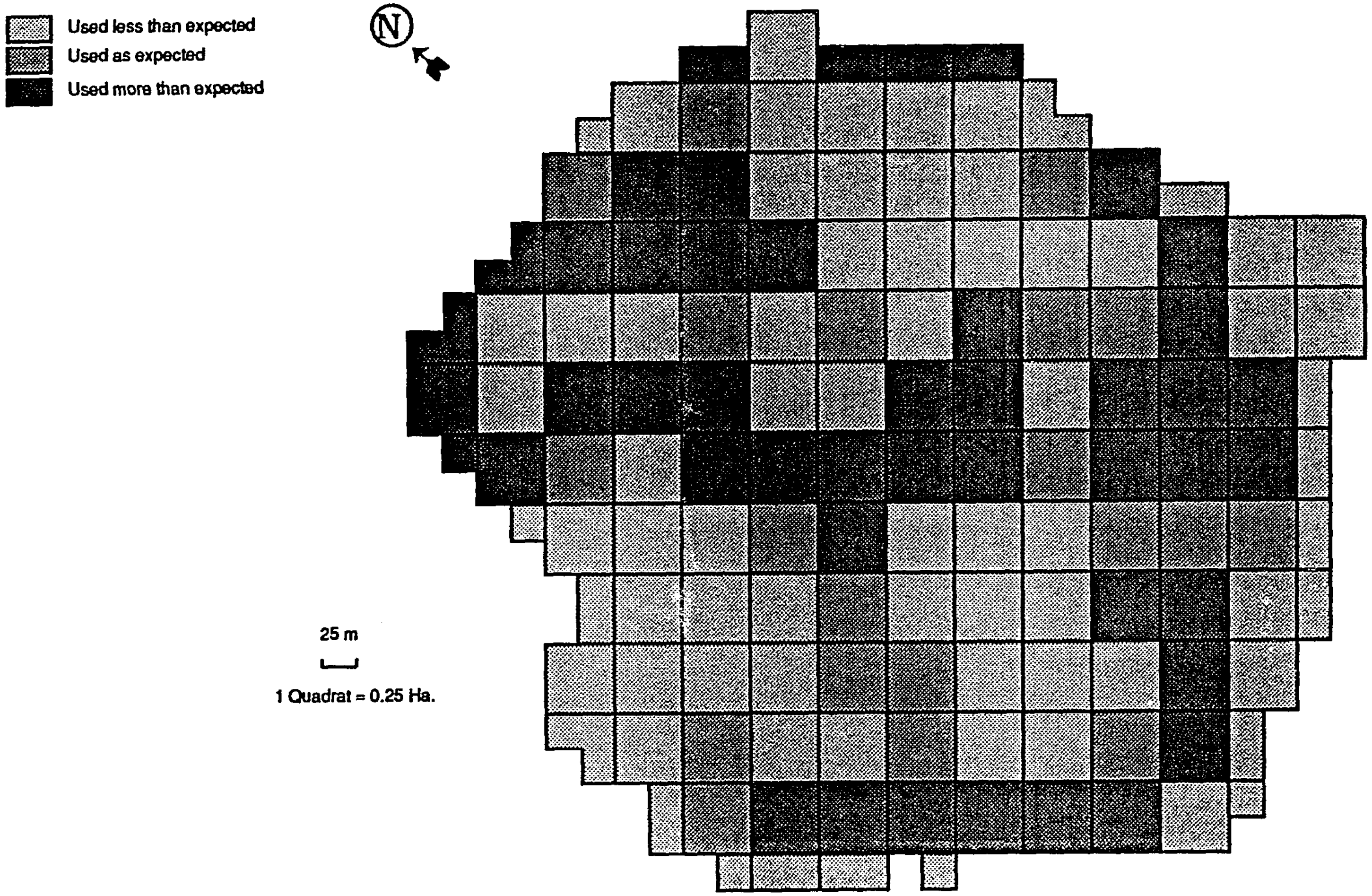


Figure 17
General Quadrat Use by Moustached Tamarins

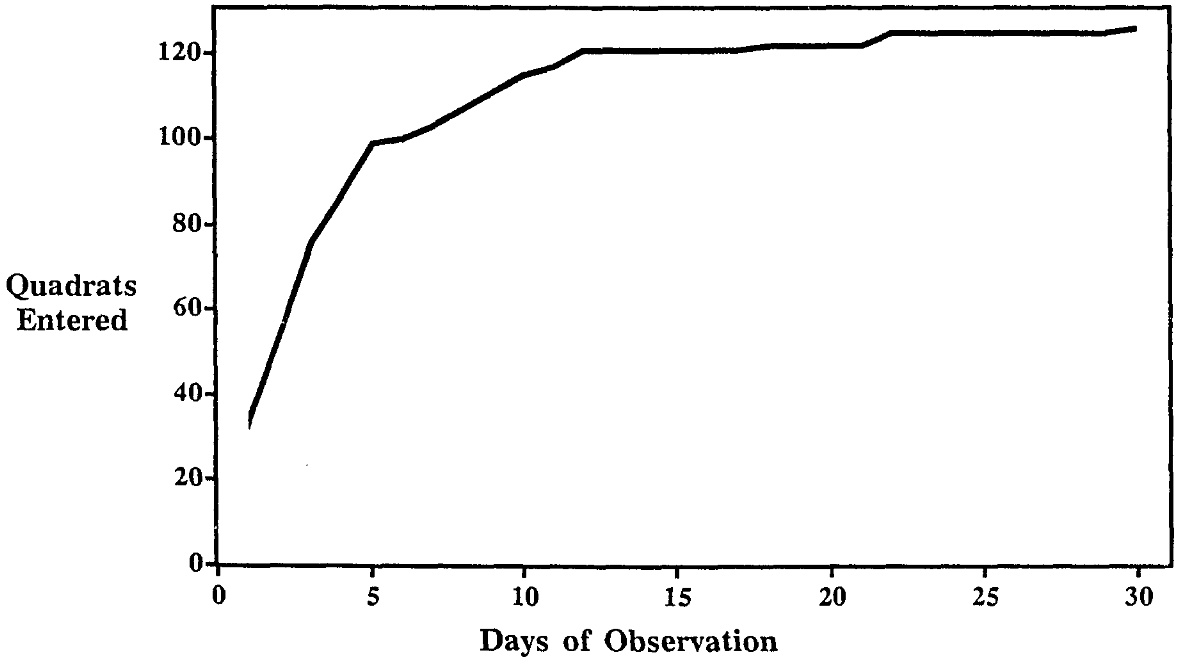


Figure 18
Cumulative quadrats entered by the Green group

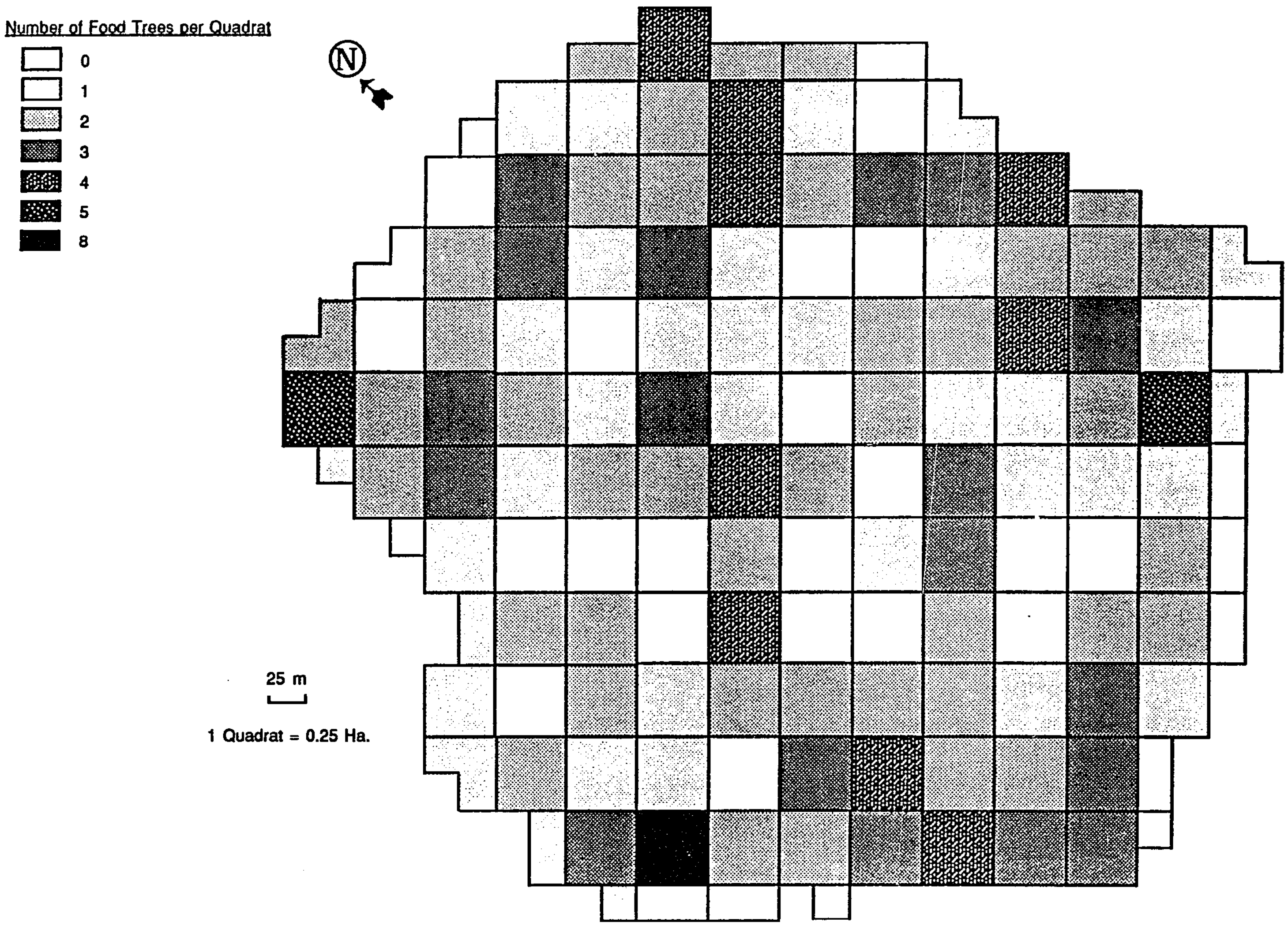


Figure 19

Distribution of Food Trees by Quadrat

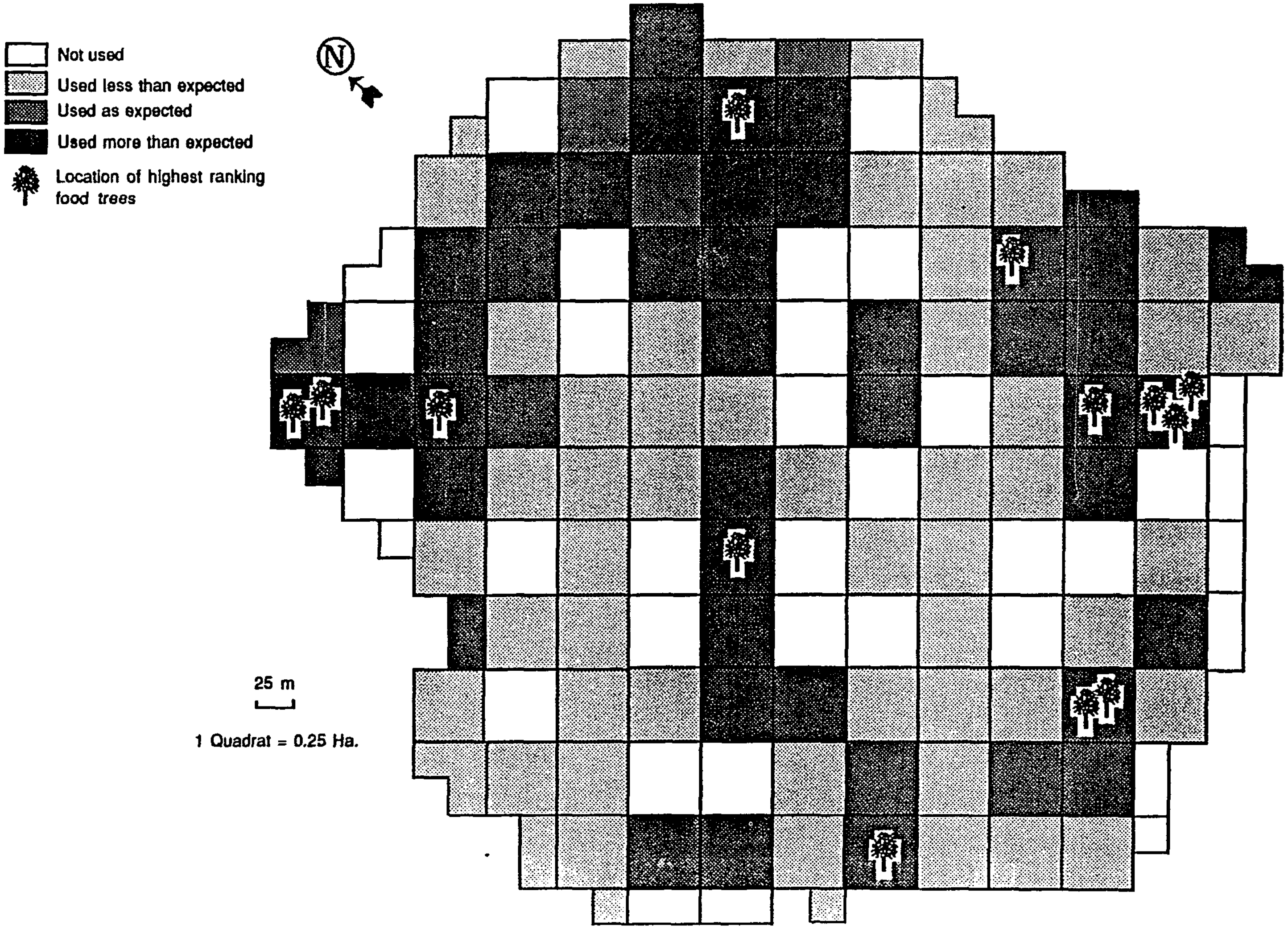


Figure 20

Cumulative Use of Quadrats for Plant Feeding

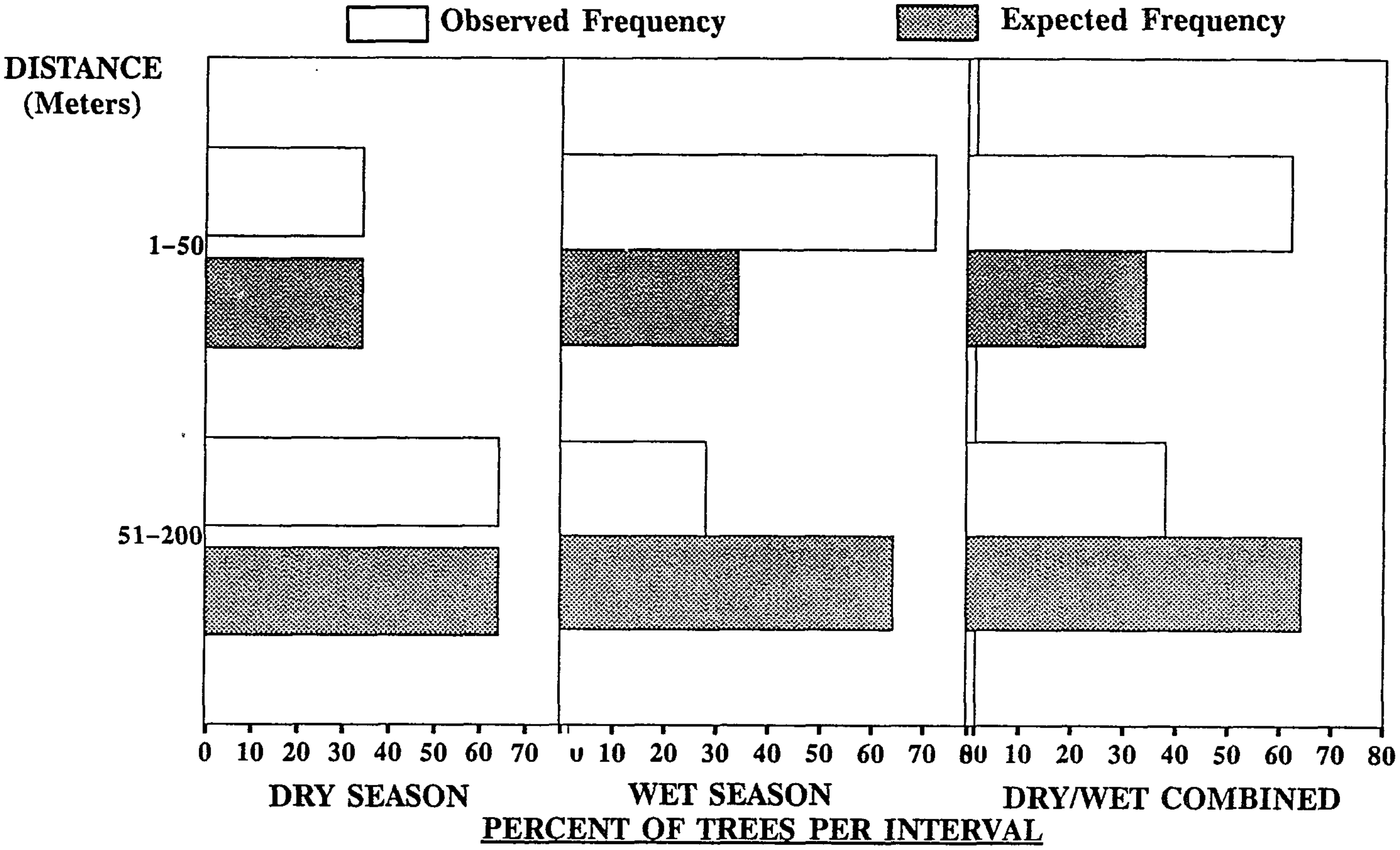


Figure 21
Distance from boundary for the four highest ranking feeding trees

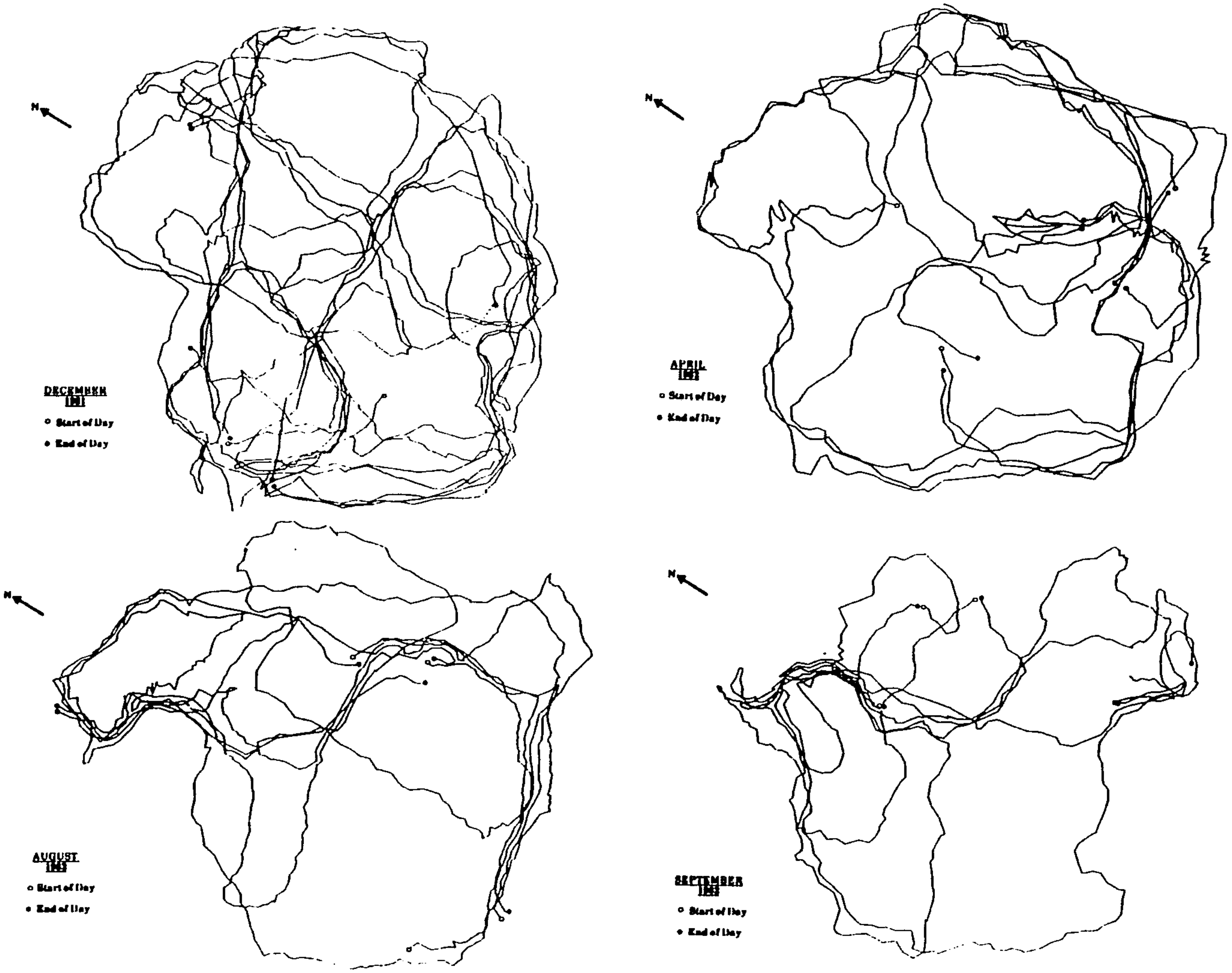


Figure 22
Paths traveled by S. mystax during wet season (top) and dry season (bottom) months

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