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ABSTRACT

BEHAVIORAL ECOLOGY OF THE PANAMANIAN TAMARIN, *Saguinus oedipus* (CALLITRICHIDAE, PRIMATES)

By

Gary Alan Dawson

The objective of this study was to gather information regarding the autecology and behavior of the Panamanian tamarin (*Saguinus oedipus*), a biomedically-important primate which inhabits areas of second growth forest from the Department of Choco, in Colombia, to at least central Panama. Toward this end, a holistic approach to data gathering was employed. Techniques utilized in order to collect this information include: observations in the field, the trapping, marking, and observations of marked tamarins, the tracking of radiotagged groups, and the examination of the diet, parasites, sex-age-class composition, and reproductive parameters of a collected sample consisting of 131 tamarins collected at biweekly intervals over the course of one year.

Estimates of population density, and the problems which arise in making such estimates, are discussed. Implications regarding the usage of these census techniques for primates inhabiting large home ranges under conditions of dense foliage and consequent low visibility are given.

Food habits, as evidenced by the stomach and intestinal contents of 129 tamarins taken over the course of a year, are discussed in relation to information regarding the relative abundance of fruits and insects over seasons, and between upland and lowland sites. Both diversity and equitability values for components of the diet is presented according to season. The relationship between the distribution and abundance of food sources, and tamarin ecology and behavior, is discussed.

Quantitative information regarding the use of time and space by this tamarin are presented. Contrary to earlier reports, this tamarin exhibits a definite rhythm of activity. Differential usage of habitats is also explored. The use of both space and time is correlated with salient ecological conditions and behavioral peculiarities. A detailed account of nesting or roosting behavior, hitherto undescribed, is also included.

Data were also collected on the size, composition, and stability of tamarin social groups. While group size and composition remained relatively stable over the course of the study, some group constituents were found to be unstable. The concept of the tamarin social group as an extended family unit is discarded; it is suggested that a "typical" social group consists of a breeding pair, the young of the year, and a revolving complement of sexually mature, but socially immature, animals. The probable evolutionary advantages of this latter system are discussed. The correlation between group stability and the degree of deciduousness of trees on a group's home range site is also explored.

The absence of pronounced sexual dimorphism, the duality of male-female roles, evidence for a one male-one female dominance system, high incidence of intragroup aggression, intraspecific communication system, foraging strategy, and distribution of resources are considered in defining the species' social structure and the adaptive significance of that structure in a seasonal environment.

Data regarding tamarin reproduction result from the examination of the reproductive tracts of sacrificed animals and observations in the field. While pregnant females or newborn young may be encountered every month of the year, most births occur from March to June, with the height of the peak being in April and May. The numerous, newly-pregnant females collected in May and June indicate another potential birth peak in August or September. The potential is rarely realized, however, and young, in fact, are seldom seen outside the March-June birth peak. No seasonal differences were noted in the reproductive tracts of either males or females. The possible significance of this pattern of reproduction is discussed.

The parasites of *S. oedipus* were also investigated. In general, the loads of intestinal parasites appear to be relatively low when compared with data for animals which have been in captivity for some time. Data regarding the incidence of blood parasites and ectoparasites are also presented and discussed.

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By

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Computer time necessary for the analysis of data on tamarin reproduction was provided by Dr. W. Magee and Dr. W. Dukelow. Other calculations herein were facilitated by the Wang 600-14 calculator in the Michigan State University Museum.

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INTRODUCTION

An Overview of Neotropical Primate Studies

Despite the difficulties in studying arboreal primates (Aldrich-Blake, 1970), many field investigations of New World monkeys (all of which are arboreal) have been conducted in recent years. The howler monkey, genus *Alouatta*, which served as the subject for the first comprehensive field investigation of New World primates (Carpenter, 1934) has been the object of the majority of studies (*e.g.* Chivers, 1969; Mittermeier, 1973). Field investigations have also been undertaken on species of the genera *Ateles, Cebus,* and *Saimiri* (*e.g.* Thorington, 1967; Thorington, 1968a; Oppenheimer, 1969; Baldwin and Baldwin, 1972). Both the quantity and the quality of the information regarding the ecology and behavior of these species are substantial. However, due to the limitations on observation imposed by the densely-foliated environment, the information regarding platyrrhines (New World primates) cannot compare with the data base that has been established for the terrestrial catarrhines of the Old World.

Nevertheless, certain generalizations can be made regarding species of the Neotropical genera named above: 1) Under pristine conditions, these species tend to form large, relatively stable social units; 2) these social units are structurally complex, with several sex and age classes represented within the unit; 3) the principal dominance hierarchy is predicated on male dominance; and 4) the dominance hierarchy may be characterized as being either uni-male or age-graded multi-male in structure (Eisenberg *et al.,* 1972).

In contrast, little is known of the ecology or social structure of those platyrrhines which form small social units, *e.g., Aotus* spp., *Callicebus moloch*, or any of the Callitrichidae. The information at hand regarding their habits and their social organizations is at best fragmentary, and often anecdotal.

Mason's (1966, 1968) study of *Callicebus moloch* may be considered the pioneer field study of a Neotropical primate species which occurs in small social units. Moynihan (1964, 1970) discussed the behavior patterns of *Aotus trivirgatus* and *Saguinus geoffroyi*, but his primary emphasis lay in laboratory study rather than in field observation. The contributions of Coimbra-Filho and Mittermeier (1973) and Thorington (1968b) add to our knowledge of callitrichid ecology, but result from casual observations rather than from comprehensive field study. While several field studies on members of the Callitrichidae are currently in progress, none of their findings has yet been published. The present study is a substantial addition to our understanding of the ecology and behavior of the medically-important Callitrichidae.

Medical Importance of the Callitrichidae

Marmosets and tamarins (Callitrichidae) have become increasingly popular in recent years as animals for biomedical research. Their small size, their relative tractability when compared to larger species, their tendency to produce twins, and, in some species, their abundance and relatively low cost are responsible for their popularity in today's budget-conscious scientific community. Moreover, while other monkey populations continue to decline due to over-exploitation and the destruction of their habitats, some callitrichid species, *e.g.*, *S. oedipus*, thrive in the dense, second-growth forests which result from man's activities in the Neotropics. Thus, potentially, some callitrichid species offer at least a partial solution to the current shortage of primates for biomedical purposes.

Marmosets and tamarins have proven to be useful laboratory animals for a variety of purposes. The presence of chimerism in their twin offspring make them particularly suitable for some genetics studies (Benirschke *et al.*, 1962). They are also widely used in the studies of virology, protozoology, psychology, and dentistry (*e.g.* Sandler *et al.*, 1966; Deinhardt *et al.*, 1967; Hunt *et al.*, 1970; Young, 1970; Dreizen *et al.*, 1972; Patterson *et al.*, 1973).

The Panamanian tamarin, *S. oedipus*, is an important reservoir host of several human diseases. For example, they are known to carry relapsing fever (Clark *et al.*, 1931), leishmaniasis (Herrer *et al.*, 1966), trypanosomiasis (Sousa *et al.*, 1974), and enteropathogenic bacteria (Kourany and Porter, 1969). Thus this tamarin, which is often found in second growth forests close to human habitations, is a potential source of sylvatic infections.

Range of *Saguinus oedipus geoffroyi*

The Panamanian tamarin, *Saguinus oedipus geoffroyi*[1] is the only member of the family Callitrichidae endemic to Central America. The ancestors of the present form apparently immigrated from South America

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[1] Follows the classification by Hershkovitz, 1966.

during the late Pliocene (Hershkovitz, 1969). The modern range extends from the Colombian province of Choco north to at least central Panama (Hershkovitz, 1949; Handley, 1966; Moynihan, 1970). Moynihan (1970) indicates that *S. oedipus (=S. geoffroyi)* is characteristic of areas of moderate humidity, and is almost absent from the humid Atlantic coast. However, the trapping records of Telford *et al.* (1972) indicate that it is extremely abundant in a strip of disturbed vegetation about 5 km wide along the Atlantic coast in the Province of San Blas. Furthermore, *S. oedipus* is reported to be abundant on edges of gallery forest in the humid Province of Darien (P. Galindo, pers. comm.). It appears then, that a lack of habitat in the appropriate seral stages, rather than a climatologically-determined habitat type, restricts the range of this tamarin in the humid lowlands of Panama.

Morphology

Saguinus oedipus geoffroyi is a small monkey; very few individuals exceed 650 g in weight. Only slight sexual dimorphism exists -- adult females (pregnant females excluded) in this study averaged 4.3 percent heavier than adult males. Average body length for adult animals of both sexes is about 235 mm; average body weight is about 500 g. The Panamanian tamarin, then, while delicate in structure, is a relatively robust animal.

As in all callitrichids, the tail is not prehensile, and is used primarily as a balancing organ as the animal forages on the tips of fragile branches and progresses in long, arching leaps from tree to tree. The position of the tail, and the presence or absence of piloerection at a discrete point in time are expressive of the monkey's behavioral state (Moynihan, 1970).

The Panamanian tamarin has well-developed claws on the front feet; the digits on the hind feet also possess claws, with the exception of the hallux, which has a nail and is apposable. The combination of claws and relatively short fore and hind limbs equip this animal for a mode of locomotion which may be characterized as squirrel-like. The apposable great toe is often used in conjunction with the rear foot in grasping a branch while the animal is hanging upside down while eating such pendant fruits as those of *Cecropia* spp. and *Genipa americana*.

The dentition reflects the tamarin's insectivorous and frugivorous diet. The dental formula is $I\frac{2}{2}$, $C\frac{1}{1}$, $P\frac{3}{3}$, $M\frac{2}{2}$, $x2=32$. The canines are especially well-developed, and are used as offensive and defensive weapons as well as for procuring food. Unlike many Old World primates, notably the baboons and drills, there are no significant differences in canine size and shape between males and females. The molars are trituberculate, a dental condition which Hill (1957) regards as primitive.

The short gastrointestinal tract reflects the demands of an insectivorous-frugivorous diet. The following measurements (in mm) were taken from the gastrointestinal tracts of 92 adults: 1) Small intestine, $\bar{x} = 476 \pm 8(SE)$; 2) large intestine $\bar{x} = 186 \pm 4(SE)$; 3) caecum $\bar{x} = 33 \pm 1(SE)$. Comparative information regarding the gastrointestinal proportions of other primates may be found in Fooden, 1964; Hladik, 1967; and Jones, 1972. A comparison of *S. o. geoffroyi* intestinal tract microstructure with that of other New World primates which exhibit different feeding habits may be found in Hladik (1967).

The suprapubic gland is larger and more highly developed in females than in males (Wislocki, 1930a; Moynihan, 1970; Epple, 1972). In this study the average suprapubic gland width was 32 percent greater in adult females than in adult males (26.6 mm vs. 20.1 mm, respectively). Seasonal changes were apparent in the gland width of females, but not males (See section on reproduction). The mean width of female suprapubic glands was greater during the peak season of parturition (March-June) than in the remainder of the year. Apparently, endocrinological changes during that period, together with increased frequency of maternal behavior, are responsible for this difference (H. Box, pers. comm.).

Coloration

The color pattern of the Panamanian tamarin, *Saguinus oedipus geoffroyi*, has been adequately described by Moynihan (1970), and is quoted here. "Individuals of both sexes have the same color pattern, which is quite complex. The face is largely bare (more so in adults than in young) and a dark gray in color, but there are stripes of white hair on the cheeks and the sides of the nose or snout. There also is a triangular patch or 'blaze' of white on the forehead and front of the crown, and the sides of the bare face are framed by another pair of whitish stripes (passing behind the naked black ears). The rear part of the head and the nape are chestnut or rufous red. The upper part of the body is largely brindled black and grayish-yellow (the precise arrangement of the black and yellow differs considerably in different individuals). The underparts and most of the arms and legs are white, sometimes tinged with yellowish-orange on the breast and belly. The proximal part of the tail is deep rufous, and the distal part is black (with a white tip in all or most infants and young juveniles)." The following can be added to this description: The yellowish tinge on the normally white underparts can be quite pronounced. The variable character is so striking that Elliot (1912) made this a character for his species *salaquiensis*, which he later withdrew. The ears are dark grey or black, as are the planar surfaces of the feet and the claw and nails. The iris of the eyes is chocolate; the pupil black.

The above description is accurate and agrees closely with my observations. However, I did not observe a white tail tip in infant or juvenile animals, nor does Mendez (1970) mention this character in his description of the animal. It is possible that white tail tips may be characteristic of some individuals in restricted, local populations, and that Moynihan's animals came from such a source.

There is no record in the literature of color mutants in *S. o. geoffroyi*. During the course of this study two types of color mutants, four animals in all, were encountered. The first mutant was a melanistic animal seen near Gamboa, Panama Canal Zone; this animal was not collected. It appeared to be entirely black in color. The other three animals exhibited incomplete pigmentation of the skin on the face, the planar surfaces, the palmar surfaces, the nails, and claws. These tamarins were collected between 6 and 7 km west-southwest of Balboa, Panama Canal Zone, and are housed in the Michigan State University Museum under catalogue numbers 22916, 22963, and 23038. Of the three, the male offers the most striking variation from normal coloration. Pigment is present in only about 10 percent of the nearly naked facial skin, and its distribution is spotty. The right and left ears are approximately 50 and 30 percent pigmented, respectively. The plantar and palmar surfaces are entirely devoid of pigment; the dark claws are noticeably lighter than normal; one claw and both nails are also devoid of pigment. Pigment is absent on the suprapubic gland of the male; the suprapubic glands of the females are blotchy.

THE STUDY AREA

The Pacific slope of the Panama Canal Zone was selected as the site for this study because it: 1) Supports high densities of tamarins, 2) contains second growth forests which have not been disturbed recently, and 3) contains a system of hard surfaced roads which provides easy accessability to the study area during both seasons. The entire study area lies within the Dry Tropical Forest life zone (Holdridge and Budowski, 1956; Holdridge, 1967). The focal point of the study, the former Rodman Naval Ammunition Depot (referred to hereafter as Rodman) is located at $8^{o}57'$N, $79^{o}57'$W.

Climate and Photoperiod

Mean monthly temperatures in the Canal Zone average about 80^{o}F (26.7^{o}C) throughout the year. Rainfall, however, is markedly seasonal with a four month dry season from mid-December to mid-April and an eight month wet season from mid-April to mid-December. On the Pacific side, rainfall over the dry season averages 5.48 inches (139.19 mm); rainfall during the wet season averages 62.83 inches (1595.88 mm) (based on 72 years of continuous records, Panama Canal Company). Rainfall during the 1973 dry season was 3.99 inches (101.35 mm) below the mean; rainfall for the 1973 wet season exceeded the mean by 16.44 inches (417.58 mm). Rainfall during the 1974 dry season was also below normal, 3.16 inches (80.26 mm) below the mean. The dry season is accompanied by desiccating winds which average 10 mph (16.1 km/hour) and often gust to over 25 mph (40.2 km/hour). Rainfall and temperature during the study are compared with historical averages for these parameters in Figure 1.

Annual changes in photoperiod at this latitude are slight -- approximately 63 minutes difference between summer and winter solstices. Other accounts of Canal Zone climate and photoperiod can be found in Kaufmann (1962) and Fleming (1971).

Topography

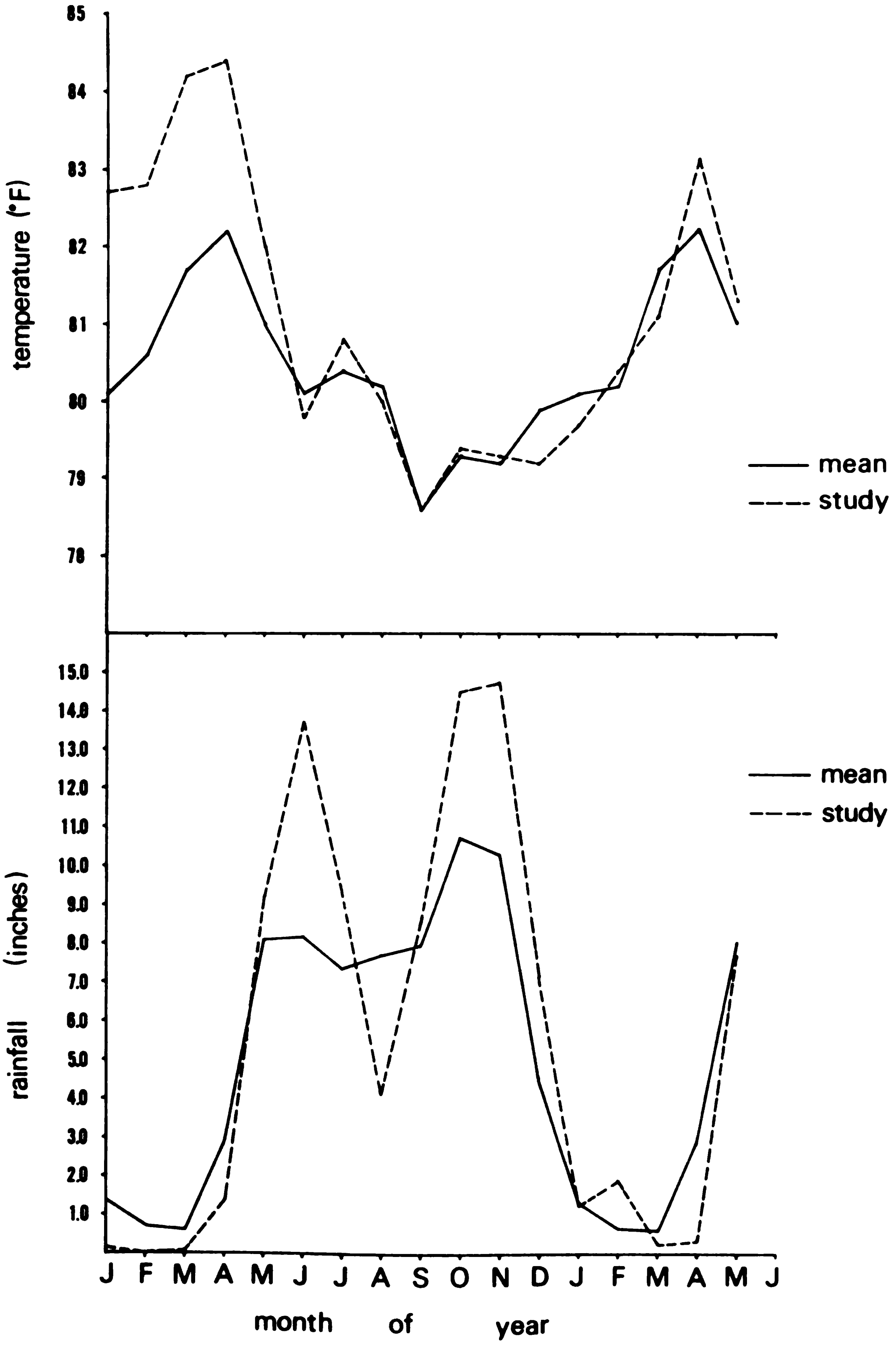
The land rises from sea level to 1180 feet (360 m) and consists of small hills and valleys. Milennia of intense weathering on a lateritic substrate have produced hills which rise abruptly from the surrounding environment. The flats between the hills are dissected by small streams, most of which are seasonally intermittent. The lower reaches of the two main rivers in the study area, the Rio Cocoli and the Rio Velasquez, are meandering, sluggish streams characteristic of peneplain surfaces. Both streams run northeastward to the Panama Canal.

Vegetation

The forest on the Pacific side of the Canal Zone is primarily a second growth forest. Physiognomically, the forest ranges from brushy vegetation of 1-2 m in height on the edge of the forest to trees about 25 m in height in the gallery forests lining the streams. The bulk of the vegetation consists of trees 10-20 m in height. There are, however, large areas on hillsides and ridges where edaphic factors prohibit the

Figure 1. Rainfall and temperature data for Balboa, Panama Canal Zone: Readings taken during the study vs. a 72 year mean.

Figure 1.


85
84
83
82
81
80
79
78
temperature (°F)
mean
study
15.0
14.0
13.0
12.0
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
rainfall (inches)
mean
study
J F M A M J J A S O N D J F M A M J
month of year

growth of large trees. Lower growth forms, particularly low brush and grasses, predominate here and render foot travel difficult.

Structurally, the forest consists of a single stratum which follows the contours of tree height. The beginning of a two to three stratum system is apparent in gallery forests, but even here the dominants are not uniformly distributed, and the canopy is incompletely closed.

A table from Fleming (1971) describing the vegetation on his study grid in Rodman has been expanded to include the common vegetation (predominantly tree species) from the study area as a whole (Table 1).

Gallery forests of *Anacardium excelsum* line both permanent and intermittent streams. Two palms, *Bactris balanoides* and *Corozo oleifera*, are commonly found in lower, wetter areas of the gallery forest. A fern, *Adiantum lucidum*, is common along stream banks.

Where a canopy exists in upland sites, its common components are *Calycophyllum candidissimum*, *Cordia alliodora*, *Enterolobium cyclocarpum*, *Ficus* sp., *Guazuma ulmifolia*, and *Luehea seemanii*. Other emergent trees which are important on some sites include *Spondias mombin*, *Cedrela* sp., *Chrysophyllum cainito*, and *Scheelea rostrata*.

As Fleming (1971) indicated, the shrub layer in this forest is well developed. Rank growth of vines, grasses and shrubs are common on certain sites where tree growth is inhibited by edaphic factors; additionally, fallen trees are commonplace -- often whole stands are toppled in high winds. These areas of windfalls and other areas without a uniform canopy are covered by thickets containing bamboo grass (*Chusquea simpliciflora*), a shrub (*Hirtella racemosa*), and, if the opening is completely unshaded, growth of grasses such as *Olyra latifolia* and *Panicum maximum*.

Table 1. Common vegetation on the Pacific slope of the Panama Canal Zone.

TREES

Anacardium excelsum (Bert. and Balb.) Skeels
Andira inermis H.B.K.
Annona reticulata
Annona spraguei Safford
Apeiba tibourbou Abul.
Bunchosia cornifolia H.B.K.
Bursera simaruba (L.) Sarg.
Byrsonima crassifolia (L.) H.B.K.
Calycophyllum candidissimum (Vahl.) DC.
Cassia moschata
Castilla panamensis
Cecropia eximia Cuatr.
Cecropia obtusifolia Bertol.
Cecropia peltata L.
Cedrela sp.
Chrysophyllum cainito L.
Cochlospermum vitifolium (Willd.) Spreng.
Cordia alliodora (Ruiz and Pav.) Roem and Schult.
Ficus sp.
Genipa americana L.
Guazuma ulmifolia Lam.
Inga sp.
Lonchocarpus sp.
Luehea seemanii Tr. and Pl.
Mangifera indica L.
Miconia argentea (Swartz.) DC.
Pittoniotis trichantha Griseb.
Sapindus saponaria L.
Spondias mombin L.
Terminalia sp.
Vochysia ferruginea Mart.
Xylopia frutescens Aubl.

PALMS

Bactris balanoidea (Oerst) Wendl.
Corozo oleifera (H.B.K.) L.H. Bailey
Scheelea rostrata (Oerst) Barret.

SHRUBS

Hirtella americana
Hirtella racemosa Lam.
Lacistema aggregatum (Berg) Rusby
Piper reticulatum L.
Psychotria cuspidata Bredem.
Psychotria undata Jacq.
Randia sp.

Table 1 (Cont'd):

GROUND LAYER

Adiantum lucidum Sw.
Chusquea simpliciflora Munro
Cyperus luzulae (L.) Retz.
Olyra latifolia L.
Panicum maximum Jacq.

Many trees, such as *Bursera simaruba, Calycophyllum candidissimum,* and *Spondias mombin,* shed their leaves during the dry season. As a result, the forest floor is generally covered with a leaf layer several inches thick. In the dry season the leaves are particularly dry, and quiet foot travel becomes impossible. During the wet season conditions are more favorable for decay, and the leaf layer diminishes somewhat, but it is never completely absent. Where the canopy is dense enough to inhibit the passage of light and thus prevent the growth of shrubs, the forest floor is relatively open. In general, however, unimpeded travel is possible only in stream beds and the gallery forests.

Description of the Rodman Area

Rodman, which served as the site for behavioral and radio-tracking portions of this study, is a 1015 ha fenced reserve administered by Gorgas Memorial Laboratory for field biomedical studies. The topography of Rodman does not differ from that of the surrounding area. The forest cover is representative of the study area as a whole, and has not been disturbed to any great extent since World War II. The tamarin population in Rodman also appears to be representative of the tamarin populations on the Pacific slope. A dendritic system of hard surfaced roads allows Gorgas personnel access to most of the area during both wet and dry seasons. As a study site, Rodman offered the additional benefit of being close (within 15 minutes drive) to Gorgas Memorial Laboratory.

Although hunting is prohibited in the area, Rodman is heavily utilized by local poachers. Fortunately, rather than tamarins, their prime targets are whitetail deer (*Odocoileus virginianus*), collared peccary (*Tayassu tejacu*), agouti (*Dasyprocta punctata*), and paca (*Agouti paca*). While tamarins are eaten in some areas of Panama, their small size and the high cost of ammunition make them an economically-marginal target at best. Hunting for meat or sport is probably a negligible factor in tamarin mortality; however, capture of young for the local pet and medical trades may be responsible for substantial losses.

Vertebrate Fauna

Fleming (1971) indicated that nearly 70 species of mammals are present in Rodman. The avifauna is also rich and varied, as is the herpetofauna. Rather than discuss these faunas in detail, I wish to touch on those species which are of probable importance to tamarins as either competitors or predators.

Mammalian competitors: To my knowledge, only three species of primates occur in the study area: *Saguinus oedipus*, *Aotus trivirgatus*, and *Cebus capucinus*. *Aotus* is not uncommon, and may be a nocturnal ecological equivalent of *Saguinus* (Moynihan, 1964). *Cebus* is locally rare -- only three were seen during the entire study, and the *Cebus* diet, which consists primarily of the larger fruits (Oppenheimer, 1969; Eisenberg *et al.*, 1972), does not broadly overlap that of the tamarin. Thus, the night monkey, *Aotus*, may be the only important primate competitor.

Other mammals which have diets overlapping that of *Saguinus* include: *Marmosa robinsoni*, *Caluromys derbianus*, *Didelphis marsupialis*, *Nasua nasua*, *Bassaricyon gabbii*, *Potus flavus*, *Sciurus granatensis*, and *Sciurus variegatoides*. The last two mammals are squirrels which compete directly with *Saguinus* for fruits, and, because they are also diurnal, are frequently involved in interspecific conflict. Fruit bats, such as *Artibeus* spp., are also competitors, particularly for the fruits of *Ficus* spp., *Cecropia* spp., and *Anacardium excelsum.*

Avian competitors: Moynihan (1970) considered several tyrannid flycatchers to be probable competitors of tamarins for both fruits and insects. My observations indicate that some flycatchers do eat the same fruits, but that the primary insect types taken by tamarins (*e.g.* Tettigoniid grasshoppers, Lepidopteran larvae, and large Coleopterans) are not prime flycatcher foods. Flycatchers usually specialize on smaller, flying insects. It is more likely that gleaning species such as motmots (*e.g., Baryphthengus martii*), the squirrel cuckoo (*Piaya cayana*), and the puffbird (*Malacoptila panamensis*) are stronger competitors for insects than are the flycatchers. Oropendolas (*Zarhynchus wagleri*) and chachalacas (*Ortalis cinereiceps*) are important competitors for the small fruits used by tamarins, and are often chased from fruit trees by this primate.

Mammalian predators: The tayra, *Eira barbara,* is an excellent climber and is capable of capturing tamarins in the treetops as well as on the ground. A tayra has been observed carrying a dead tamarin (Moynihan, 1970). A second predator, the yaguarundi (*Felis yagouroundi*) may catch tamarins when the latter are foraging on the ground or travelling in the very low brush. On two occasions, yaguarundis approached the investigator while he was carrying traps which contained vocalizing tamarins. Finally, the ocelot (*Felis pardalis*), an arboreal cat, is also capable of taking tamarins.

Avian predators: The large hawks and hawk-eagles are probably the most important predators of *S. oedipus*. Important raptors in this area include: the black hawk-eagle (*Buteogallus urubitinga*), the white hawk (*Leucopternis albicollis*), the tyrant hawk-eagle (*Spizaetus tyrannus*) and the ornate hawk-eagle (*Spizaetus ornatus*). The tyrant hawk-eagle has been observed to prey upon tamarins (N. G. Smith, pers. comm.). I observed the black hawk and the ornate hawk-eagle preying upon the variegated squirrel (*Sciurus variegatoides*), which is about tamarin size and, as noted above, occupies the same habitat. All of the hawks listed above are certainly potential predators of *S. oedipus*.

Moynihan (1970) indicates that *S. oedipus* are "... very much afraid of most birds of prey," and that, "... the only bird of prey that does not provoke such reactions is the Double-toothed Kite (*Harpagus bidentatus*)." Moynihan (*ibid.*) noted that even perched birds of prey evoked an antipredator response on the part of the tamarins. I observed tamarins vocalizing at a Grey-headed Kite (*Leptodon cayanensis*), which was perched in a tree at least 50 m from the group. Tamarins vocalize and initiate escape behavior upon the appearance of most large, flying objects, including low-flying aircraft. Moynihan (1970) observed that *S. oedipus*, "... burst into high intensity escape behavior when a Turkey Vulture (*Cathartes aura*) flies by, even though the vulture, ... probably could do them little damage even if it wanted to." In general, this statement is probably true. However, N. Smythe (pers. comm.) once saw Turkey Vultures diving at a group of tamarins, apparently in an attempt to dislodge twin infants from the back of one of the adults. I once observed a toucan (*Ramphastos sulfuratus*) attempting to do the same. (All names of birds cited herein follow Eisenmann, 1955).

METHODS AND MATERIALS

Introduction

The field study of forest-dwelling primates requires some rather specialized methods, particularly when the monkey involved is small and easily alarmed, as are tamarins. Aldrich-Blake (1970) discussed some of the problems involved in gathering ecological and ethological data on arboreal species. These problems include: 1) Extreme restrictions in contact time occur due to interference of thick vegetation and the altitudinal hiatus which occurs between the arboreal primate and the earth-bound observer. Habituation of the animal to the observer is thus more difficult than it might be in an open, terrestrial environment; 2) Heavy foliage makes it difficult to see all animals involved in a given behavioral interaction. In addition, the stimulus which releases various behaviors, or the complete response of the part of all or even one group member, may not be visible; 3) Animals are often difficult to observe initially, since they remain motionless in heavy foliage; 4) Once the monkeys have been located, it is difficult to follow them in the forest habitat; 5) Some sex and age classes, because of behavioral biases, are more easily observed than others. This bias is reflected in the data regarding species behavior; 6) Accurate accounts of group size and/or composition are difficult, and often impossible to make; and 7) The use of various resources by the animals cannot be readily quantified. All of these problems were present in the current study, and are responsible for the development of much of the methodology that follows.

Trapping of Live Tamarins

Tomahawk Live Traps (Tomahawk Live Trap Co., Box 323, Tomahawk, Wisc. 54487) measuring 41 cm x 14 cm x 14 cm were used in trapping live tamarins. Traps were baited either with banana (*Musa paradaisica*) or mango (*Mangifera indica*), and wired to trees and vines 3-10 m above the ground in areas frequented by tamarins. Traps were generally set in clusters of from 3-5, since the vocalizations of trapped individuals often drew the attention of other tamarins, which were then captured in the remaining traps. Traps were washed in stream water, as necessary, to remove accumulated bait and the odor of trapped animals.

Tamarins are adept at stealing bait from traps. They may enter the trap only a few inches and then stretch forward and remove the bait without tripping the pan, or they may insert their paws from the outside of the trap and extract the bait a fingerful at a time. I found that wrapping the bait in 1/4" (7.6 mm) mesh hardware cloth and suspending it from a wire above and posterior to the pan, or placing it underneath the pan so that it was more difficult to extricate, increased my success.

One attempt was made to capture an entire group through the use of a banana and brown sugar "stew" liberally laced with ethyl alcohol. The bait was accepted readily, but the alcohol did not have the desired effect, *i.e.* the monkeys did not lose their locomotory capabilities, albeit they were obviously impaired.

Anesthesia

Ketamine anesthesia (Drake, 1972) was used routinely before handling live-trapped animals in the laboratory. Ketalar (Parke Davis Co.) was administered intramuscularly in dosages of: 0.2 cc for infants, 0.3 cc for young juveniles, 0.5 cc for older juveniles and adults. This dosage proved sufficient for the half hour period necessary to perform the needed operations. Complete recovery occurred 6-8 hours following injection. No mortality occurred in anesthetizing 104 tamarins.

Radio-location Study

Two tamarin social groups were chosen as subjects for detailed studies regarding the utilization of time and space within their respective home ranges. The first group, the lowland group by designation, occupied a lowland area on one of the tributaries of the Rio Velasquez. The second group, the upland group, occupied an upland area which became xeric during the height of the dry season. I intended to compare the use of time and space between two groups inhabiting these disparate sites in order to test a hypothesis formulated by Janzen and Schoener (1968) which holds that insectivorous vertebrates (tamarins require large quantities of animal protein) inhabiting seasonally-xeric upland areas must radically alter their patterns of spatial and temporal usage in order to exploit the seasonal insect resources, while insectivores occupying lowland areas in which insect populations are more stable maintain their pattern of usage throughout the year.

The area occupied by the lowland group is typical of the lowland sites where *S. oedipus* is commonly found. A seasonally-intermittent stream, a branch of the Rio Velasquez, bisects the home range. A gallery forest of *Anacardium excelsum* (to 23+ m) occurs along the watercourse; trees typical of increasingly drier sites appear as one moves out of the river valley and onto the uplands bordering the river. The area is relatively flat in aspect, rising from 12 m to 55 m above sea level at the highest point. The flatness of the area lent itself to the construction of a grid system of trails, which divided the area into squares 100 yards (91.5 m) on a side. The 12,500 ft (3813 m) trail system supplemented the existing road system in creating a well-mapped study area in which precise estimates of group location were possible.

The elevation of the area inhabited by the upland group ranged from 43 m to 127 m above sea level. The vegetation here was markedly different from that in the lowland group's area. Many of the tree species on this site were deciduous in the dry season; the average height of the forest here was also lower due to edaphic factors and the seasonal lack of moisture. The terrain was rugged in aspect, which necessitated the construction of a modified trail system, rather than a strict grid system, for the purpose of determining group location. Where the terrain permitted, the grid system outlined above was constructed. However, when the grade became too steep or the undergrowth and windfalls prohibitively thick, paths were cut following passible routes which lay as close to the intended grid line as possible. The approximate location of these paths was determined through the use of a measuring tape and a lensatic compass. Over

16,000 ft (4880 m) of trail were cut in the upland group area to supplement the existing system of roads. This trail system permitted the monitoring of the upland group over much of its home range. The large home range of the group, however, and a lack of time and funds precluded the construction of a trail network which encompassed the complete home range.

Radio location telemetry equipment used in this study was manufactured by the A. V. M. Instrument Company (808 W. Springfield Ave., Champaign, Ill. 61820). Model St-1 transmitters mounted on bioperm plastic collars equipped with whip antennas constituted the transmitter package. Originally, both continuous signal and pulsating transmitters were used, but the former were abandoned in favor of the lighter (20-25 g), longer-lasting, pulsating models. The weight of the pulsating transmitter package was approximately 4-5 percent of animal body weight, a permissable load for the study of the movements of free ranging animals (Brander and Cochran, 1969). The output frequency of all transmitters was controlled by a crystal which oscillated in the 50 MHz range. The system was designed for maximum output at the third harmonic (150 MHz), and permitted the reception of weak signals at the ninth harmonic (450 MHz) for close range locations (see Montgomery *et al.*, 1973, for details).

A custom-made LA-11 receiver mounted with a two element yagi antenna was used to receive directionally the 150 MHz signal. The effective range of the 150 MHz signal was much less than the 1200 m indicated by Montgomery *et al.* (1973) due to the presence of signal-impeding vegetation and topographic discontinuities. In most cases, reception of the 150 MHz signal was not possible at distances greater than 300 m; reception of the 450 HMz signal was limited to about 100 m.

After the trail system had been constructed in the study areas, the 450 MHz frequency was used almost exclusively since it allowed more precise determination of location than the 150 MHz frequency. In most cases the location of the group (or, at times, only the telemetered animal) could be determined to within 10 m of the actual location. Vocalizations and the sound of moving foliage often aided in obtaining precise locations. When the group was hidden in dense foliage, triangulation from the grid lines determined location to within 20 m.

As noted previously, only the lowland group was radio-monitored for whole-day periods. In preparation for a day of radio-tracking, the lowland group was located about 2 hours prior to sunset on the preceding evening and then followed until it reached its roost tree for that night. The tamarins were watched for at least 30 minutes as they sat on the roost. I then returned to the roost before sunrise on the following day to begin the day's tracking routine.

The behavior in the roost tree was observed, and the exact time the first tamarin left the tree was noted. Locality and behavioral data were then recorded throughout the day at 15 minute intervals.

Since I wished to observe the behavior of undisturbed animals, and since I wished to monitor the natural movements of a free-ranging group rather than the movements of a harassed group of tamarins fleeing from an observer, I found it necessary to employ certain tactics which rendered my presence less obtrusive: 1) Olive drab and camouflage clothing was worn in order to merge more perfectly with the forest environment. I also applied mud to my face to avoid facial "shine"; 2) I attempted to remain at least 30 m from the group when following it to avoid alarming its constituents. This was usually sufficient under dense foliage conditions. Careful stalking of the group from this position was frequently rewarded by glimpses of undisturbed behavior; 3) once the direction of travel had been ascertained, it was often possible to use the path system to "circle" ahead of the tamarins and observe them from a hidden position to the side of their path of travel; 4) binoculars were used in observing their behavior at a distance; and 5) when, despite precautions, my presence was detected, I immediately retreated and hid myself from view. Almost invariably, the tamarins resumed their activity and did not flee from the area.

In addition to elucidating the differences in temporal and spatial utilization between two groups inhabiting upland and lowland sites, the radio-tracking segment of the study had the following purposes: 1) To determine the activity pattern of *S. o. geoffroyi*; 2) to quantify variability in usage of habitat types within the home range and to integrate these findings within the scheme of home range usage; and 3) to observe and interpret intra- and intergroup behavior.

The linear distance travelled by the lowland group within two-hour time periods was used as a measure of activity. Location of the group was determined every fifteen minutes, and the information was transferred to a map of the area. Linear distances travelled in each two-hour period were compiled from these maps after the study had been completed. In analyzing the activity data, I adopted the null hypothesis that the distance travelled in any given time period would be proportional to the total time amassed for that period. Expected values for each time period were obtained by multiplying the proportion of total time in each time period by the total linear distance travelled over all time periods. A Chi-square test (Sokal and Rohlf, 1969) was used *a priori* to test whether or not significant differences occurred among hourly periods. An *a posteriori* test employing the Bonferroni Z statistic (Neu *et al.*, 1974) was used to identify significant components of the Chi-square analysis.

The home range of the lowland group was divided into eight habitat types using height of vegetation, associated tree species and physiognomy of the upper strata as criteria. My null hypothesis stated that habitat usage would be proportional to the area encompassed by each habitat.

The amount of time spent within each habitat and the distance travelled therein were used as measures of habitat usage. A Chi-square test (Sokal and Rohlf, 1969) was used in testing the null hypothesis of proportional usages. Following the rejection of that hypothesis, an *a posteriori* test suggested by Neu *et al.* (1974) for usage-availability data was used to identify those habitats which were preferred, those which were used in proportion to habitat size, and those which were used significantly less than expected.

The acceptance of an hypothesis which predicts proportional usage of habitats which are not uniformly distributed in size or over space requires the assumption that usage is independent of location. I feel that this assumption is reasonable since: 1) the tamarin is capable of moving rapidly enough to traverse the home range in any 15-minute observation period, and thus may be expected to use those habitats within the range by preference rather than by accident of location; and 2) a Chi-square test testing the distance travelled and time spent in the inner vs. outer one-half of the home range indicated that usage did not differ significantly between the two elements -- *i.e.*, there was no trend apparent which indicates higher usage either of a central or core area, or of the peripheral portion of the home range.

Group Composition and Stability

Live trapping of study group constituents began in Rodman in January, 1973. Groups were selected whose estimated home ranges lay at fairly discrete intervals along a moisture-vegetation continuum which extended from the moist bottomlands with evergreen gallery forests to seasonally-xeric uplands which support scrubby, highly deciduous forests. This sampling scheme was based on an hypothesis suggested by Janzen and Schoener (1968) which holds that insectivorous vertebrates inhabiting seasonally xeric tropical uplands must employ different patterns of spatial utilization than their lowland counterparts in order to exploit the more seasonally variable insect resources characteristic of upland areas.

Sixty-eight tamarins were captured during the study. All were marked with leather collars wrapped with from one to three strips of brilliantly-colored plastic tape according to a predetermined code relating the animal to its group. Longevity of the collars and readability of the tape proved excellent; only 3 of 68 collars required replacement during the study period, and all collar codes were readable throughout the study. Small mammal ear tags (Salt Lake Stamp Co., Salt Lake City, Utah) were attached to the left ear of each of the color-marked animals as an additional means of identification.

Five complete social groups were trapped, marked, and observed during the study. Immigrants were trapped and marked after they had been observed with the group. Groups were retrapped and observed at regular intervals from February 1973 to December 1973. From January to May, 1974, each group was observed at monthly intervals. Observations were made from blinds while the group fed at pre-baited platforms 3-5 m above the ground. Identification was aided by the use of 7-14X binoculars. Each group was observed for two consecutive days during each of the observation periods in 1974. No changes in group composition were noted on any of the second day counts.

Estimates of Population Density

Tamarin densities in Rodman were estimated using a modified version of the strip-census method described by Hayne (1949). Tamarins were censused by two observers from a car travelling slowly (less than 10 mph or 16 kmh) on the Rodman road system. The effective width of the strip was 30 m during the wet season and 50 m during the dry season. Estimates were further divided by time of day, 0645-0830 hours and 0830-1045 hours in order to compensate for differences in activity levels and choices of early morning sites noted while observing animals. In all, 1,712 km were traversed during the censusing. Estimates of population density obtained by this strip census were compared to animal densities based on home range size as indicated by telemetry data.

Data From Collected Tamarins

One-hundred thirty-one tamarins were collected with a 20 gauge shotgun in areas peripheral to Rodman at the rate of five animals every two weeks over the course of one year. Collection sites were changed frequently to avoid the decimation of local populations. All collecting sites were located at least 1 km from the nearest observation blind; most were located at least 3 km from Rodman. Individuals, which had been under observation for 5-15 minutes in order to ascertain group size, were collected without known bias. Upon collection, tamarins were placed in a portable cooler to prevent tissue degeneration. Data obtained from this collection, and the methods employed, are outlined below.

Weight and standard measurements: The body weight of intact individuals was determined to the nearest 0.1 g on an Ohaus triple beam balance (Ohaus Scale Corp., Union, N. J. 07083). Standard mammalogical measurements were taken (in mm) and include: 1) Total length, 2) tail length, 3) length of ear from notch, and 4) length of hind foot.

Sex and reproduction data: Males were divided into two classes, mature and immature (see section on sex-age classes). Testes were preserved in AFA prepared according to a formula from Mosby *et al.* (1969). Measurements taken on the preserved material include, for each testis: 1) Length, 2) width, 3) breadth, and 4) weight. Histological cross sections stained with eosin and hematoxylin were made of the testes of one male from each month's collection. The testes of the sampled individuals approximated the mean testis size of all adult males examined for that month. This was done to determine whether or not changes in gross morphology occurred even though testis size remained constant over time.

Females were divided into five reproductive classes by means of obvious and traditional criteria: 1) Imperforate, 2) perforate, 3) pregnant, 4) lactating, and 5) post-lactating. Incidence and crown-rump length of embryos were recorded. Female reproductive tracts were preserved in AFA as indicated above. Measurements of preserved female reproductive tracts include: 1) Right and left ovary length, 2) right and left ovary width, 3) right and left ovary breadth, 4) right and left ovary weight, 5) length of right and left oviducts, 6) cervico-vaginal length, 7) cervix length, 8) uterus depth, 9) uterus width, and 10) uterus weight.

Reproductive measurements, together with body length, body weight, and the length, breadth, and degree of pigmentation of the suprapubic gland (see below) were compared over three trimesters: 1) November to February, the peak breeding season; 2) March to June, the peak season of parturition; and, 3) July to October, a period of comparative reproductive quiescence. Differences among catagories were determined using single classification analysis of variance with a two-sided hypothesis. Actual analysis was conducted by computer using the Michigan State University Bastat system. Immature individuals were excluded from the entire analysis; weights and uterine measures of pregnant females were also excluded.

Sex-age classes: Tamarins were divided into four sex-age classes; mature males, mature females, immature males, and immature females. The criterion used for the separation of immature from mature animals was the degree of pigmentation of the suprapubic and the circumgenital glands (gland length and width was also recorded, in mm). These apocrine and holocrine structures are unpigmented or very slightly pigmented in prepuberal tamarins (Epple, 1967a). Tamarins reach puberty at approximately 18 months of age (Hampton *et al.*, 1966); my observations on known-age animals indicate that the suprapubic gland becomes pigmented at 16-18 months of age. This change in pigmentation is striking and appears to be a reliable method of determining age. Body weight can also be used as a criterion of division, but it is less proximally related to the physiological changes which occur at puberty than is the degree of pigmentation of the suprapubic gland. Only 3 of 38 juveniles in the collected sample exceeded 425 g, no mature tamarins weighed less than this.

Food-habits analysis: Gastrointestinal tracts were preserved in 10 percent formalin as soon as possible upon returning to the laboratory. The esophagus, jejunum, and rectum were secured with string to prevent loss of internal materials. Fixed food material was examined as time permitted.

In analysing the material, the small intestine, large intestine, and caecum were first measured (in mm). Stomach contents and identifiable intestinal contents were then taken from the gastrointestinal tract and placed in petri dishes. A dissecting scope aided in separating this material for measurement. Insects were identified to order; plant material was given a number and preserved in 95 percent alcohol for subsequent identification (plant materials were identified by Dr. Robin Foster, University of Chicago). All foods were quantified volumetrically according to the water-displacement method outlined by Korschgen (1969). Tabulation follows the aggregate volume method of Martin *et al.* (1946).

No attempt was made to assess the availability of foods; hence no strict assessment of food preference is possible. Foods are listed according to volume and frequency of occurrence. As Korschgen (1969) indicates, however, "high frequency and high volume indicate a food of high quality or preference."

Smythe (1970a) and Fleming (1971) outlined the major phenological differences which occur annually in the Canal Zone. On the basis of their findings, I wished to compare the diversity and equitability of tamarin diets over three periods: 1) The dry season, mid-December to mid-April; 2) the first half of the wet season, mid-April to mid-August; and 3) the latter half of the wet season, mid-August to mid-December. Comparisons of diversity and equitability of both animal and plant material as measured by both volume and occurrence were made using the standard Shannon-Weiner function as found in Krebs (1972).

Parasites and their preservation: Helminths encountered while examining gastrointestinal contents were further preserved in AFA. Identification of helminths was undertaken by Capt. L. Hendricks of the Middle American Research Unit, Balboa, Canal Zone.

Ticks, which were attached to the nasal septum, were removed and preserved in 95 percent ethyl alcohol. Ticks were identified by Dr. K. Yunker, Rocky Mountain Laboratory, Hamilton, Montana.

Nasal mites were obtained by irrigating the turbinal bones with water and examining the effluent. The mites were preserved in 95 percent ethyl alcohol and mailed to Dr. F. Lukoschus, Katholicke Universitiet, Nijnegan, The Netherlands, for identification.

Blood smears and capillary-tube blood samples were obtained from the blood of 148 tamarins. The presence or absence of trypanosomes and microfilaria was determined through direct examination of thick and thin, giemsa-stained smears by Dr. O. Sousa and his staff at Gorgas Memorial Laboratory. The trypanosomes of 15 animals were identified using the techniques of direct blood smear examination, animal inoculation, hemoculture, and xenodiagnosis described in detail by Sousa *et al.* (1974).

Preservation of skin and skeletal materials: Flat skins or study skins were made of all collected specimens. Borax was used as a preservative, and skins were dried in an air-conditioned room to prevent putrification.

Excess tissue was removed from the skeletons; the skeletons were then placed in a dry, heated container for desiccation. Dried skeletons were shipped to the Michigan State University Museum, where their further cleaning was facilitated by the use of dermestid beetles. Both skins and skeletal material are housed in the mammalogical collection of the Museum, Michigan State University.

Skeletal measurements herein were made with needle point calipers to the nearest 0.01 mm. Canine measurements follow Kinsey (1972).

RESULTS AND DISCUSSION

Results: Estimates of Population Density

The strip census technique outlined in the methods section was used on 181 days during the study as part of the standard operating procedure. Data presented herein are from a 168-day subset of this period, and represent the information obtained from days on which the same 4340 m strip was sampled twice, from 0645-0830, and from 0830-1045 hours. These records were collected on 45 days during the 1973 dry season, 70 days during the 1973 wet season, and 53 days during the 1974 dry season. In all, 1458 km were traversed; 729 km during the prime activity period from 0645-0830 hours, and 729 km between the hours of 0830 and 1045.

Estimates of population densities (simply animals seen per square kilometer censused) are given in Table 2. Such density estimates are commonly found in the current primate literature. No estimates of precision are given, since the distribution of individual density estimates over days is highly skewed (Figures 2a, 2b, and 3). In and of themselves, these data are of little value; they are included here for heuristic purposes which will be explained in the discussion section.

Estimates of population density were also obtained from information on home range and territory usage by the two telemetered groups. Population density within the home range of the lowland group was

Table 2. Estimates of population density for the *S. oedipus* population in Rodman, Panama Canal Zone. January, 1973, to May, 1974.

Season	Time	Animals/km^2	Censuses(n)
Dry season, 1973	0645-0830	9.7	45
Dry season, 1973	0830-1045	4.2	45
Wet season, 1973	0645-0830	23.1	70
Wet season, 1973	0830-1045	6.5	70
Dry season, 1974	0645-0830	28.0	53
Dry season, 1974	0830-1045	11.0	53

Figure 2a. Number of tamarins seen per census of a 4340 x 50 m strip of forest. Rodman, Panama Canal Zone. Dry season of 1973.

Figure 2b. Number of tamarins seen per census of a 4340 x 50 m strip of forest. Rodman, Panama Canal Zone. Dry season of 1974.

Figure 2a and 2b.

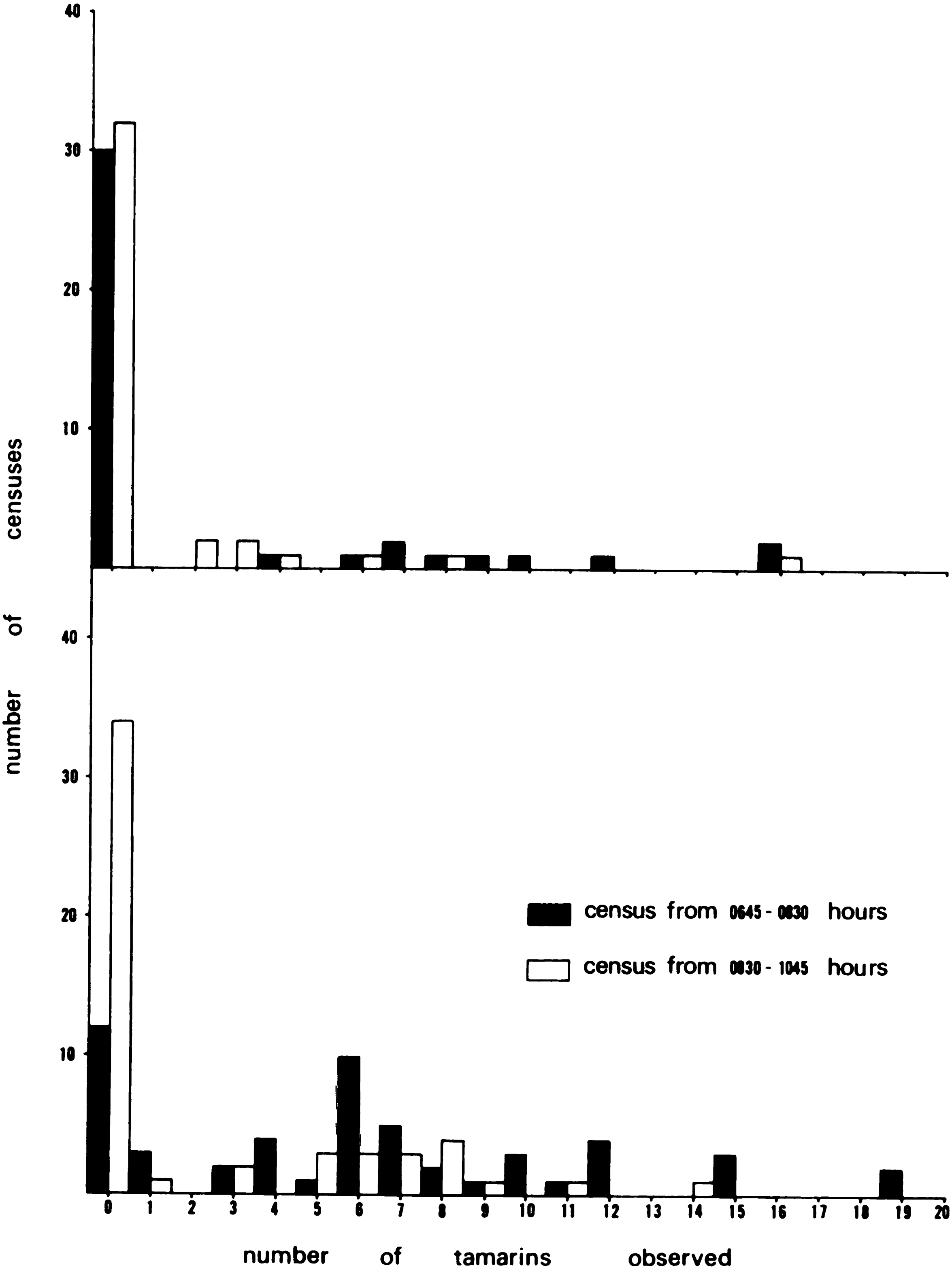
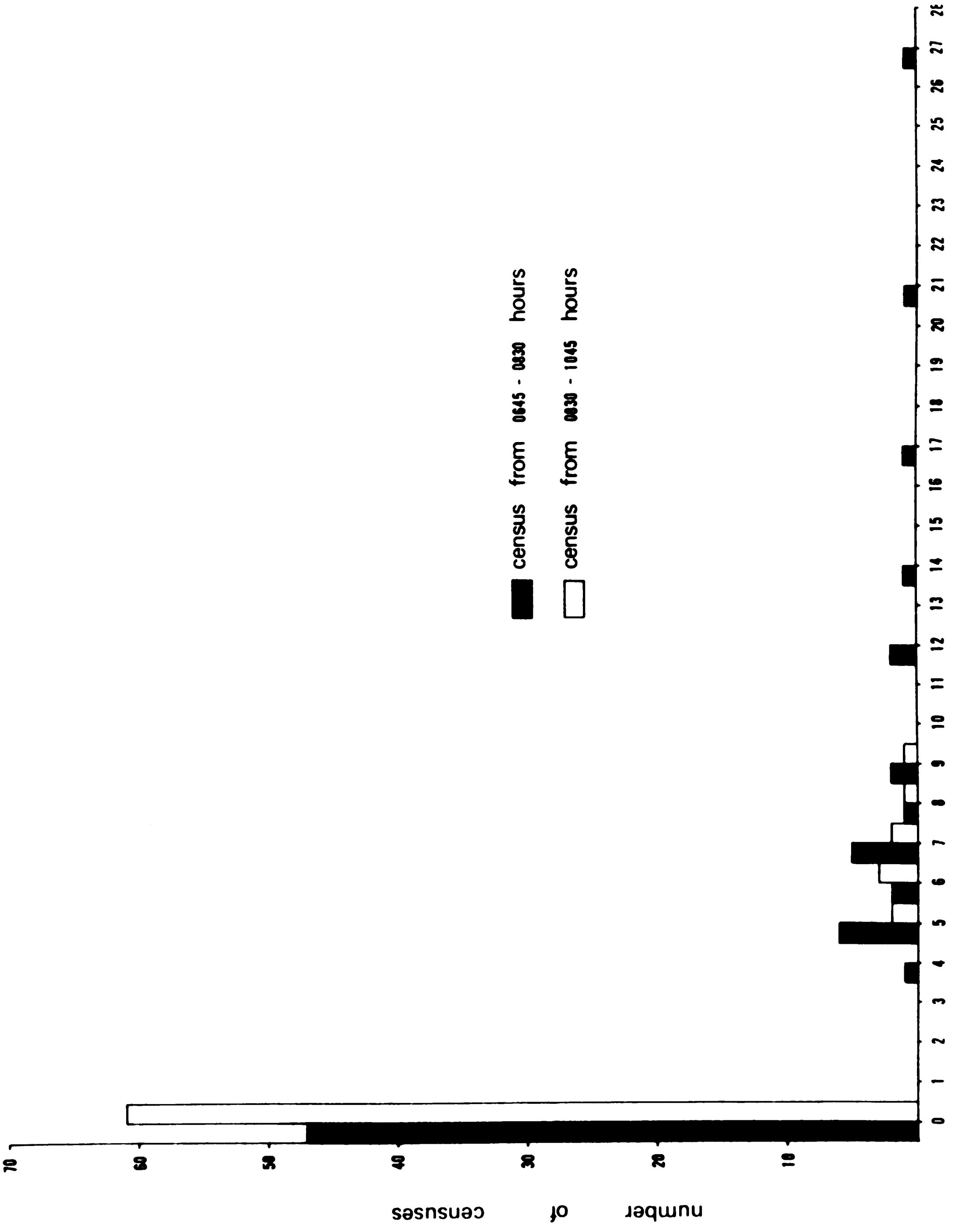


Figure 3. Number of tamarins seen per census of a 4340 x 30 m strip of forest. Rodman, Panama Canal Zone. Wet season, 1973.

Figure 3.


census from 0645 - 0830 hours
census from 0830 - 1045 hours
number of censuses
number of tamarins observed
10
20
30
40
50
60
70
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
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estimated at approximately 27 tamarins per square kilometer. The density estimate for the wet season home range of the upland group was approximately 36 tamarins per square kilometer. The dry season estimate of population density for the upland group's home range was about 20 tamarins per square kilometer. These observations, combined with a knowledge of approximate home range size and usage patterns for three non-telemetered groups, point to a year-around population density figure of about 20-30 tamarins per square kilometer.

Discussion: Population Density

As the populations of wild primates dwindle in the face of habitat destruction and overexploitation, the need to estimate primate numbers becomes increasingly important. If we are to preserve the rarer primate species from extinction, and if we intend to assure the existence of the viable populations that currently serve as reservoirs for those primates used in biomedical programs, then we must begin to gather data on population densities as the first step in the conservation program. In order to make appropriate management decisions, we must first have a knowledge of what species are still extant, where they are found, and in approximately what numbers. This basic information is necessary before the most rudimentary of management strategies can be employed. Census figures should not be misconstrued to be estimates of primate availability; allowable rate of "harvest" or "offtake" cannot be determined without a detailed knowledge of a species' population dynamics.

The current interests in primate conservation by such organizations as the Institute for Laboratory Animal Resources of the National Academy of Sciences-National Research Council, the World Health Organization, and the International Union for the Conservation of Nature have provided the impetus for much of the current study of Neotropical primates. Most studies involve estimates of population density; for several studies with which I am familiar, this is the major objective (see Southwick, C. H., 1975).

According to Thorington (1968b), direct visual censusing, *i.e.* going out into an area and counting all animals that can be seen, is the most common census method. This technique is most appropriate for larger, more visible species, where the recognition of individual group members precludes the possibility of repeated counts. Thorington (1972) also indicates that strip censuses are commonly used visual censusing techniques, particularly where estimates of relative abundance are required.

Thorington (1971), on the basis of his earlier work (Thorington, 1968b), concluded that, "... tamarin populations can be assessed in a meaningful way by strip censuses." In addition to visual estimates, he indicated that tamarin vocalizations might prove useful both in locating nonvisible individuals and in attracting tamarins from a distance through the use of the actual or taped calls of a captive animal (Thorington, 1972; Eisenberg and Thorington, 1973). He also suggested (Thorington, 1972), that radio telemetry might prove to be the most useful technique for studying marmosets (tamarins).

Data from strip censuses conducted during this study are presented in Table 2 and Figures 2a, 2b, and 3. On the surface, the differences in density estimates appear to be sufficiently gross to merit explanation. Typically, one might explain the presence of uniformly lower density estimates for the 0830-1045 census periods by observing that tamarins are most active and vocal early in the morning, and therefore density estimates taken after this time are likely to be lower. One might explain the differences between dry season estimates by noting that the dry season in 1973 was unusually severe, which forced groups to leave their upland ranges earlier than in that for 1974, when the moderate dry season allowed them to remain in the upland portions of their range over a greater number of censuses. Additionally the differences between wet season densities and the densities from the 1974 dry season could be attributed to increased foraging activity in response to lower levels of both insect and plant foods. These figures may not, however, be compared in this manner.

As evident from Figures 2a, 2b and 3, the distribution of the number of tamarins seen per census is decidedly skewed. Because this distribution in no way approximates a normal distribution, no estimates of precision can be meaningfully applied to the estimates of density (means). Thus the apparent differences between these estimates cannot be compared by parametric methods. Nonparametric tests are also inapplicable, since samples of this size require a modified comparison with an approximate "t" distribution, which is in fact an approximation of a normal distribution (Sokal and Rohlf, 1969). Even if nonparametric tests were applicable, a comparison of means for distributions where the modal values and the bulk of the observations equal zero would not be of great applied interest.

Because of the variability among censuses taken on different days, the high incidence of the mode, zero, and the considerable variability of the density estimates themselves, this method is impractical for censusing tamarins which inhabit densely-foliated habitats affording low levels of visibility.

The failure of this census method is due to the low probability of tamarin-observer contact in a large (20-40 ha) home range under conditions of low (30-50 m) visibility. If one were studying a species or population that occupied smaller home ranges and/or lived in a more open habitat that allowed greater visibility, the probability of contact would be increased, and the census technique would be more precise.

It might be argued that precision might also be gained by either increasing the number of transect censuses taken or by increasing the length of the transects. While this is undoubtedly true from a theoretical point of view, practical constraints prohibit such sampling in the habitats normally occupied by tamarins. The number of repetitive census taken during this study, and the length of the transect itself, exceed the time, energy, and monetary budgets for most field studies. The length of potential transects is further limited by chronological considerations, *i.e.* the transect must be short enough to be traversed over the period of peak activity if it is to yield the desired results. In the current study, transect length would be limited to that distance which could be traversed during the peak morning activity period, which is less than three hours in length.

The most reliable density estimates in this study result from data on the home range usage of two telemetered groups and from data obtained from the approximate home range sizes and usage patterns for three additional groups of marked animals. On the basis of these data, an all-season density figure of about 20-30 tamarins per square kilometer was obtained. While this figure is not precise, it allows one to compare the relative abundance of tamarins from this area with that of other areas. Such an index of relative abundance, rather than an exact estimate of animal abundance, should be the goal of most studies.

It should be noted that while some of the density estimates obtained during the strip census fall within the above range, the relationship of these figures with the true density are strictly fortuitous. A glance at Figures 2a, 2b and 3 reveals that on most days one would conclude that no tamarins existed in the study area. On other days, density estimates might reach 200 tamarins per square kilometer.

Results: Analysis of the Diet of the Panamanian Tamarin

A cautionary note must precede the presentation of data. The majority of tamarins collected were taken during the morning hours since they were more visible and vocal, and hence more vulnerable, at that time. Observations of foraging animals in Rodman indicated that tamarins spent much of this time foraging for insects rather than fruit. This particular feeding strategy is most efficient since winged insects (*e.g.* large Orthoptera, Lepidoptera), as poikilotherms, have a lower metabolic rate in the cool temperatures of early morning and are less likely to fly or escape, than during the warmer daylight hours. Janzen (1973) observed that sweep samples for tropical insects did not yield high numbers of insects until about 0800 hours (presumably after the insects' metabolic rates had reached levels conducive to activity). The proportion of insects in the diet, then, may be exaggerated. In support of this view, large quantities of fruit, presumably ingested during the afternoon and evening of the previous day, were found in the intestines. However, C. M. Hladik, in a personal communication to M. Moynihan (1970), indicated that this tamarin may eat relatively more fruit in the morning and relatively more insects in the afternoon.

The relative amounts of plant and animal material in the diet, and the diversity and equitability of these food items in the diet, are recorded by season in Table 3. The three "seasons", dry season, the first half of the wet season, and the second half of the wet season, are distinctly different in regard to the abundance and diversity of insects and plant phenology. The various components of the animal complement of the diet, and the seasonal incidence in the diet, are reported in Table 3. Identified fruits and their importance in the diet are recorded in Table 4.

Discussion: Analysis of the Diet of the Panamanian Tamarin

As Thorington (1970) indicates, the food habits of free-ranging primates are poorly known, despite the fact that foraging behavior is a major component of the daily behavioral repertoire of most primate species. A knowledge of the availability and distribution of a species' food resources is absolutely essential in both defining the ecological niche occupied by that species and in interpreting its social behavior. Deinhardt (1970), in reviewing the nutritional requirements of callitrichids, commented on both the paucity of data on the natural diet of marmosets and the contradictory nature of the

Table 3. Values for diversity (H') and equitability (E) of tamarin gastrointestinal contents, April 1973 - April 1974.

	Dry Season Mid December Mid April(n=41)	First half Rainy Season Mid April Mid August(n=48)	Second half Rainy Season Mid August Mid December(n=40)
Stomach, Total Volume (cc)	118.9	276.85	225.95
Stomach, Mean Volume (cc) per animal, ±SE	2.90±.38	5.77±.81	5.65±.78
Stomach, % Animal Components	44.34	63.70	35.92
Stomach, % Plant Components	55.66	36.30	65.08
Stomach, Animal Component, H' (vol.)	1.138	1.605	1.806
Stomach, Animal Component, E (vol.)	0.380	0.535	0.387
Stomach, Animal Component, H' (occ.)	1.880	2.284	2.008
Stomach, Animal Component, E (occ.)	0.627	0.761	0.715
Stomach, Plant Component, H' (vol.)	2.804	1.670	3.085
Stomach, Plant Component, E (vol.)	0.758	0.393	0.740
Stomach, Plant Component, H' (occ.)	3.261	3.811	3.564
Stomach, Plant Component, E (occ.)	0.882	0.909	0.855
Intestine and Caecum, Volume plant material (cc)	285.10	483.75	633.55
Intestine and Caecum, Plant Component, H' (vol.)	3.545	3.451	3.485
Intestine and Caecum, Plant Component, E (vol.)	0.697	0.725	0.733
Intestine and Caecum, Plant Component, H' (occ.)	4.563	4.179	4.132
Intestine and Caecum, Plant Component, E (occ.)	0.897	0.846	0.869
Intestine and Caecum, Animal Component (occ.)	2.639	1.939	1.700
Intestine and Caecum, Animal Component (occ.)	0.713	0.646	0.658

Table 4. Identified plant components of the diet of *S. o. geoffroyi*, based on observations in the field and the stomach and intestinal contents of 129 individuals collected from April 1973 to April 1974.

Palmae
  Desmoncus sp.
  Bactris balanoidea (Oerst.) Wendl.
  Scheelea rostrata (Oerst.) Barret.
  Corozo oleifera (H.B.K.) L. H. Bailey
Araceae
  Philodendron sp.
  One species of undetermined genus
Bromeliaceae
  One species of undetermined genus
Smilacaceae
  Smilax sp.
Zingiberaceae
  Two species of undetermined genera
Piperaceae
  Piper spp. (2)
  Piper reticulatum L.
Lacistemaceae
  Lacistema aggregatum (Berg) Rusby - B4
Loranthaceae
  One species of undetermined genus
Moraceae
  Cecropia obtusifolia - B3
  Cecropia exima
  Pourouma sp. - B3
  Ficus insipida Willd.
  Ficus sp.
  Castilla panamensis Cook
Polygonaceae
  Coccoloba sp. - C3
Euphorbiaceae
  Hieronyma laxiflora Muell. Arg.
Anacardiaceae
  Mangifera indica L. - A2
  Anacardium excelsum (Bert. & Balb.) Skeels - AB4
  Spondias mombin (*S. lutea* L.) - BC4
Sapindaceae
  Paullinia sp.
  Cupania sp.
Vitaceae
  Vitis sp.
  Two species of undetermined genera
Tileaceae
  Apeiba tibourbou Aubl.
  Luehea seemanii Tr. & Pl.
Dilleniaceae
  Doliocarpus sp.
Flacourtiaceae
  Zuelania guidonia Britt. & Millsp.
  One species of undetermined genus
Melastomaceae
  Miconia argentea (Swartz) DC. - A2
  Three species of undetermined genera - B1, B1
Passifloraceae
  Passiflora spp. (2)
Myrtaceae
  Syzguim sp.
  ? *Eugenia* sp.
Sapotaceae
  Chrysophyllum cainito L. - A3

Table 4 (Cont'd):

- Annonaceae
  - *Annona spraguei* Safford - C3
  - *Annona* sp. - C2
  - *Xylopia aromatica* Baill.
- Chrysobalanceceae
  - *Hirtella americana* L.
- Leguminosae
  - *Inga* spp. (2) - A1, B2, C2
  - *Cassia moschata* H.B.K.
  - One species of undetermined genus
- Burseraceae
  - ? *Bursera* sp.
- Meliaceae
  - *Cedrela* sp.
- Malpighiaceae
  - *Byrsonima crassifolia* (L.) H.B.K.
- Solanaceae
  - *Solanum* sp. - B1
  - One species of undetermined genus - C1
- Rubiaceae
  - *Coussarea* spp. (2) - C2
  - *Randia* sp.
  - *Faramea* sp.
  - *Pittoniotis trichantha* Griseb. - C2
  - *Genipa americana*
  - *Alibertia* sp. - A3
- Guttiferae
  - *Vismia* sp.
- Cucurbitaceae
  - Two possible species
- Acanthaceae
  - ? *Mendoncia* sp. - A1

A - Dry season
B - First half wet season
C - Second half wet season
1 - 5-10% of diet by volume or occurrence in any trimester
2 - 10-20% of diet by volume or occurrence in any trimester
3 - Greater than 20% by volume or occurrence in any trimester
4 - Not present in stomach contents, but observed to be an important food source

data that are available. One might assume *a priori,* on the basis of their primitive, tri-tubercular molars (Hershkovitz, 1972), their relatively short gastrointestinal tracts -- indicative of insectivorous primates (Jones, 1972), and a highly-developed system of villi in their small intestines (Hladik, 1967), that callitrichids are, in general, highly insectivorous, and possibly frugivorous as well. However, Enders (1930) working with *S. o. geoffroyi,* reported only fruits and seeds from gastrointestinal contents, although he observed that captive tamarins showed a fondness for insects. Fooden (1964) found only fruit in the stomach contents of *Saguinus midas* collected in Surinam during the December-February rainy season. In contrast, Hladik (1967) estimated that the diet of *S. midas* contained about 1/3 insect material and 2/3 fruits, flowers, and seeds, and Jones (1972) considered the callitrichid genera *Callithrix, Cebuella, Leontideus,* and *Saguinus* to be euryphagus. Furthermore, Hladik *et al.* (1971), in an admittedly fragmentary description of the diet of *S. o. geoffroyi,* concluded that this tamarin utilized both fruit and a large number of insects.

Hershkovitz (1969) states that, "Marmosets also eat animals other than insects, such as worms, or small birds, and also seeds and much fruit when available, but insects appear to be the chief food, particularly at times when food is scarce." In summary, the majority of accounts indicate that most Callitrichidae are rather catholic in their food preferences.

Temporal distribution of food resources: As indicated earlier, the climate is markedly seasonal in the Dry Tropical Forest Life Zone (Holdridge and Budowski, 1956). The seasonality of rainfall, as one might expect, profoundly affects the availability of both fruits and insects, the two most important items in the tamarin diet. Rather than attempting to measure the seasonal availability of either fruit or insects, I relied on data compiled by others regarding gross phenological characteristics of the forests in Panama, and insect abundance in the Dry Tropical Forest Life Zone.

Janzen and Schoener (1968) discussed differences in insect abundance and diversity between wetter and drier sites in a Costa Rican Dry Tropical Forest during the dry season, and also discussed, both implicitly and explicitly, the differences between wet and dry season abundance and diversity. Their more pertinent findings and observations may be summarized as follows: 1) Insect abundance and diversity decrease over all habitats during the dry season. Smaller forms, because they are more subject to desiccation than larger forms, are most affected; 2) Immature stages, particularly caterpillars, are uncommon in all habitats during the dry season; 3) Biomass of all insects, including the large orthopterans and lepidopterans, increases as one moves from dry, upland sites to wetter, lowland sites; 4) Total dry weight of all arthropods (including spiders) decreases as one moves from wetter to drier areas, although the decrease is less severe than the decrease in numbers, since many of the larger forms persist, albeit in reduced numbers, at drier sites; 5) The greater proportion of some insect groups in respect to biomass (*e.g.*, Orthoptera, Hemiptera, Coleoptera) means that predictions made concerning the biomass and adaption of vertebrate predators in the understory should give disproportionate weight to the properties and changes in abundance of these more abundant prey groups; and

6) During the dry season, an insectivore which specializes on a particular taxon is more likely to encounter its prey in the wetter, lowland area than in the drier, upland areas. The reverse situation is postulated for the wet season, when insect biomass should be greater in upland areas rather than lowland areas. From this last suggestion, one might infer that lowland habitats harbor fairly stable insect populations, while the insect populations inhabiting upland areas experience periods of population irruption followed by rapid decline.

An account of the seasonal variation in fruit availability in tropical monsoon forest on Barro Colorado Island in the Panama Canal can be found in Smythe (1970a, b). While the forest on Barro Colorado is more mature and the climate there is somewhat wetter than that found in the study area, both support many of the same tree species, and both areas experience marked seasonal changes in phenology due to the yearly monsoon pattern of precipitation. The timing of phenological changes by tree species common to both areas is roughly the same. This is expected since rainfall is dependent upon the pervasive trade winds, and these two localities, which are less than 25 km apart, are not separated by major orographical barriers.

Smythe (1970a, b) divided fruits into two categories: Type 1, fruits with diameters greater than 1.5 cm, and type 2, fruits with diameters less than 1.5 cm. While tamarins do feed on type 1 fruits, type 2 fruits are the mainstay of their diet. In general, the seeds of type 2 fruits are dispersed by birds and small mammals (Hladik, 1967; Smythe, 1970a; personal observations), and usually pass through tamarin gastrointestinal tracts intact.

The primary fruit peak begins with the coming of the rains in mid-April or early May and continues until about the middle of August (Smythe, 1970a; Fleming, 1971; personal observation). The greater biomass of fruit observed during this period is due to the increased number of all species in fruit, but is primarily attributable to the abundance of the large type 1 fruits. The secondary peak of fruit abundance noted by Smythe on Barro Colorado Island did not occur in the study area. Type 1 fruits are almost nonexistent from mid-August to mid-April. The fruiting of smaller, type 2 fruits is, however, more evenly distributed throughout the year (Smythe, 1970a, b; personal observations). Nevertheless, the biomass of type 2 fruits is quite low in the late wet season (October, November, and the first half of December), and remains low throughout the dry season (mid-December to mid-April).

Thus the tamarins in the study area must survive a period of both insect and fruit scarcity from the latter part of the wet season through the dry season. Foraging activity comprises a larger proportion of the tamarin's daily routine, particularly in upland areas, and patterns of spatial utilization change as upland groups move to lower, moister habitats in order to secure both insect and plant foods. The volumes of food found in tamarin stomachs at this time of year tend to be lower when compared with values for the first and second halves of the wet season (Table 3). However, variability of individual stomach volumes renders this comparison rather imprecise ($F = 2.792$, $.1 > p < .2$, using log-transformed data). Adult tamarins collected during the dry season also weighed considerably less than adults weighed during the last half of the wet season ($\bar{x} = 484$ g vs. $\bar{x} = 530$ g; $F = 23.732$,

$p < .002$). While the occurrence of recently-matured tamarins in the sample may have been responsible for a portion of the difference, the loss of weight by adults during this period of stress is a real phenomenon. The omental fat reserves accumulated during the type 2 fruit peak in the wet season are almost totally absorbed during the dry season, and individuals lack their earlier robustness. The effects of the food shortage in the late wet season on various Panamanian mammals are discussed in Smythe (1970a, b) and Mittermeier (1973).

Spatial distribution of food resources: The preferred habitats of the Panamanian tamarin are the early seral stages of second growth. The distribution of these cover types was patchy, but the patches of second growth in the study area were very large. In fact, areas of early second growth were the predominant cover type. The spatial distribution of both insect and fruit resources within these patches may be characterized as being dispersed and of low density. The insect types favored by tamarins are most abundant in areas of low brush and in the vine covered trees bordering the forest edge. "Edge" habitats contain more surface area per unit ground area than level stands, and the productivity in regard to both plant and animal biomass is greater here than in the mature forest. This well-known "edge effect" is discussed in many ecology texts (*e.g.*, Odum, 1971). The large folivorous insects sought by tamarins are themselves dispersed in space due to the ubiquitous dispersion of their food resources. Thus the tamarin must travel widely to capture insect prey. Tamarins do not forage cooperatively, but rather as individuals in a loose group. Most foraging for animal foods occurs at 2-15 m above the ground, although at times one may observe them foraging in the tops of such trees as *Anacardium excelsum,* 20 m or more above the ground. Similar observations were made by Moynihan (1970). Once, however, I came upon a group of tamarins foraging for grasshoppers in the tall grass bordering a road, and on another occasion, during the dry season, I observed a single animal foraging for insects among the leaves on the forest floor.

As indicated above, the plant foods most commonly utilized by tamarins are dispersed by birds and small mammals. It follows that within the large patches suitable for their growth, the plants which bear these fruits are scattered rather than clumped, and that, spatially, these fruit types comprise low density resources.

Altmann (1974) observed that low density, dispersed resources are most efficiently exploited by small social groups utilizing partitioned (territorially discrete) home ranges, where insect and plant resources necessary for sustenance are usually available throughout the year. In upland areas, both fruit and insect biomasses alternate between prodigious wet season highs and abyssmal dry season lows. During the wet season, individual food items remain dispersed, but their overall density in the patch is so high that the patch itself may be considered an abundant food source. Such a temporally delimited food source is most effectively used by groups with overlapping home ranges. This manner of spatial utilization was used by *S. o. geoffroyi* groups inhabiting a seasonally dry upland area. Nomadism, another efficient mechanism for using temporally delimited resources, was not observed, but long-distance travel by upland groups to lowland areas was observed during the dry season.

Altmann (1974) would predict the existence of large group size given abundant resources. However, the small group size noted in upland groups may be a parsimonius concession to conditions during the six months of the year when food is scarce. Phylogenetic history may also be an influencing factor here.

The analysis of the diet of almost any mammal, let alone one living in a tropical habitat exhibiting a high diversity of plant and animal life, is an ambitious undertaking, and may require years of painstaking collection and effort. The results presented herein must be considered a preliminary estimate of the diet of *S. o. geoffroyi*. It should be stressed, however, that this estimate, incomplete as it is, is the most detailed and quantitative estimate to date of the diet of any of the Callitrichidae, and, with the possible exception of the work by Hladik *et al.* (1971), of any Neotropical primate species.

The stomach contents of this tamarin lend themselves well to quantitative analysis since, in general, individual food items are poorly masticated. Many fruits are swallowed whole, and the insects, while chewed more thoroughly, can be separated easily due to their colorful and distinctive chitinous exoskeletons. It is also possible to identify and measure the relative volumes of seeds and fruits in the intestines; the frequency of occurrence of insects may also be determined because of the longevity of their durable chitinous remains. Analysis of the intestinal material greatly increased the number of fruits in the dietary estimate; two additional orders of insects were recorded as well.

Components of the diet: Arthropods and small vertebrates comprised almost one-half (49.5 percent) of the aggregate volume of the stomach contents examined. While this estimate may be too high due to the behavioral biases mentioned above, the figure does demonstrate that animal material is an important component of the diet. As noted in Table 3, the importance of the animal complement of the diet varied seasonally, as did diversity and equitability of the components of the diet.

Diversity of animal components by volume was lowest during the dry season, when large orthopterans and coleopterans formed the bulk of the diet, and increased through the wet season. Equitability by volume, however, was greatest during the first half of the wet season, when insects of small and intermediate size were presumed to be abundant. The equitability values for dry season and late wet season were lower due to a dependence on fewer, but larger, prey items in fewer categories. Diversity and equitability values based on occurrence of food items in the sample favor the first half of the wet season, but differences among seasons using this measure are probably non-significant. On the other hand, the diversity and equitability values based on the occurrence of insect types in intestinal contents may be a more useful measure since this analysis permits the sampling of animal types taken over a longer time period. The high diversity and equitability values for the dry season indicate that the tamarins took a variety of animal foods, and probably captured what they could find rather than expending time and energy in the search for the more preferred foods.

The incidence and proportion of arthropod and vertebrate prey items in the diet of 129 collected tamarins are summarized in Table 5. The importance of each category in the diet will be discussed separately

Table 5. Seasonal distribution of animal components in stomach contents of *S. o. geoffroyi*.[1]

	Dry Season (mid-Dec.-mid-April)[2]		1st half Wet Season (mid-April-mid-Aug.)[3]		2nd half Wet Season (mid-Aug.-mid-Dec.)[4]		Total Over Year[5]	
	%Volume	%Occurrence	%Volume	%Occurrence	%Volume	%Occurrence	%Volume	%Occurrence
Orthoptera	77.35	63.4	65.89	79.2	75.91	80.0	70.46	74.74
Lepidoptera	0.19	4.9	15.37	45.8	15.90	32.5	12.93	28.68
Coleoptera	9.38	12.2	9.36	33.3	0.99	7.5	7.17	18.60
Lizard (Iguanidae)	10.43	2.4	2.67	2.1	---	---	3.29	1.55
Spider (Araneae)	0.95	7.3	2.72	16.7	6.90	17.5	3.51	13.95
Homoptera	---	---	3.91	14.6	0.12	7.5	2.26	3.22
Hemiptera	1.52	4.9	0.06	4.2	0.06	2.5	0.31	3.88
Hymenoptera	0.09	2.4	0.02	2.1	0.12	5.0	0.06	1.29
Diptera	0.09	2.4	---	---	---	---	0.01	0.77

[1] Based on identifiable material only.

[2] Aggregate volume = 52.75 cc, n = 41.

[3] Aggregate volume = 176.35 cc, n = 48.

[4] Aggregate volume = 81.15 cc, n = 40.

[5] Aggregate volume = 310.25 cc, n = 129.

in the following paragraphs. Since no data were gathered regarding the availability of these food items, no definite statements can be made regarding food preference. However, as Korschgen (1969) indicates those foods comprising a high percentage of the aggregate volumes, and exhibiting a high frequency of occurrence, may be thought of as preferred foods.

Orthoptera: Orthopterans, which constituted over 70 percent of the aggregate volume, were easily the most important prey items. Hladik (1970) and Hladik *et al.* (1971) also reported that large orthopterans were major items in the diet of this tamarin. Large long-horned grasshoppers (Tettigoniidae) were the most important orthopterans encountered. During the dry season and late wet season the size of Tettigoniids taken by tamarins was larger than that observed during the rest of the year. These larger species (and also mature stages of species with smaller, immature forms extant in the early wet season) are probably more capable of withstanding the rigors imposed by the torrential rains during the late wet season and the effects of desiccation in the dry season than are their smaller relatives and immature stages. Walking sticks (Phasmidae) were the only other orthopterans present in the stomach samples. One cockroach (Blattidae) was discovered in the intestinal contents. The paucity of cockroaches in the diet was surprising, since cockroaches are readily eaten by captive tamarins and were abundant in old squirrel nests and leaf litter which accumulated in the crotches of trees. The rarity of cockroaches (which serve as intermediate hosts for acanthocephalans, Dunn, 1963) in the diet may help to explain the low incidence of this parasite in the collected samples (see section on helminths).

Lepidoptera: Both larvae and adult moths (Suborder Heterocera) and butterflies (Suborder Rhopalocera) were represented in the diet. Larval biomass, however, far exceeded adult biomass. Adult lepidopterans in flight are elusive prey for the tamarins; probably the majority of adults are captured in the early morning dampness when they are unable or less able to fly than during the latter part of the day. The tamarins do, however, attempt to catch adult lepidopterans throughout the day. The presence of lepidopteran wing scales in the turbinal bones of virtually every weaned tamarin attests to this prey's popularity. Lepidopterans, second only to Orthopterans as wet season food items, were all but absent from the diet in the dry season (Table 5). This is in keeping with the findings of Janzen and Schoener (1968), who noted that lepidopterans, and especially lepidopteran larvae, were practically nonexistent during the dry season.

Coleoptera: Large Coleoptera, primarily cerambycid beetles, were important food items in the dry and early wet seasons. Janzen and Schoener (1968) stated that large coleopterans were among the three common orders of large insects conspicuous during the dry season. Their presence in stomach samples in the dry season supports this. The increased frequency of occurrence of coleopterans in the diet in the early wet season might be predicted on the basis of the existence of more equitable environmental conditions for most insect species at that time. No explanation is offered, however, for the absence of these insects in samples taken during the late wet season.

Homoptera: A number of small homopterans of the family Cicadidae were present in stomach samples taken in the wet season. Homopterans are of very minor importance in this tamarin's diet.

Hemiptera: Hemipterans of the family Reduviidae were found in five stomachs. Low volumes and low frequency of occurrence of this insect family should indicate that it is probably not a preferred food. It should additionally be observed that the dry season values for this order are low, despite the fact that Janzen and Schoener (1968) found Hemiptera to be one of the three fairly abundant orders during the dry season. No individuals of the Triatominae, which serve as vectors for trypanosomiasis, were encountered. This implies that the high incidence of trypanosomiasis present in Panamanian tamarins (see section on blood parasites) is due more to an active host-parasite relationship rather than to the ingestion of the vector and associated pathogens by the monkey.

Hymenoptera: Only ants (Formicidae) were encountered in the sample. These may have been taken incidently as the tamarins foraged on fruits.

Diptera: The one dipteran found in the sample was probably ingested incidently with fruit.

Thysanoptera: Thrips, which were probably ingested with fruits, were occasionally found in the intestinal contents.

Araneae (Spiders): Spiders were relatively common components of the diet, particularly during the wet season. The majority of spiders utilized appeared to be large and medium-sized orb weavers.

Vertebrata: Two stomachs contained the remains of Iguanid lizards, one of which was identifiable to the genus *Anolis*. While the animal biomass gained per lizard captured is high, lizards are apparently uncommon items in the *S. o. geoffroyi* diet.

Tamarins were also observed eating bird eggs, although no evidence of eggs was seen in the stomach samples. This primate also eats nestling birds (H. Van Horn, pers. comm.).

Plant complement of the diet: A total of 101 fruit types thought to be distinct species were obtained from the gastrointestinal tracts of collected tamarins. The flowers and fruits of seven additional species were eaten by tamarins in the study area. Of the 108 species, 69 were identified to family, 54 (at least tentatively) to the generic level, and 26 to species. Since many trees fruit only every other year, and since Panamanian tamarins occupy a wider range of habitats than that sampled, the probable number of plants used by this monkey for food is much higher.

In Table 4 the identified plants are listed by family; their relative importance in the diet is indicated by footnotes. Those species without footnotes are considered to be of minor importance, at least under the environmental conditions which prevailed during the study. Most plants listed have fruits, in the broadest sense, or seeds, which tamarins utilize. However, for three trees, *Cassia moschata, Byrsonima crassifolia,* and *Luehea seemanii,* only the flowers were observed to be eaten. For a fourth, *Cedrela* sp., the new leaf buds are the only portions of the plant having gustatory appeal for tamarins.

In Table 3, the diversity by volume of plant material in the stomach contents is shown to be lowest during the first half of the wet season and highest in the second half. The first value appears to be out of place, since this time period should mark the time of greatest diversity for available food species. This apparent anomaly is due to the fact that the fruit of one plant, *Cecropia obtusifolia*, accounted for 69 percent of the aggregate volume of plant material. The selection of this fruit over all others at the time of greatest fruit diversity indicates a very strong preference for this fruit. A glance at the diversity of occurrence values for stomach contents reveals that the values correspond with the expected trend based on the phenological information discussed previously. It is apparent from the first wet season values that those tamarins which fed heavily on *C. obtusifolia* also "snacked", as it were, on a wide variety of other plant material.

The volume of plant contents in the intestine was lowest during the dry season and highest during the two wet season trimesters. The low dry season value is undoubtedly due to the scarcity of fruits during that season. The intermediate value recorded for the first half of the wet season, when fruits are most abundant, indicates, in light of the plant/animal ratio listed above, that, given an abundance of animal material and an abundance of plant material, the tamarins will exploit the former over the latter. The high value recorded for the third trimester is indicative of the shift from animal to vegetable material as insects become scarcer late in the wet season, and also of the availability of fruits during at least the first half of the trimester.

The diversity of plant material in the intestine appears to be slightly higher in the dry season than in the other trimesters. This reflects the usage of a wider variety of plants, each of which is relatively uncommon. The low equitability value for dry season volume is attributable to the predominance of *Alibertia* sp. (33 percent) and *Miconea argentea* (11.2 percent) in the sample. The equitability by occurrence of dry season plant materials provides a more realistic assessment of the situation.

Miscellaneous materials: One cubic centimeter of red clay was recovered from the stomach of one tamarin collected during the dry season. The clay may have been ingested for its mineral content.

Ticks, primarily nymphs of the genus *Amblyomma*, were recovered from the stomachs of eight tamarins. These, and the tamarin body hair found in most stomachs, are probably ingested during grooming behavior.

Results: Utilization of Time and Space

Quantitative measures of daily activity and habitat usage reported herein result from detailed observations of one tamarin social group, the lowland group, which occupied a site along a tributary of the Rio Velasquez. The majority of the quantitative measurements are based on 26 complete days of radio tracking during the wet season and 3 during the dry season. Other data were obtained from the remainder of over 500 hours of tracking the lowland group. The home range size of the lowland group and degree to which that range was overlapped by other social groups, are compared with that of the upland group, which occupied a seasonally dry hillside site. Home range size and usage for the upland group are based on more than 100 hours of radio-tracking for 14 wet season days and 17 dry season days. Other data regarding the upland group home range size and the degree of overlap by other groups result from frequent observations in this group's home range over the course of the study.

Initiation of daily activity: I define initiation of daily activity as the time when the first group member left the roost tree. Signs of activity were seen before this, including the movement of group members in the roost tree and/or urination and defecation. These behaviors were quite variable; thus the time the first animal left the tree was used as the criterion for the beginning of daily activity.

I observed the egress of apparently undisturbed (by me) tamarins from roost trees on 35 days. The average time of egress was official sunrise time (local) plus 11.7 minutes, with a standard deviation of ± 22 minutes. Available light at that time of morning varied with the cloud cover and the density of vegetation surrounding the roost tree. On a few days a flashlight would have been useful in approaching the roost tree at the time the tamarins left it, although I avoided using one for fear of disturbing them. On these days it would not have been possible to observe animals leaving the tree were it not for the fact that the roost trees were "backlighted". On other days, it was light enough to read when the tamarins began their diurnal activity.

Extremely early and extremely late times of activity initiation appeared to be roughly correlated with conditions which influenced the cessation of activity on the previous day. For example, when heavy rains caused the tamarins to cease their movements in mid afternoon, activity began earlier the next morning. Conversely, when the tamarins foraged after the time of official sunset, they tended to become active somewhat later the following day.

Cessation of daily activity: Tamarins of the lowland group were observed entering the roost trees on 47 occasions. The average time of entrance was official sunset time (local) minus 34.2 minutes, within a standard deviation of ± 33.7 minutes. Heavy afternoon rains which continued until after dark had the effect of depressing this average. In general, however, group activity ceased at least one half hour prior to sunset. Light levels on most days would have allowed foraging for an hour or more following the cessation of daily activity.

Total activity time: Average activity time (minutes) of the lowland group for 26 wet season days was 676 ± 62 S.D. Daily activity time ranged from 426 minutes, for a day when heavy rain fell from 1410 hours until dark, to 731 minutes. Total activity time for 14 days in the early wet season (May-July) did not differ from activity time observed for 12 days during the late wet season (August-November; $F = .113$, $p > .75$). Rainfall, which was fairly evenly distributed within and among days, did not suppress activity in any one time period. A comparison of the total activity time for each of 3 dry-season days with mean wet-season total activity-time using a technique for comparing single observations with means of samples (Sokal and Rohlf, 1969) indicated no significant differences ($p > .1$ for all tests).

Quantification of daily activity: A summary of daily activity using linear distance travelled (path distance) as the criterion is presented in Table 6. The highly significant Chi square value ($p < .001$ 6 d.f.) indicates that distance travelled over time periods is not proportional to the available time within periods. A definite activity pattern is apparent -- tamarins travelled significantly farther than one would expect during the early morning hours, began to slow down in late morning, experienced a lull in activity during midday, and resumed rapid travel at significantly higher rates than one would expect on the basis of available time during the late afternoon and evening hours. The behavioral significance of this pattern will be discussed.

Characteristics of trees used as roosts: Tamarins were observed on their night roosts on 61 occasions. At least seven tree species were used as roosts; many were used repeatedly. On six of the 26 days of radio-tracking, the lowland group returned to the same roost which it left that morning. A summary of tree types and frequency of usage is presented in Table 7.

Trees used were primarily of two types: tall, usually evergreen trees such as *Anacardium excelsum* which possessed broad, leafy crowns; or shorter, often deciduous trees which supported dense tangles of evergreen vines. The mean height of the roost above the ground was 16.0 ± 3.5 m (SD) in the former type and 6.6 ± 1.7 m (SD) in the latter tree type. The mean height above the ground of all roosts was 14.0 ± 5.0 (SD). Tamarins roosted in the crown or within tangles of vines; tree cavities were not used, although they existed.

Table 6. Activity pattern of the Panamaian tamarin, *S. oedipus*, based on linear distance travelled during hourly periods over 26 wet-season days.

Hourly Time Period	Proportion of Total Time(Pe)	Expected Linear Distance(m)	Observed Linear Distance Travelled(m)	x^2 Values	Proportion of Observed Distance(Pi)	"Family" of 95% Confidence Intervals on Pi
0500-0700	.062	3323	3898	99.842	.073	$.070 \leq P_1 \geq .076$**
0700-0900	.175	9379	9452	.568	.176	$.172 \leq P_2 \geq .180$
0900-1100	.180	9647	8865	63.390	.165	$.161 \leq P_3 \geq .169$*
1100-1300	.180	9647	7495	480.056	.140	$.136 \leq P_4 \geq .144$*
1300-1500	.180	9647	9202	20.527	.172	$.168 \leq P_5 \geq .176$*
1500-1700	.171	9165	9830	48.252	.184	$.179 \leq P_6 \geq .189$**
1700-1900	.052	2787	4853	1531.524	.090	$.087 \leq P_7 \geq .093$**
				$x^2=2244.159$		

* Observed proportion significantly lower than expected proportion (Pi<Pe).

** Observed proportion significantly higher than expected proportion (Pi>Pe).

Table 7. Night roosts of the Panamanian tamarin: Tree species and frequency of usage.

Tree Species	Number of Trees Used "n" Nights Nights 1	2	3	4	5	9	Total Trees	Total Nights
Anacardium excelsum	5	2	1	3	1	0	12	29
Spondias mombin	2	0	0	0	0	1	3	11
Cassia sp.	1	1	0	1	0	0	3	7
Luehea seemanii	0	0	1	0	1	0	2	8
Cupania sp.	0	1	0	0	0	0	1	2
Ficus sp.	1	0	0	0	0	0	1	1
Dead trees, vine covered	1	1	0	0	0	0	2	3
Total	10	5	2	4	2	1	24	61

The locations of the various roosts are given in Figure 5. While apparently suitable trees are located throughout the home range, the distribution of those used for roosts is distinctly clumped. Most roost trees are located in the northeast corner of the home range, far from the areas of overlap depicted in Figure 4. The others are clumped near the areas of overlap. This distribution, the relationship between roost tree site and the surrounding vegetation, and behavior at or near the roost trees, will be discussed.

Patterns of movement within the home range: The travels of the lowland group within its range were not random; they appeared to be influenced by a number of factors. The foremost were territorial behavior and distribution of food resources. As noted in Figure 4 a total of approximately 15 percent of the lowland group's home range (territory) was overlapped at four locations by four other social groups. Of the four groups, three were observed to engage in social altercations with the lowland group quite frequently; only one agonostic encounter was recorded between the lowland group and the fourth group. On 19 of the 26 days monitored, the lowland group entered, or passed within, vocalizing distance of at least three of the four areas of overlap which it contested with these three groups. The observation is not incidental; the lowland group often travelled rapidly to their areas of overlap, and usually two of the four areas were visited from early to mid morning, the time of which most territorial disputes took place. On six of the remaining seven days, the lowland group visited the areas of overlap of two of the three groups. On one day in 26, the group visited only one area of overlap.

Figure 4. A comparison of home range size and degree of overlap of a group of tamarins inhabiting a lowland area and a group inhabiting an upland area.

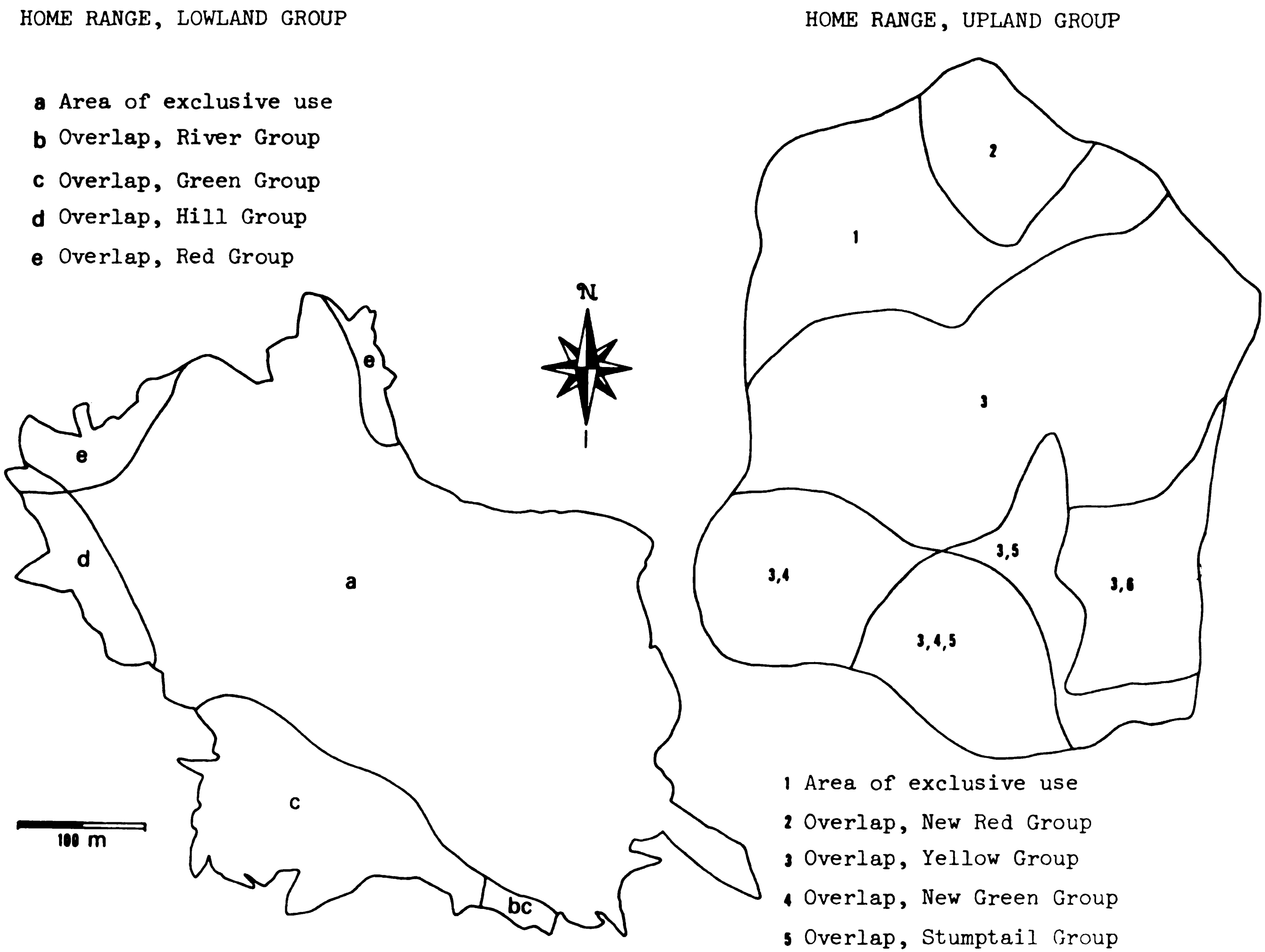
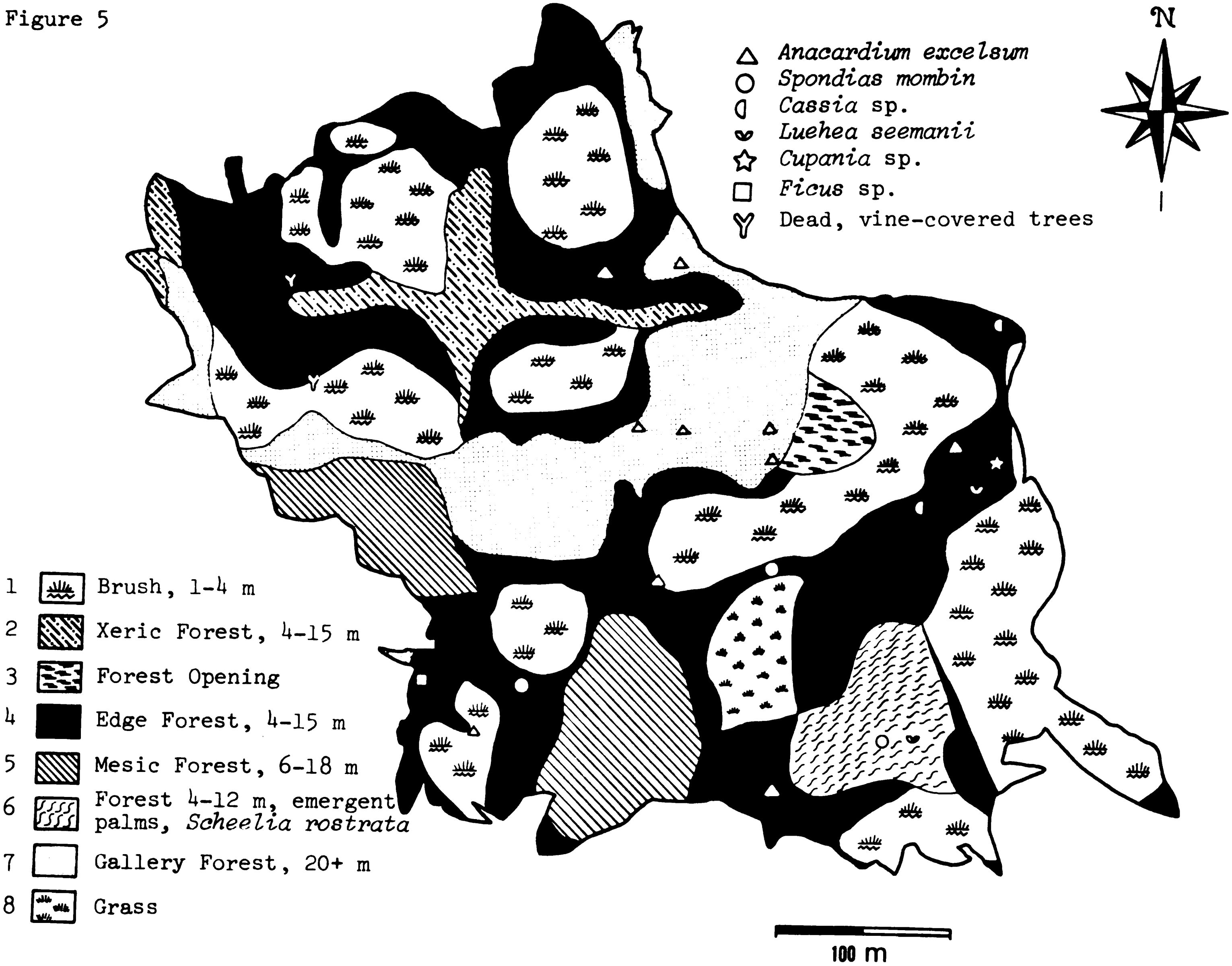

HOME RANGE, LOWLAND GROUP
a Area of exclusive use
b Overlap, River Group
c Overlap, Green Group
d Overlap, Hill Group
e Overlap, Red Group
a
bc
c
d
e
e
100 m
N
HOME RANGE, UPLAND GROUP
1
2
3
3,4
3,5
3,4,5
3,6
1 Area of exclusive use
2 Overlap, New Red Group
3 Overlap, Yellow Group
4 Overlap, New Green Group
5 Overlap, Stumptail Group
6 Overlap, Spur Group

Figure 4.

Figure 5. Distribution of habitat types and roost trees within the home range of the lowland group.

Figure 5


△ *Anacardium excelsum*
○ *Spondias mombin*
Cassia sp.
Luehea seemanii
☆ *Cupania* sp.
□ *Ficus* sp.
Y Dead, vine-covered trees
N
1 Brush, 1-4 m
2 Xeric Forest, 4-15 m
3 Forest Opening
4 Edge Forest, 4-15 m
5 Mesic Forest, 6-18 m
6 Forest 4-12 m, emergent palms, *Scheelia rostrata*
7 Gallery Forest, 20+ m
8 Grass
100 m

Food availability also influences movements. Marked changes in movement patterns were noted when *Anacardium excelsum, Lacistema aggregatum,* and a wild grape, *Vitis* sp., came into fruit. The response to fruits and stems of *A. excelsum* during the late dry season, a time of fruit scarcity, was particularly impressive. For several weeks the movements of the group appear to be highly correlated with the distribution of fruiting *A. excelsum* in the home range.

The distribution of suitable roost trees may also influence movement.

Daily travels within the home range: The mean linear distance or path length travelled per day was 2061 m, with a standard deviation of 402 m. Mean path length travelled per hour was 183 m (600 ft.). The mean travel distances (the distance between the two extreme locations on a given day, defined by Mason, 1968) was 468 m, with a standard deviation of 66 m. The mean area of the home range encompassed by the daily path travelled was 9.4 ha with a standard deviation of 0.6 ha. Thus approximately 36 percent of the home range was encompassed by the group's movement on any given day. Path distance travelled in the outer 1/2 of the home range did not differ from the path distance travelled in the inner 1/2 of the home range, $x^2 = .006$, 1 d.f., $p > .9$. Mean daily path length and home range size are compared with those of other Neotropical species in Table 8. Tamarins can, however, travel much faster than this. A single radio-tagged animal from the upland group averaged 952 m/hour over a one hour period, and the lowland group once travelled 221 m in six minutes enroute to a roost tree, a rate of 2210 m/hour.

Table 8. Daily path length and home range size for selected Neotropical primates.

Species	Path length/day (km)	Home Range Size (ha)	Reference
Saguinus oedipus geoffroyi	2.06±.40(S.D.)	26-32	Dawson (present study)
Saimiri oerstedi	2.5-4.2	17.5	Baldwin and Baldwin (1972)
Saimiri sciureus	---	14.3	Thorington (1968a)
Cebus capucinus	1.6+	85.2	Oppenheimer (1969)
Alouatta villosa	0.18	80-120	Carpenter (1934)
Alouatta villosa	0.29	14.4-20	Chivers (1969)
Callicebus moloch	0.57	0.4	Mason (1968)

Differential habitat usage as measured by time spent within habitats: The home range (=territory) of the lowland group was divided into eight habitat types (Figure 5). Time spent within each habitat type is summarized in Table 9. The significant Chi-square value ($p < .001$, 7 d.f.) indicates that the time spent in the various habitats is not proportional to habitat area. Low brush (0 - 4.0 m), forest edge (4.0 - 15 m) and the gallery forest of *Anacardium excelsum* may be considered preferred habitats, since they were used significantly more than expected on the basis of habitat area, while xeric forest, mesic forest (open canopy, 6 - 18 m), sparsely forested openings, and areas of grass were used significantly less. The habitat which included vine-covered trees with emergent palms (*Scheelia rostrata*) was used in proportion to its area. A Chi-square contingency test (7 X 26) indicated that time spent within the seven utilized habitats was highly dependent on the day monitored ($x^2 = 5264$, 6 d.f., $p < .001$). The variation in time spent within each of the habitats is quantified in Table 10. Note that the variability in usage was lower in the preferred habitats. Cumulative time spent in the outer one half of the home range was not significantly different from cumulative time spent in the inner one half of the range ($x^2 = .804$, 1 d.f., $p > .1$). Thus, there was no apparent tendency to use central areas of the home range more than peripheral areas. A single sample test (Sokal and Rohlf, 1969) was used to compare time spent within each habitat during each of three dry season days with the mean time spent in each habitat over the wet season. No significant differences were evident, with $p > .1$ for all comparisons.

Table 9. Habitat utilization by *S. oedipus:* Habitat preference determined by time spent among 8 habitats during 26 wet-season days.

Habitat Number	Area (Ha)	Proportion of total area (Pe)	Time Expected (min)	Time Observed (min)	x^2	Proportion of Observations (Pi)	95% "Family" of Confidence Coefficients on Pi
1	7.25	.274	4790.15	5631	147.601	.323	$.313 \leq P_1 \geq .333$**
2	1.21	.046	800.57	538	86.117	.031	$.027 \leq P_2 \geq .035$*
3	0.21	.008	141.37	44	67.605	.002	$.001 \leq P_3 \geq .003$*
4	9.28	.351	6127.22	8095	631.960	.464	$.454 \leq P_4 \geq .474$**
5	4.63	.176	3060.91	682	1848.866	.039	$.035 \leq P_5 \geq .043$
6	0.74	.028	491.13	492	.002	.028	$.025 \leq P_6 \geq .031$
7	2.55	.097	1686.66	1971	47.935	.113	$.106 \leq P_7 \geq .120$**
8	0.54	.020	354.99	0	$\underline{354.999}$ x^2=3184.545	.000	No confidence limits possible

* Observed proportion significantly lower than expected proportion (Pi<Pe).

** Observed proportion significantly higher than expected proportion (Pi>Pe).

Table 10. Variability in daily habitat usage by *S. oedipus* during 26 wet-season days.

Habitat	Time (min)		Distance (m)	
	$\bar{x}$	SD	$\bar{x}$	SD
1	216.58	97.84	559.39	158.70
2	20.69	21.08	67.69	55.48
3	1.69	5.12	4.28	13.13
4	311.35	83.49	943.39	265.20
5	26.23	27.35	145.05	114.93
6	18.92	23.24	70.15	88.07
7	75.61	68.65	271.39	121.07
8	0	0	0	0

Differential habitat usage as measured by distance travelled within habitats: The home range (territory) of the lowland group was divided into eight habitat types (Fig. 5). In Figure 6, the paths of group travel for the entire study period are recorded as lines. The patterns of usage in this figure are further elucidated by the information in Table 11, where the distance travelled within each habitat type is compared with the expected distance travelled per habitat type, based on the hypothesis that distance travelled within the habitat is proportional to habitat area. The significant Chi-square value ($p < .001$, 7 d.f.) indicates that habitat usage as estimated by distance travelled among habitats was not proportional to habitat area. Less travel distance was logged in areas 2, 3, 5, and 8 than expected, while more distance was logged in areas 4, 6, and 7 than expected. On the basis of this analysis, habitats 4, 6, and 7 are considered to be preferred habitats. The distance travelled in area 1 was proportional to the area of that habitat type in the home range. A Chi-square contingency test (7X26) indicated that the distance travelled within given habitat types was highly dependent of days samples ($x^2 = 34{,}713$, 6 d.f., $p < .001$). The variability of habitat usage within each habitat type is evident from Table 11. Two of the habitats (1 and 4) which were preferred by the tamarins have proportionally smaller standard deviations than those which were not preferred. The relatively high standard deviation for habitat 6 is due to its isolation as a single habitat block near the border of the home range. When habitat 6 was used, it was used intensively, as evidenced by both the time and distance measurements from Tables 9 and 11.

The lowland group vs. the upland group: A comparison of home range size and utilization: Home range size and the degree of home

Figure 6. Cumulative daily movements of the lowland group over approximately 500 hours of radio-tracking.

Figure 6.

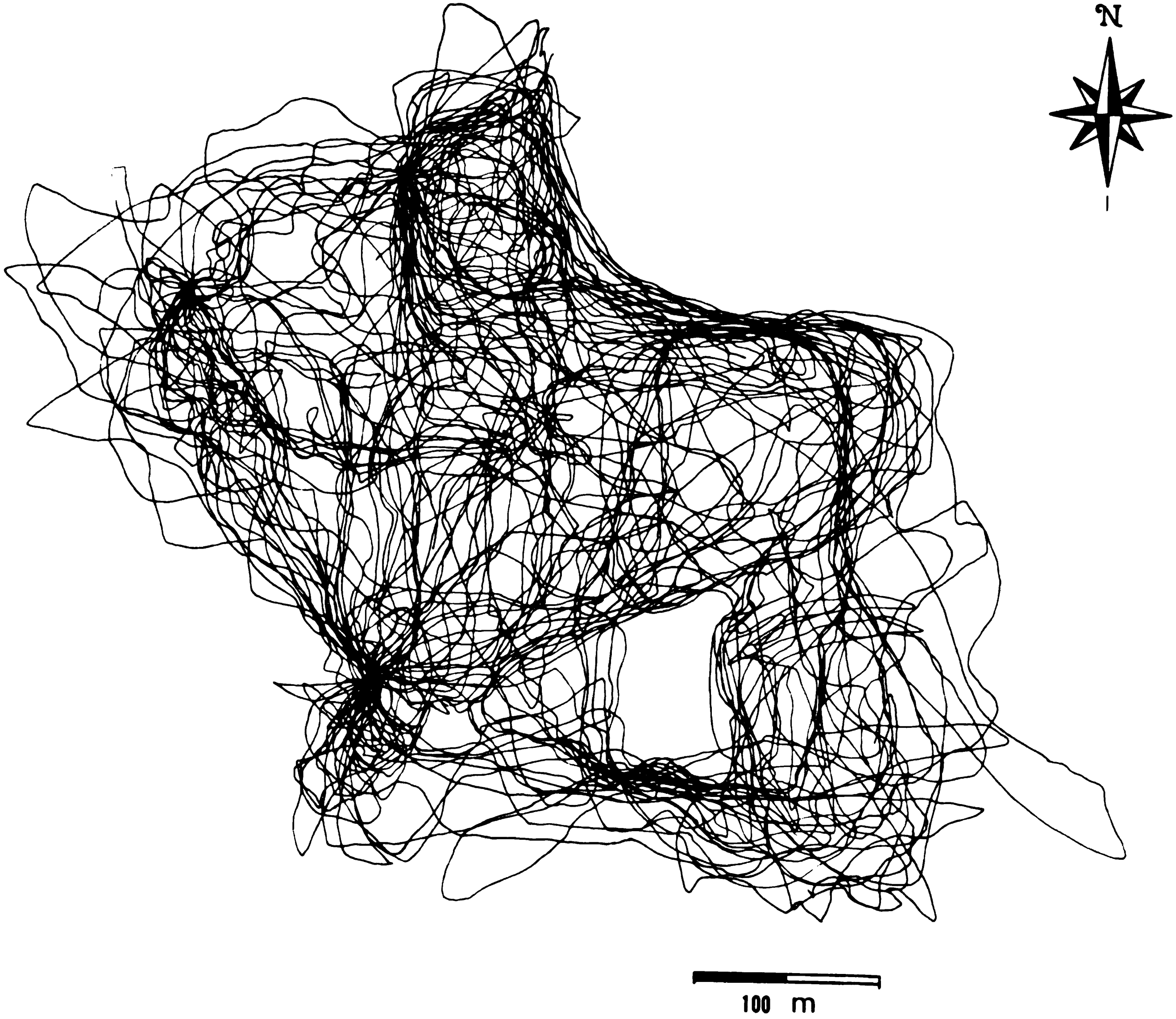


Table 11. Habitat utilization by *S. oedipus:* Habitat preference determined by distance travelled among 8 habitats during 26 wet-season days.

Habitat Number	Area (Ha)	Proportion of Total Area (Pe)	Expected Distance Travelled (m)	Observed Distance Travelled (m)	x^2	Proportion of Observations (Pi)	95% "Family" of Confidence Coefficients on Pi
1	7.25	.274	14709.57	14544	1.865	.271	$.266 \leq P_1 \geq .276$
2	1.21	.046	2458.38	1760	198.482	.033	$.031 \leq P_2 \geq .035$*
3	0.21	.008	434.12	111	240.011	.002	$.002 \leq P_3 \geq .003$*
4	9.28	.351	18815.46	24528	1734.438	.458	$.452 \leq P_4 \geq .464$**
5	4.63	.176	9399.42	3771	3369.931	.070	$.067 \leq P_5 \geq .073$*
6	0.74	.028	1508.15	1824	66.106	.034	$.032 \leq P_6 \geq .036$**
7	2.55	.097	5179.38	7056	680.077	.132	$.128 \leq P_7 \geq .136$**
8	0.54	.020	1090.11	0	1090.111 x^2=7381.021	.000	No confidence limits possible

* Observed distance travelled significantly lower than expected (Pi<Pe).
** Observed distance travelled significantly higher than expected (Pi>Pe).

range overlap with other tamarin groups are presented in Figure 4. The home range of the lowland group was approximately 26 ha in area. The lowland group defended this area as a distinct territory; during the wet season only about 13 percent of its home range was overlapped by the ranges of other groups. The home range size of the upland group during the first six months of the wet season encompassed an area of about 32 ha. During the late wet season and the dry season the home range included this area and at least 11 additional hectares. This home range was not defended as a fixed geographical entity, but was rather shared with five other groups through spatial and temporal segregation.

During the first six months of the wet season, upland areas appeared to support higher densities of tamarins than the lowland areas. A comparison of population densities in the effective home ranges of the lowland and the upland groups demonstrates this. If one apportions all areas of home range overlap according to the size of the groups using these areas and subtracts that proportion of the home range used by other groups from the total home range figure, one obtains a crude estimate of the foraging area, or the effective home range, available for that group. The density estimates arrived at in this manner are approximately 27 tamarins/km^2 for the lowland range and approximately 36 tamarins/km^2 in the upland range. It must be kept in mind that these figures result from data for only two groups, and must be regarded cautiously. They do, however, offer an objective estimate in support of my subjective impressions regarding population densities in the two habitat types.

Discussion: The Use of Time and Space

No animal exists in a vacuum; all living animals occupy three dimensional space during even the briefest moment of time. The location of an animal in space is the result of a multitude of interactions between that animal and the environmental milieu in which it finds itself, and, to a greater or lesser extent, chance. The coevolutionary history of the animal and the associated biota have a bearing on the use of space, as do more proximate ecological occurrences. Phylogenetic history is responsible for providing the animal with a potential behavioral repertoire with which to respond to environmental stimuli; impinging stimuli, the strength of the primary stimulus, experience, and the behavioral state of the animal will determine precisely how the animal reacts. Use of time and space, then, are dependent on the interplay of many ecological and ethological parameters. The purpose of this discussion is to attempt to interpret the patterns of temporal and spatial utilization used by Panamanian tamarins in light of available ethological and ecological information.

Before proceeding further, it is necessary to define two terms which will appear from time to time in the discussion. The first, home range, is defined as "The area in which an animal normally lives, exclusive of migrations, emigrations, or unusual, erratic wanderings" (Brown and Orians, 1970). For the second term, territory, this paper will follow the usage suggested by Noble (1939) and Burt (1943), which is any area defended against encroachment by extra-social-unit conspecifics. Definitions, such as that suggested by Schoener (1968), which require that the territory be an area of exclusive use for the occupant, are not flexible enough to account for the frequent acts of trespass which occur on the periphery of large territories.

Daily activity pattern: Moynihan (1970), in describing the habits of *S. o. geoffroyi,* observed that "unlike other diurnal monkeys with which I am familiar, and most other diurnal mammals and birds in the same habitats, these tamarins do not become active at, or very shortly after, dawn. In the wild they are never seen moving around until at least a quarter of an hour after it has become light. In most cases, they apparently do not get up until approximately three quarters of an hour, or more, after full light." He also observed that, "It is only approximately one hour or half hour before sunset that they gradually stop feeding and drift off in the general direction of their sleeping trees." He further states that with this unusual activity pattern, "... one wonders if the animals do not become torpid or semitorpid at night."

My data support Moynihan's (1970) observations. Unlike the squirrel monkey (*Saimiri sciureus*), another small insectivore-frugivore (Eisenberg *et al.,* 1972) whose activity pattern has been documented (*e.g.* Thorington, 1967; Baldwin and Baldwin, 1972), this tamarin neither begins foraging at dawn nor does it customarily forage in the twilight following sunset. Furthermore, my observations of roosting tamarins suggest that they may become torpid, or semi-torpid, at night, as Moynihan hypothesized.

If, for example, one waits for 10-15 minutes before approaching the roosting animals, they maintain their formation, and, if they respond to the observer's presence at all, they turn their heads groggily, stare at the observer, and then resume their former position. The same response can be elicited in the early morning hours. Apparent torpor has also been observed in *S. o. geoffroyi* housed under laboratory conditions (S. H. Hampton, pers. comm.).

Whether or not actual torpor does occur, the unusual activity pattern which precludes activity in the crepuscular hours is a real phenomenon which begs an explanation. At present, theories relating to the adaptive significance of this behavior must, because of the limited knowledge available, be regarded as conjectural. A few hypotheses, however, will be suggested.

Moynihan (1970) advanced the idea that this activity pattern was adaptive in that it temporally removed the tamarins from competition for insects with flycatchers, which forage extensively and intensively during crepuscular periods. While this view may have some merit, flycatchers, as indicated earlier, tend to specialize on smaller insects and flying insects, which are more difficult for tamarins to obtain and probably prohibitively "expensive" in terms of the tamarins' energy budget. Given the temporal segregation of the flycatchers and tamarins and the difference in the type of insects utilized, I find his suggestion that the similarities between many flycatcher calls and the vocal repertoire of the tamarins represent social mimicry to be unlikely. On the contrary, similarities between flycatcher and tamarin vocalizations are probably the result of the convergent evolution of vocalization frequencies which are most efficient in the general habitat occupied by both forms. If the vocalizations of the two forms were broadly overlapping in time, one would expect to find distinctly different types of vocalizations occurring in order to prevent the reception of extraneous auditory signals by either form.

A more probable explanation might be that the tamarin's activity may revolve around the time of optimal vulnerability of its insect prey. Large orthopterans, lepidopterans, and coleopterans, because of their low surface to volume ratio, warm at a slower rate than do the smaller insects. Hence, while the small insects favored by flycatchers are warmed quickly and become active shortly after dawn, these larger-bodied insects remain farther down in the foliage, gradually absorbing heat and becoming more metabolically active. The time of their greatest vulnerability to tamarins must occur when they are emerging from their nocturnal resting places and have not yet achieved their optimal capacity to escape.

A similar hypothesis might be advanced regarding their early cessation of activity. When the sun has dropped from its zenith and cooler temperatures and higher humidities prevail, flying insects and insects in the outer layer of the foliage become more numerous, and because of their locations, more vulnerable to flycatchers and gleaning birds than they were in the heat of the day. The large insects which the tamarins prefer lose their heat more slowly than the smaller forms because of their lower surface to volume ratio. Thus, they are relatively invulnerable to predation by non-aerial predators until quite late in the evening. The early cessation of activity by *S. oedipus*, may be a feasible response when insect food cannot be obtained, except at high energetic cost, until late in the evening. Cessation of activity and the assumption of an apparently torpid or semitorpid condition may have an additional value in predator avoidance. Small tamarin groups may be less capable of repelling predators than, for example, larger *Saimiri* groups, which may forage well after sunset (Baldwin and Baldwin, 1972).

The tamarin may also have adopted this behavioral pattern in order to escape competition from crepuscular (and nocturnal) insectivorous and frugivorous mammals. The night monkey, *Aotus trivirgatus,* which appears to be the nocturnal counterpart of *Saguinus* (Moynihan, 1964, 1970), is fairly common in the study area, and was occasionally observed in the crepuscular hours. An evolutionary history of widespread sympatry may be responsible for the temporal segregation of these two species. The wooly opossum, *Caluromys derbianus,* an abundant animal in Rodman, is another possible competitor that is temporally segregated from *Saguinus.*

Quantification of the daily activity pattern and behavioral attributes: Upon examining Table 9, it is apparent that tamarins travelled significantly farther than expected during the first two hours of the morning. The relatively longer distances logged are partially attributable to the tamarin's predilection for feeding on insects at this time of day. On the majority of days monitored, foraging began at or very near the roost; usually in areas of low, brushy vegetation, but occasionally in the top of *Anacardium excelsum,* 20 m or more above the ground. On other days, the tamarins travelled 100-200 m as a group and then began foraging after having passed over other areas which appeared to be equally as productive as the area in which they began foraging. Upon leaving the roosts, the monkeys began to forage individually and to move as a loose group through the forest. Group scatter at this time was usually 40-70 m. Foraging was generally extensive rather than intensive, hence the longer path length. Insects appeared to be the primary objective during at least the first half hour of the activity period, although fruit was taken occasionally. Approximately an hour after leaving the roost the emphasis in foraging activity shifted to fruits. Contact calls (called long whistles by Moynihan, 1970) which were commonly heard early in the time block became less frequent as the tamarins reduced their group scatter. During the latter portion of this time period and the beginning of the next the monkeys were often seen eating fruit in single trees and concentrated food patches. On the majority of days monitored, the group began to move as a unit toward areas of home range overlap between 0645 and 0800 hours. These movements added, in part, to the significantly higher movements per unit time before 0700 hours.

Most of the behavior involving intergroup encounters occurred between 0700 and 1000 hours; the major part of the distance travelled to areas of intergroup conflict was accomplished between 0700 and 0900 hours on 20 of 26 days. While foraging for both fruits and insects occurred en route to areas of overlap, the path of travel was much more linear than during the early morning hours, when the animals were scattered in their foraging. Upon reaching areas of overlap, the group often devoted much of its time to foraging. In two areas, *Spondias mombin* and *Inga* sp. were common and, during their fruiting seasons, were attractive sources of fruit.

The opposing group often did not arrive at the overlap area at the same time as the lowland group. Often the lowland group remained in the area for an hour or more before the other group appeared; on some days the other group did not visit the area of overlap at the same time as the lowland group did, if at all. In following the lowland group, I obviously could not remain at the area of overlap to determine whether or not the other group appeared at some other time during the day.

When the groups did encounter one another in an area of overlap, the behaviors observed were variable. Often a group would leave the area before the opposing group entered. One could frequently hear the "long whistle" vocalizations (Moynihan, 1970) of the incoming group before they were visible. As Moynihan (1970) indicates, "long whistles" are a bivalent signal which attract group members and repulse members of other groups. It seems likely that these calls enable the tamarin groups to mutually avoid one another. When the groups did come within visual contact of each other, the confrontations were accompanied by choruses of long whistles by both groups. Moynihan (1970) also observed that these vocalizations were the principal ones heard in intergroup agonistic encounters. In seven instances, chases occurred between members of opposing groups. In three instances actual physical contact was made. These physical contacts were punctuated by "rasping" vocalizations (a group of vocalizations defined by Moynihan, 1970).

Marking behaviors, *i.e.* "sit rubbing" and "pull rubbing" (Moynihan, 1970), and especially the former, appeared to be more frequent in areas of overlap than in other parts of the home range. However, since thick brush in all areas made observation of the animals difficult, comparable quantitative data were not obtained. Scent marking both preceded and followed agonostic confrontations, and sit rubbing also occurred in the absence of the opposing group. Pull rubbing, as Moynihan (1970) indicates, is rare except in the more intense behavioral situations, such as those involving overt conflict, or possibly the sudden appearance of terrestrial predator. Pull rubbing was observed only four times, twice following encounters involving physical contact with members of the other group and twice when the observer appeared to be the stimulus. Marking was usually initiated by the dominant (*i.e.* reproductive) female. The tamarins tended to perform their rubbing behaviors on protruding knots, stubs, and rough bark rather than on smooth branches. No evidence was found for the existence of fixed, customarily-used territorial markers or sign posts. While differences of opinion exist regarding the function and information content of scent marking behaviors (Epple, 1967b; Epple and Lorenz, 1967; Moynihan, 1970; Epple, 1972), they are an integral component of territorial behavior.

By approximately 1000 hours the tamarins had began moving out of areas of low brush and into the shade. (Thorington, 1968b, observed the same tendency in *Saguinus midas*). On 12 days the tamarins travelled less than 200 m from the area of overlap before slowing their pace and engaging in intermittent resting and foraging activities; on 10 days the group travelled relatively rapidly across the range to another area of overlap before their cadence of activity diminished. On 19 of the 26 days mid-day activity revolved around stands of *Anacardium excelsum* and the large, shady trees in Habitat 4. While activity did not stop between 1000 and 1500, path distance became significantly shorter than expected due primarily to frequent periods of quiescence and to less directionality in group movement. Individuals and subgroups foraged sporadically between rest periods, during which the tamarins sat relatively motionless in the trees or very occasionally sprawled full length on a branch. Autogrooming and allogrooming behaviors were seen more frequently during those hours than during the remainder of the day, with the possible exception of the first few minutes following periods of rain, when autogrooming was a common, and possibly obligatory, comfort behavior.

On most days the tempo of activity began to increase at about 1500 hours. Travel between this hour and dark was directional and relatively rapid, which resulted in significantly longer distances travelled over the last two to four hours of the day. While insects were taken during the late afternoon and evening, most travel seemed oriented toward fruit trees. The animals might travel 100 m or more in five or fewer minutes and then spend 15-30 minutes in a fruit tree. The path followed during late afternoon did not appear to be random; it appeared to be directed by the ultimate goal, the roost tree, and the location of fruit trees. That a given roost tree was the ultimate goal was indicated by: 1) The direct nature of the route of travel; 2) the fact that former roost trees and other presumably suitable trees were passed en route to the nights' roost; 3) the fact that individual roost trees were often used on several successive nights; and 4) the rapidity of group movement over the last 100-300 m before arriving at the roost. The rapid movement to roost trees, the direct movements between fruit trees, and the brief interludes of multidirectional foraging for insects, are responsible for the significantly higher rates of travel evident in the ultimate and penultimate time periods.

Roost trees: Location and associated tamarin behaviors: When the locations of roost trees (Figure 5) are compared with the map showing areas of home range overlap (Figure 4), it is apparent that most roost trees are located in the northeastern portion of the home range, while the remainder occur near areas of group overlap. Since apparently suitable trees are located throughout the area, the reason for this distribution of roosting sites is not apparent. One might surmise that the location of roosts is dependent upon a number of factors, the most important of which are patterns of territorial travel, which might be affected by intergroup relationships, and temporal variations in the availability of food.

Roost trees, in 22 of 24 cases, were either much higher than the surrounding vegetation and/or lacking extensive vine connections with other trees. This lack of physical connection with the surrounding strata might lessen the probability of detection by nocturnal, arboreal predators and might also provide an effective "lookout" from which to observe the surrounding vegetation before beginning the next day's activity.

I was able to observe clearly the tamarins on the roost in only 13 of the trees. In each case, the roost was located toward the periphery of the tree rather than close to the trunk. In all 13 instances a pad of small sticks, leaves and fibrous material was located in the multiple branches where the animals roosted. The presence of this material poses an interesting question, "Do tamarins build nests?" I saw no evidence of tamarins carrying large pieces of vegetation in their mouths or otherwise participating in nest building activity. The five "pads" which I examined, however, appeared to have been constructed masses of material instead of an accumulation of debris. They may have been constructed by squirrels, or partially constructed by tamarins. Regardless of their origin, these "pads" of vegetation did exist, and tamarins sat on them.

The existence of nest pads may be important in the epidemiology of trypanosomiasis with which these tamarins are heavily infected (Sousa *et al.*, 1974; see also section on blood parasites). The nest pad, which may remain moist during the dry season, harbors a variety of insect life. While no triatomine bugs were encountered in the five pads examined, the existence of the pads and periodic visitation by the tamarins suggest that such a vector-host relationship is feasible. This situation merits further study.

As indicated in the prior section, the tamarins often move both directly and rapidly to the roost tree. They also travel silently, without vocalizing. Rapid, silent movement to sleeping trees is probably advantageous in predator avoidance.

Upon reaching the roost the monkeys huddle together either on the pads discussed earlier or within a mass of thick leaves or vines. The tails are held forward and close to the body, as described by Moynihan (1970). Their heads are oriented downward and toward the center of the huddle, thus obscuring the white blaze on the head. Small infants are carried on the ventral sides of group members. This series of behaviors would seem to have the effect of making the animals less conspicuous while at the same time reducing individual heat loss through huddling.

If the tamarins were disturbed within approximately 10 minutes of assuming the huddling posture, they usually left the tree. On three nights I unintentionally disturbed the lowland group while trying to get close enough to see them. On these three occasions the huddle veritably exploded, with tamarins exiting in all directions. In each case the troop regrouped and settled into another roost tree within 15 minutes. On two other occasions the reproductive female left the group and wandered slowly away from the group, at the same time uttering low volume, high pitched, single notes of about a second's duration. After I followed her away from the roost tree, she returned to the group. This behavior pattern appears to be analogous to the wing-dragging of female birds protecting a brood. Further observations must be made to determine whether or not these behaviors are real components of the species' behavioral repertoire.

In the morning tamarins began moving in the roost at least 10 minutes before leaving it. Few vocalizations were given until after they had left the roost. Tamarins sometimes left the roost singly; at times two or three or the entire group left at once.

Effects of rain on tamarin activity: Measurable amounts of rain occurred on 21 of 26 tracking days. The loss of foraging time due to rain falling between initiation and cessation of activity averaged 15 minutes/day. This is a low figure, since one cannot determine how early the tamarins would have begun or ceased activity had it not been for the rain. Heavy rain, and prolonged rain, definitely affect tamarin activity.

Patterns of home range usage: That patterns of home range usage exist is evident from the above information having to do with activity over the day and the distribution of roost trees. The salient factors which influence these spatial and temporal patterns include territorial behavior, thermoregulatory behavior, anti-predator behavior, foraging behavior, temporal and spatial distribution of resources, and cover types. Upon comparing the travels of the lowland group (Figure 6) with the figure depicting those areas of the lowland group's home range that are overlapped by other groups (Figure 4), the relationship between movements and territoriality are obvious. When the accumulated travels of the lowland group (Figure 6) are compared with a map showing the cover types in the lowland group's home range (Figure 5), the relationship between cover type and usage is also apparent.

Daily travels within the home range: In perusing Table 8, one observes that the daily path length of *S. o. geoffroyi* in this study was second only to that of the *Saimiri oerstedi* studied by Baldwin and Baldwin (1972). Both forms are insectivorous and frugivorous; the long daily path lengths reflect the longer travel distance necessary to obtain animal protein. The path length of the white face monkey, *Cebus capucinus*, which is primarily frugivorous but somewhat insectivorous (Eisenberg *et al.*, 1972) occupies an intermediate position. Howlers (*Alouatta villosa*) and the ti-ti (*Callicebus moloch*) are primarily frugivorous and folivorous (Carpenter, 1939; Mason, 1966); their shorter daily path lengths reflect the nature of their less demanding diet.

Home range size and rate of travel observed are reasonably close to the figures predicted by Moynihan (1970), but the tamarins did not, as he suggested, travel throughout their home range several times a day or even once a day. They did, however, visit most of the points of overlap, even on extreme ends of their range, on most days.

Differential utilization of habitat types: Chapman (1929) and Enders (1930, 1935) wrote that this tamarin preferred areas of second growth, and the latter author indicated that they were common in areas of low, brushy vegetation not inhabited by other local primate species. Moynihan (1970) stated that this callitrichid had a pronounced preference for the vegetation along the edges of taller forests. He further refined this general statement by saying that *S. o. geoffroyi* prefers to inhabit "the vicinity of the edge" rather than "the edge itself." Moynihan also indicates that extensive areas of tall forest are not favorable for tamarin populations, and cited as evidence the inverse relationship between forest growth and tamarin abundance on Barro Colorado Island.

The above authors based their opinions of habitat usage on visual observations made while gathering natural history and behavioral data. I chose to quantify habitat usage in order to provide additional, more definitive information regarding habitat preference. The reader is referred to Figure 5 for a breakdown of the lowland group's home range by habitat; the cumulative group travels in Figure 6 give a rough idea of travel patterns within and among habitat types. Tables 9 and 11 present data on time spent and distance travelled in each of eight habitat types as indices of habitat preference.

Areas of low brush (Habitat 1) and forest edge (Habitat 4), as expected, were clearly preferred habitats. While path distance travelled in low brush was not greater than expected, the time spent within the area was significantly higher than expected. These values reflect the usage pattern for this habitat: intensive, multidirectional foraging. Areas of forest edge were used extensively for foraging activities, resting and grooming areas, and as primary arteries of travel. Intensive use of edge vegetation in foraging undoubtedly reflects the greater abundance and diversity of both fruits and insects which commonly occur in such ecotones (Odum, 1971). The abundant vines and the high foliage density also provide readily accessible escape cover from predators, a characteristic described and appreciated by Moynihan (1970).

The gallery forest of *Anacardium excelsum* (Habitat 7) was also a preferred habitat. This habitat type was used extensively as a loafing area during the heat of the day. Some foraging for insects occurred in the upper levels of this habitat type during the early morning hours and on several evenings; when the trees were in fruit during the latter part of the dry season and the early part of the wet season, these fruits and the fleshy area immediately above the fruit were a preferred food. The importance of *A. excelsum* as a roost tree influenced early morning and late evening movements within this habitat, which resulted in higher scores in both distance travelled and time spent within the habitat.

Habitat 6, an area which, save for the abundance of emergent palms, resembled the forest edge habitat, was utilized heavily in foraging for insects and also as a staging area for disputes with the river group, which occupied a home range to the south of this location. The tamarins foraged widely in the palm crowns, and frequently used the fronds as trail runways. Thus my observations disagree with those of Moynihan (1970), who stated that these tamarins avoid palms and other monocots. The trapping records of Telford *et al.* (1972), who commonly captured this tamarin on the ground in clumps of *Heliconia* spp., also cast doubt on Moynihan's observation.

Four habitat types were definitely avoided by the lowland group. These included areas of open, seasonally deciduous forest (Habitat 2), areas of open forest on mesic sites (Habitat 5), a sparsely forested opening (Habitat 3), and the grass which bordered roads and former ammunition bunkers (Habitat 8). The forest types held one characteristic in common - they were all relatively open, with a scarcity of vines. Productivity of tamarin foods in these areas was undoubtedly lower than in the surrounding areas. In addition, these open areas may not have offered sufficient escape cover. That the areas of grass were not used is surprising, since these areas abut the edge vegetation most commonly used by tamarins and, at the same time, contain high densities of orthopterans. A tamarin could easily dash out into the grass, capture a few insects, and return to the adjoining cover, as was observed in a small area of grass bordering an old road in another part of the area. However, the increased risk of predation, and particularly the vulnerability to aerial predators, may make the use of these large areas of grass undesirable.

On the basis of the above findings, the ideal tamarin habitat appears to be areas of low brush and vine-covered "edge" vegetation interspersed with taller, non-deciduous trees. The former habitat types provide both food and cover; the latter provides night roosts and shelter from the sun in the heat of the day. Thorington (1968b) also recognized the importance of this mixed habitat type in his observations of *Saguinus midas* in Guiana.

The lowland group vs. the upland group -- a comparison of home range size, home range utilization, and territoriality: Bates (1970) in a review of territorial behavior in primates, stated that, "territorial relations between primate groups are far from universal, even among those species which do establish territories." Struhsaker (1967a and b), in his study of the vervet monkey (*Cercopithecus aethiops*), found that home range and territory are functions of vegetational composition and distribution rather than group size. The validity and widespread applicability of the concept are recognized by Altmann (1974), who states, "Home range overlap depends primarily on those essential resources with the most restricted spatial distribution: it will be low in relatively uniform habitats and will be extensive if several essential resources have very restricted distributions." The temporal restriction of resources, however, is also important, and the word "temporal" may be substituted for "spatial" in the above quote. The observations of Jolly (1972) confirm this. In her study, *Lemur catta* groups which had formerly lived in discrete, well-defended territories, adopted a system of time-space segregation with extensive home range overlap in response to a scarcity of food resources during a severe dry season.

The wet season home ranges of the lowland and upland groups, and the extent to which they were overlapped by other social groups, are presented in Figure 4. The differences in degree of overlap between the two home ranges are striking. The entire home range of the lowland group was defended as a territory; hence the small degree of overlap. The home range of the upland group, on the other hand, was widely overlapped by five groups. Territorial defense, when defined as the defense of an exclusive area (Schoener, 1968) did not occur. Rather, the upland group appeared to defend the integrity of the area around the group rather than a fixed geographical territory.

One might further differentiate between the use of space by the two groups by observing that while the travels of the lowland group conformed to regular patterns of home range usage, those of the upland group appeared to be more random. The wet season home range size of upland group exceeded that of lowland group, which implies that resources in the upland area were less available to individual animals and thus necessitated more widespread foraging. Furthermore, while the lowland group maintained a relatively stable home range and pattern of travel throughout the late wet season and the dry season, the upland group expanded its home range by at least 11 ha and wandered widely. Seminomadic behavior was common during the late wet season and the dry season among those groups inhabiting upland areas. DeMoor and Steffans (1972) observed similar contrasts between vervet monkeys (*Cercopithecas aethiops*) living in gallery forests and those inhabiting a sandy hillside.

The key to this disparity in usage patterns between the two groups appears to lie in the temporal distribution of resources. Lowland mesic areas along streams support relatively stable quantities of food throughout the year, while upland areas undergo great seasonal changes in insect abundance and diversity (Janzen and Schoener, 1968).

The territorial pattern of usage exemplified by the lowland group is the expected pattern for a territorial primate inhabiting a relatively uniform habitat (Altmann, 1974). He further states that "The natural tendency of animals to occupy all available parts of the habitat while minimizing competition with conspecifics, combined with the advantages of an established familiar area, tends to produce a mosaic distribution of home ranges, with contiguous or minimally overlapping boundaries." The efficient exploitation of predictably stable and more or less uniformly distributed, low density food resources, in conjunction with the advantages accrued by living in an exclusive area, make territoriality the most feasible utilization strategy for *S. oedipus* groups inhabiting lowland areas.

In contrast, the usage pattern of upland groups is a feasible alternative for exploiting resources which are predictably limited in time. The formation and defense of territories would probably be energetically unfeasible in areas which provide adequate resources for only six months of the year. If food resources are richer in the uplands than the lowlands during the early wet season (as the higher density of tamarins per unit area for upland group's home range suggest), the energetic costs of defending territories in the time of food abundance would undoubtedly be higher in the uplands than in the lowlands due to the "attractiveness" of the rich resources to contiguous groups.

Results: Group Composition and Stability

Trapping success: Trapping success was low, averaging 39.04 trap days/tamarin (68 captures over 5,388 trap days). Of those tagged animals, only 50 figured prominently in the study. Six infants in the five groups died or disappeared before I could capture them. Juveniles were more susceptible to capture and recapture than adults ($x^2 = 10.356$, $p < .005$) with expected values for their capture based on the proportion of juveniles in the combined collection and study group samples.

Group size: Mean group size was determined for 71 groups. Rounded mean size was used for 24 groups seen frequently in Rodman; the remainder of the data results from single observations. Mean size was found to be 6.39 ± .31 when carried infants were excluded from the count, and 6.93 ± .36 when the infants were included (Figure 7).

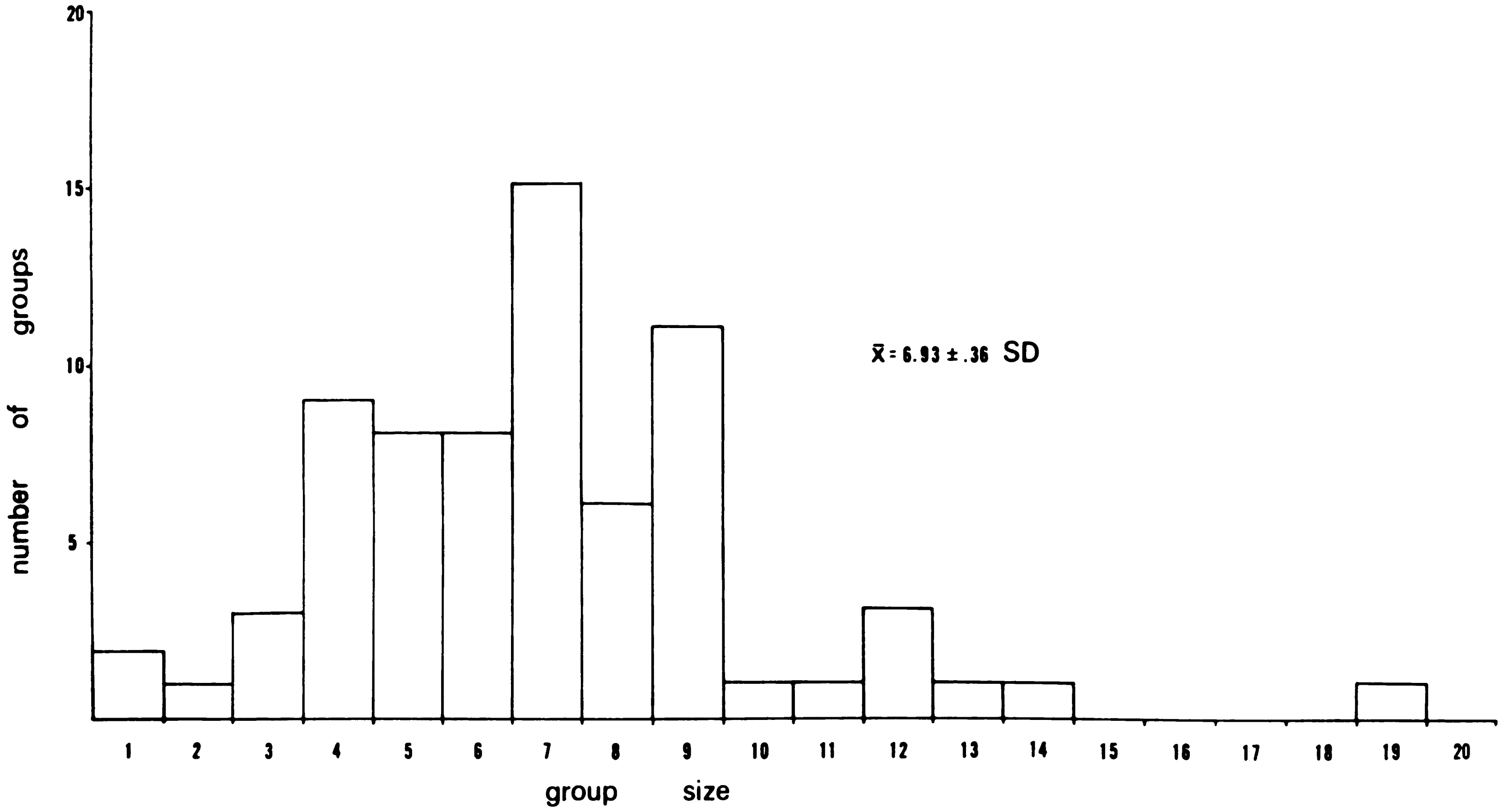
Individual tamarins and aggregates smaller than the mean were often observed during periods of casual observation. However, observations of such small groups over a longer time period (5-30 minutes) or in a "mobbing" situation directed toward the investigator, revealed that these individuals and aggregates were almost invariably constituents of larger groups. No "floating" population of extra-group individuals was evident.

The above data must be further qualified by the observation that the two largest groups appeared to be casual groupings of tamarins at concentrated food sources rather than permanent social groups. Both "groups" were observed only once, although I often passed through that area.

Group size was compared over three trimesters: 1) November to February, the peak breeding season, 2) March to June, the peak season of parturition, and 3) July to October. Carried infants were excluded from the analysis since they are incapable of participating actively in intergroup movement, and, moreover, their numbers could be expected to increase group size in the third trimester. Analysis of variance indicated that no differences in group sizes existed over trimesters ($F = .249$, $p > .75$, d.f. = 2,68).

Figure 7. Group size for 71 distinct groups of the Panamanian tamarin (*S. oedipus*) encountered on the Pacific slope of the Panama Canal Zone from January, 1973, to May, 1974.

Figure 7.


20
15
10
5
number of groups
$\bar{X}$ = 6.93 ± .36 SD
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
group size

Population sex ratio: The sex ratio for *S. o. geoffroyi* in this study did not differ significantly from a 1:1 ratio. This held true for both immature and mature age classes collected by trapping or by shooting (Table 12). No sex specific mortality factor appears to be affecting either age class.

Composition of monitored groups: A summary of the sex-age class compositions for the five monitored groups is given in Table 13. No definitive statement on either group or population sex-age class structure can be made on the basis of the composition of five groups. Neither can a definitive statement be made regarding the sex-age class structure of a population on the basis of a collected sample of 131 tamarins. The small sample size of the first estimate militates against the probability of it being a representative sample of their population; hidden biases, particularly behavioral ones, might influence the latter estimate. A comparison of the sex-age class distributions arrived at by the two methods, while inconclusive in a strict sense, would, if favorable, lend credence to the validity of these estimates.

To this end a Chi-square goodness of fit test was used to compare the sex-age class distribution of the five groups of known composition with the sex-age class distribution from the collected sample. The two distributions did not differ significantly; in fact, they proved practically identical ($x^2 = 0.359$, $p > .9$, 3 d.f.). This supports the contention that the sex-age class structures found in both samples are representative of the population's sex-age class structure. On the basis of this evidence both distributions are assumed to be representative, and, for the purpose of this study, valid estimates of population composition.

Table 12. Sex ratios within tamarin age classes.

	n	x^2	P
A. Collected Tamarins			
1 Mature males	53	.495	$p > .1$
Mature females	46		
2 Immature males	18	.500	$p > .1$
Immature females			
B. Trapped Tamarins			
1 Mature males	21	.100	$p > .5$
Mature females	19		
2 Immature males	18	2.286	$p > .1$
Immature females	10		

Table 13. Sex-age class composition of five social groups of the Panamanian tamarin, *S. oedipus*.

	Sex-age Classes				
	Mature Males	Mature Females[1]	Immature Males	Immature Females	Total
Group (n)[2]	$\bar{X}$ SE	$\bar{X}$ SE	$\bar{X}$ SE	$\bar{X}$ SE	$\bar{X}$ SE
Lowland (14)	2.0 ± 0.1	2.6 ± 0.1	1.3 ± 0.3	0.3 ± 0.1	6.1 ± 0.3
Green (7)	2.1 ± 0.5	2.3 ± 0.2	1.1 ± 0.5	1.4 ± 0.3	7.0 ± 0.4
Red (7)	1.9 ± 0.1	2.3 ± 0.8	1.1 ± 0.0	0.0 ± 0.0	5.1 ± 0.3
Upland (9)	4.0 ± 0.4	0.8 ± 0.1	0.7 ± 0.4	0.9 ± 0.3	6.3 ± 0.5
Yellow (8)	2.0 ± 0.4	2.4 ± 0.5	1.3 ± 0.3	0.8 ± 0.3	6.4 ± 0.5
Total[3]	2.4 ± 0.4	2.1 ± 0.3	1.1 ± 0.1	0.7 ± 0.2	6.2 ± 0.3

[1] Carried young excluded.

[2] n = number of censuses.

[3] Average of means as estimate of group composition.

Group stability: While the five monitored groups maintained relatively stable group sizes and sex-age class proportions (Table 13) their particular complements of individuals proved unstable. Forty-one immigrations and emigrations (considering emigration and subsequent immigration by the same individual as separate events), fourteen disappearances, and one death were recorded while observing the five groups over a period of from 10-15 months per group. Since systematic, *i.e.* monthly counts, were made only during the last five months, additional changes in group composition may have gone unnoticed. Twenty immigrations and emigrations, and six disappearances were recorded during 19 observation periods during the wet season. Twenty-one immigrations and emigrations, eight disappearances, and one death were recorded over 29 dry season counts, 25 of which were made during the 1974 dry season. Rates of mobility between wet and dry seasons are not comparable due to the irregular intervals among wet season censuses. The data demonstrate, however, that changes in group composition occurred frequently during both seasons.

Comparison of group stability: Two measures were used to compare stability among groups: 1) The percentage of individuals associated with a group above the mean for that group; and 2) comparisons of median stability, where group stability is based on the stability value of its components, and stability itself is defined as the frequency of occurrence of individuals over pertinent sampling periods. The first measure is crude in that it is sensitive only to gross changes in group association; the second is more finite since it also measures the tenure of individual constituents.

In Table 14, groups are organized along a gradient according to the relative availability of moisture and degree of deciduousness of the vegetation in their home ranges. It is apparent that the number of individuals associated with groups above and beyond the mean varied directly with the degree of deciduousness in their home range and inversely with the availability of moisture.

Median group stability was tested in the 1974 dry season, when each group was censused monthly for five months, and in the 1973 wet season. Median stability values for the 1974 dry season are listed in Table 14. No values of median stability are presented for the dry season since uneven, inadequate sampling precluded comparisons among all groups. For the eight of ten wet season comparisons which were possible, a separate index of median stability, based on common census periods, was developed for each paired comparison in order to correct for unbalanced sampling. Formulae for comparing the median stabilities of groups are found in Hays (1963).

An *a priori* test to determine whether differences in median stability occurred among the five groups during the 1974 dry season indicated that significant differences did occur ($x^2 = 8.444$, $.1 < p > .05$, 4 d.f.). *A posteriori* paired comparisons indicated that two groups, lowland and upland, exhibited significantly higher dry season stabilities than yellow group ($x^2 = 4.549$, $p < .05$, 1 d.f., and $x^2 = 5.519$, $p < .025$, 1 d.f., respectively). All other comparisons were non-significant, with $p > .1$ or more for all comparisons.

Paired comparisons of group median stability during the wet season indicated that the lowland group was significantly more stable than Yellow group ($x^2 = 3.976$, $p < .05$, 1 d.f.). Median stabilities among other groups did not differ, with $p > .1$ or more for all comparisons.

Table 14. Comparison of mean group size and the number of associated individuals for five tamarin social groups whose home range lie along a moisture-vegetation gradient.

River Valley	Estimated percent deciduousness-Dry Season 1974	Group	$\overline{X}$ ± SE	Associated Individuals[1]	% Associated Above Mean	Median Stability Dry Season 1974
Moisture gradient	10	Lowland[4]	6.143 ± .254	10	62.79	100[2]
	20	Green	7.000 ± .436	12	71.43	80
	20	Red	5.143 ± .261	9	75.00	80
	30	Upland	6.334 ± .500	13	105.24	100[3]
	40	Yellow	6.375 ± .518	17	166.67	40
Hillside						

[1] Includes recruitment by birth.

[2] Median dry season stability differs from that of Yellow at $p < .05$.

[3] Median dry season stability differs from that of Yellow at $p < .025$.

[4] Median wet season stability differs from that of Yellow at $p < .05$.

Stability among sex-age classes: The median test was also used to test for differences in stability among sex-age classes, both for the entire study period and the 1974 dry season. No significant differences in stability among sex-age classes were noted for either period (x^2 = 4.402, p > .1, 3 d.f., and x^2 = .483, p > .975, 3 d.f., respectively).

In a separate test, emigrations and disappearances for all sex-age classes over all counts were compared with the expected number of emigrations and disappearances per class based on the proportion of each sex-age class in the overall population (Table 15). The results, x^2 = 9.245, p < .05, 3 d.f., indicate that the expected numbers of emigrations and disappearances per class differed signficantly from the numbers observed. It can be seen from Table 15 that mature tamarins of both sexes disappeared and emigrated somewhat less than expected, while the immature tamarins emigrated and disappeared more frequently than their numbers in the population would predict. A comparison of the observed proportion of emigrations and disappearances per age class with the expected proportions was made using the Bonferroni Z statistic in order to determine whether or not the significant Chi-square value could be attributed to extreme differences between observed and expected values in one or more of the sex-age classes (see Table 15). The results indicate that while the differences between observed and expected proportions approached significance (.2 < p > .1) for each comparison, the significant Chi-square value was not attributable to significant differences in any sex-age class.

Table 15. Emigrations and disappearances among sex-age classes: Expected values based on sex-age class proportions in the five monitored groups and the collected sample.

Sex-age Class	Proportion in Population (Expected Proportion)	Observed Emigration and Disappearance	Expected Emigration and Disappearance	Chi-Square Values	Proportions Observed	90% Family Confidence Coefficient on Observed Proportion
Mature males	.405	8	12.947	1.890	.250	$.079 \leq p \geq .421$
Mature females	.351	9	11.325	.445	.281	$.103 \leq p \geq .459$
Immature males	.137	9	4.397	4.996	.281	$.102 \leq p \geq .459$
Immature females	.107	6	3.421	1.944	.188	$.038 \leq p \geq .338$
				$x^2=9.245$		

Immature tamarins, then, tend to emigrate and disappear more frequently than adults. This observation seems to be at odds with the stability comparison, which revealed no differences in stability among sex-age classes. This can be explained, however, by noting that the prolonged dependence of the young on the group early in life, which results in high stability scores, compensates for the higher rates of emigration and disappearance which occur among older immature tamarins.

Group losses by emigration or disappearance were recouped by immigration and natality. The sex-age class proportions of 18 immigrants entering the monitored groups for the first time did not differ significantly from expected proportions bases on sex-age class proportions in the collection ($x^2 = .992$, $p > .5$, 3 d.f.). A second source of recruitment, immigrating animals which had formerly emigrated, was found to be substantial (13 animals). Emigrants were found to reunite with their former groups in proportion to the numbers of each sex-age class which were known to have emigrated ($x^2 = 1.092$, $p > .5$, 3 d.f.).

While emigration to adjacent groups was a common phenomenon (11 observations), long-distance emigrations were also observed. One male about 18 months of age traveled 6.5 km from the home range of his original group. Several tamarins, including one female of about 12 months of age, were known to have travelled at least 2 km from their group of origin.

Home range data: An attempt was made to quantify both home range size and utilization patterns for two groups, the lowland, on the humid extreme of the moisture gradient, and the upland, on the dry side. The lowland group occupied a home range of about 26 ha. This home range was defended as a territory in the strictest sense - a defended area with a distinct geographical boundary (Bates, 1970). The approximately 13 percent of this range overlapped by three other groups was the site of frequent intergroup contact and territorial marking. The lowland group maintained the boundaries of its home range throughout the year; in contrast, the boundaries of the upland group's home range were flexible and were expanded in the late wet season and the dry season. During the wet season, the upland group was known to occupy an area of 32 ha; its home range during the dry season encompassed at least 43 ha. The 32 ha portion of the home range was not defended as a geographical entity - at least 83 percent of it was overlapped by at least five other groups. The groups using this area apparently did so through separation from other groups in time and/or space. Although frequent aggressive encounters and agonistic displays between groups occurred, both offense and defense seemed directed toward defending the immediate area around the group rather than toward defending a geographic territory *per se*.

Importance of group components: Perhaps the most important observation to be made here is that practically no sexual dimorphism exists in this species. In Table 16 parameters of nine characters which are commonly sexually dimorphic in primates are listed, and the intersexual differences tested (pregnant females were excluded from the samples). The only parameter which differed significantly between sexes was body weight, where females averaged 4.3 percent heavier than males. Mature males and females are roughly equal in size, weight, and dental armament, and are thus equally capable, in a

Table 16. Comparison of body weight, body length, and selected cranial and dental measurements of mature male and female *S. o. geoffroyi*.

	$\overline{X}$	SE	n	F	P
Body length (mm) males	232.43	± 1.43	53	2.249	$p > .20$
Body length (mm) females	241.52	± 3.47	48		
Body weight[1] males	486.42	± 5.89	53	4.628	$p < .10$
Body weight[2] females	507.46	± 8.11	41		
Skull length (mm)[3] males	51.16	± 1.73	48	.913	$p > .50$
Skull length (mm) females	50.92	± 1.08	44		
Zygomatic breadth (mm) males	35.38	± 1.30	48	.031	$p > .50$
Zygomatic breadth (mm) females	35.34	± 1.06	41		
Effective ($\overline{X}$) maxillary canine length males	6.12	± .17	52	1.691	$p > .20$
Effective ($\overline{X}$) maxillary canine length females	6.39	± .11	46		
Longer maxillary canine length[4] males	6.84	± .09	48	.536	$p > .50$
Longer maxillary canine length females	6.93	± .07	45		
Labiolingual breadth, maxillary canine males	2.38	± .02	48	3.515	$p > .10$
Labiolingual breadth, maxillary canine females	2.33	± .02	44		
Left mandibular canine length males	6.59	± .09	48	1.523	$p > .20$
Left mandibular canine length females	6.49	± .08	44		
Left mandibular canine breadth males	2.67	± .02	48	2.741	$p > .20$
Left mandibular canine breadth females	2.61	± .02	45		

[1] Individual weights to nearest .01 g.

[2] Pregnant females excluded.

[3] This and following measurements using needle-pointed calipers to .01 mm.

[4] Canine measurements follow Kinsey, 1972.

physical sense, of overt participation in aggressive encounters, both inter and intragroup, and in predator defense.

On the basis of morphological similarities, one might expect a more equal apportionment of roles between sexes than is found in most primate societies. My field observations bear this out. Both males and females participated actively in the care of infants, a fact which is already well substantiated in the literature (*e.g.* Hampton, 1964; Shadle *et al.*, 1965; Epple, 1967a, 1970a; Weber, 1972). Both sexes were observed to actively participate in territorial defense. In the majority of instances, this consisted of uttering "long whistles" (Moynihan, 1970) at the other group, with perhaps a few rushes toward the opposing group being made by individuals of either group. However, six intergroup encounters were observed where opponents made physical contact; of these, three took place near artificial feeding sites and three took place in natural situations. Males tended to be more aggressive in the six altercations involving contact. Both sexes were seen to mark vegetation with their suprapubic and circumgenital glands following both the aggressive encounters and those involving only agonistic display. Females appeared to mark more frequently than males, and to initiate marking behavior following an encounter. Both sexes exhibit behavior indicative of "control" animals in the sense of Bernstein (1964, 1966).

The absence of pronounced sexual dimorphism and the duality of roles noted above might lead one to suspect the existence of a social structure with a one male, one female dominance system such as the one described by Epple (1967a, 1967b, 1972) for laboratory groups of *Callithrix jacchus*. Observations at feeding platforms during the dry season indicated that certain males and females occasionally dominated members of their own sex in competition for food. I also observed that a single female per group had priority to reproduction - *i.e.* only one infant or set of twins was found in any one group at a given time, although the group might contain two or more sexually mature females. Epple (1970a), who apparently observed the same phenomenon in laboratory groups of *S. o. geoffroyi*, indicated that only alpha females bore young.

A further test of Epple's hypothesis that one and only one alpha (reproductive) female occurs per group was made by comparing the expected number of reproductive females (18.9/131) based on 1 female per average group of 6.93 animals, with the observed number found in the collected sample (25/131). A Chi-square test yielded a value of $x^2 = 1.820$, $p > .1$, 1 d.f., which indicates that the hypothesized number of reproductive females did not differ significantly from the number observed.

Reproductive females appear to be older than nonreproductive females as evidenced by the criteria of a higher frequency of scarring, especially on the ears and the face, and the high incidence of damaged canine teeth (7/22 vs. 1/26, $x^2 = 5.604$, $p < .025$, 1 d.f., and 8/22 vs. 3/26, $x^2 = 4.433$, $p < .05$, 1 d.f., respectively). Hershkovitz (1970) observed that dental caries and damaged teeth occurred only in the older marmoset age classes. The incidence of a highly developed suprapubic gland was higher in reproductive females than in nonreproductive females (21/22 vs. 6/26, $x^2 = 11.112$, $p < .001$, 1 d.f.).

Males did not differ from females in regard to the number of torn ears and facial scars (12/52 vs. 8/48, $x^2 = .512$, $p > .1$, 1 d.f.) or broken canines (16/52 vs. 11/48, $x^2 = .570$, $p > .1$, 1 d.f.). When combined with observational data, these findings offer further support for the coexistence of a single dominant male per group and also the lack of sex-specific mortality.

Discussion: Group Composition and Stability

Carpenter (1952, 1954) initiated the synthesis of primate studies toward the end of presenting an integrated classification system for primate social structures. More recent reviews (*e.g.* Crook and Gartlan, 1966; Bernstein, 1970) attempted to order the various primate taxa according to somewhat arbitrary evolutionary grades based on social "complexity." Eisenberg *et al.* (1972) reassessed this system and developed a more workable system which relates social structure with the ecology of a given species. The following discussion has as its goal the redefinition of the position of *S. o. geoffroyi* on this continuum. Group size and structure of the Panamanian tamarins will be discussed in relation to habitat, diet, and methods of communication. The transitory nature of some group constituents, and its implications, will also be discussed. A new category of social organization for primates, the age-dependent, one-male, one-female dominance system will be presented. It is suggested that other species of *Saguinus* and other callitrichids occupy similar positions, although further studies are needed to confirm this hypothesis.

Epple (1972), in summarizing the accounts from older literature, reported that callitrichid group size varied from 2-12 animals. Thorington (1968b) observed groups of *Saguinus midas* to vary from 2-6 individuals, and reported that other researchers in Surinam had seen groups of *S. midas* numbering up to 20 animals. Hladik and Hladik (1969) and Moynihan (1970), working in Panama with *S. o. geoffroyi*, found groups numbering 2-9 tamarins, with single individuals also in evidence. The last author considered an account of group sizes of up to 12 animals (Chapman, 1929) to be grossly inaccurate.

My own observations of 71 groups yielded a mean of 6.93 ± .36 animals per group, with a range from 1 to 19. The few single animals observed were almost always seen to join a group if watched for a half hour or more. The two largest groups, one of 14 and one of 19, were observed only once each at localized food sources, and thus may represent casual groupings of tamarins rather than permanent social groups. Most groups observed during the study ranged from 3-9 animals.

The mean size of specific social groups is determined by a multitude of factors: *e.g.* phylogenetic history, population density, diet, foraging system, spatial and temporal distribution of resources in the environment, relative distribution and the magnitude of population depressants such as predation and parasitism, and the recent history of epizootics (Crook and Gartlan, 1966; Bernstein, 1970; Eisenberg *et al.*, 1972). It would be pointless to pursue a discussion of *Saguinus* group size as determined by these factors, since so many of them remain unqualified. However, some general comments can be made.

For the most part, callitrichids inhabit "edge" vegetation in the broadest sense, which can generally be considered dense vegetation offering low levels of visibility (Thorington, 1968b; Moynihan, 1970; Coimbra-Filho and Mittermeier, 1973). Under these conditions, it is not surprising that the visual system of communication is rather primitive and rudimentary (Moynihan, 1970), and that the auditory and olfactory systems are highly developed (Epple, 1967a, 1967b, 1968, 1970a, 1972; Moynihan, 1970). High frequency vocalizations, which form the bulk of the acoustical repertoire (Epple, 1968; Moynihan, 1970), have the probable advantage of being absorbed rapidly by the foliage, thus enabling the passage of specific information to group conspecifics at short range, without attracting predators, of which there are many, from a distance (Marler, 1965; Moynihan, 1967, 1970).

As noted previously, tamarins, particularly *Saguinus*, are highly insectivorous and frugivorous. The fruits most often used are small, and their seeds are generally dispersed by birds and small mammals. These small fruits are more uniformly distributed over time and space than are the large, fleshy fruits (Smythe, 1970b), which are the mainstay of larger primate frugivores. The callitrichid food sources are more or less uniformly distributed rather than clumped.

Observations from this study indicated that little, if any, cooperation occurs in the capture of individual food items, although at times an insect flushed by one tamarin might be captured and eaten by another. Of more significance is the observation that individual group members act in a sentinel capacity, warning those engaged in feeding of the approach of an aerial or terrestrial predator. Increased probabilities of individual survival through group cooperation in predator detection, and through the "mobbing" of predators by the group are probably the primary advantages accrued to individuals in the *Saguinus* social system. The number of "alarm" vocalizations in the acoustical repertoire of these small, vulnerable primates (Epple, 1968;

Moynihan, 1970), and the high frequency with which they are uttered at a variety of stimuli on any given day seem to support this view. Mobbing of natural predators was not observed. However, tamarins often rushed toward the investigator while he was removing live-trapped individuals from the trees in which they were captured. These rushes, which were both vigorous and accompanied by intense vocalizations, sometimes ended only a few feet from the observer. It thus seems probable that tamarins would mob a smaller predator. Other possible advantages of group behavior, such as thermoregulatory benefits which may be gained in nocturnal huddling behavior, should not be ignored.

When taken together, the limited range of intragroup communication, the relatively uniform distribution of food resources within a given season, and the space required by foragers in a non-cooperative, individually-oriented foraging system may also militate against the formation of large social groups. The high levels of aggression exhibited by group dominants (Epple, 1967a, 1970b, 1972) and territorial behavior noted by Thorington (1968b) and Moynihan (1970), are probably instrumental in maintaining both individual and group foraging space required in the efficient exploitation of dispersed, low density food resources.

Carpenter (1952, 1954) observed that troop size tended to be standard for a given species, and that sex-age ratios also appeared to be stable. Eisenberg *et al.* (1972) indicated that habitat differences cause widespread variation in intraspecific social structure within some taxa and not others. One may infer from their discussions that, within a given habitat at a given point in time, the factors governing modal group size are fairly constant, although the habitat type itself may be quite "patchy" (as defined by MacArthur and Levins, 1964). This appeared to be true in this study where, although home range sites varied greatly in regard to the availability of food and moisture during the dry season, group size and group sex-age ratios remained relatively constant.

The mechanism necessary for the maintenance of stability in both group numbers and sex-age class proportions is obvious - immigration and natality must compensate for losses (emigration and mortality) in proportion to the loss in each sex-age class. Natal recruitment alone is insufficient to compensate for these losses. The data demonstrate that these vacancies are indeed filled, and that immigration is the primary mechanism.

The source of immigrating animals appears to be from other social groups rather than a population of extra-group individuals. Evidence for this is partly negative - single animals and small groups were almost always associated with larger groups and rarely remained isolated for extended periods. Moreover, baited feeding platforms were never visited by single animals. In contrast, ten immigrants, roughly one half of the total, were marked animals from other groups. It might be surmized that immigrants come from two sources: 1) Groups which maintain their integrity while exhibiting a turnover of constituents, and 2) groups which for some reason prove to be nonviable and thus dissipate. The existence of the latter source is necessary if one is to explain the maintenance of group size with no existing extra-group population as a source of replacements.

Four of the five groups each contained a reproductive female which remained with its respective group for the course of the study. Epple (1970a), working with *S. o. geoffroyi*, observed that only alpha females bore young, although "inferior" but sexually mature females copulated with the fertile male (alpha male). It appears likely, then, that the reproductive females in these free-ranging groups are alpha animals. In addition, at least one adult male remained a permanent member of each group throughout the study. In three of five groups the resident males were observed to supplant other associated males at feeding platforms and in some natural feeding situations. They were also observed to "lead" in chasing an intruding group from the feeding platform or territory. Evidence exists, then, for a stable group core of one reproductive or alpha female and one resident, probably dominant, male. The other stable element of the group is the dependent young, usually the survivor of twins, which does not leave the group for extended periods until it is roughly a year or more of age. In light of their temporary existence, the remainder of the group constituents may be considered transients.

The above observations, when combined with those in the prior section regarding the relative roles of male and female tamarins, suggest that the typical *S. o. geoffroyi* group consists of an alpha male, an alpha female, sedentary young of the year, and a transient complement of presumably subordinate animals of both sexes, which appear to be younger than the alpha female, and probably the alpha male as well. These subordinate animals may or may not be sexually mature (see section on reproduction). Using terminology parallel to that used by Eisenberg *et al.* (1972), this configuration may be considered an age-related, male-female troop. The existence of the dual dominance system is plausible given the lack of sexual dimorphism and the duality of roles discussed previously. The statistically equivalent rates of intergroup movement by males and females add credibility to the concept - *viz.* unisexual dominance systems should generate higher rates of movement, and perhaps extra-group individuals, of the dominated sex.

As noted previously, the existence of the dual dominance system in free-ranging callitrichids was predicted by Epple (1967a, 1967b, 1970a, 1970b, 1972) on the basis of laboratory observations in which *Callithrix jacchus* was the primary model. She garnered supportive evidence from less intensive observations of other callitrichids, including *S. o. geoffroyi* (which she referred to as *Oedipomidas spixi,* after Hill, 1957). She thought of this system as existing within a family group consisting of one or two adult pairs and their offspring of successive years. This was in keeping with the traditional concept regarding the social structure of the Callitrichidae, and was strengthened by her observation that, while dual dominance systems did form in groups of unrelated *C. jacchus* and *Saguinus fuscicollis* as well, they were rarely stable over long periods of time, whereas family groups remained peaceful over the three-year study. The social configuration which I observed appeared to be identical to those in Epple's "artificial" *i.e.* unrelated groups.

Epple (1967a, 1967b) indicated that the alpha animals "tolerated" juveniles. A "tolerance" for juveniles was also observed in an artificial feeding situation by Nelson (1975). In the current study a juvenile female approximately 12 months of age was tagged in the upland group in June, 1973. During the two subsequent weeks she was alternately a member of the upland group and adjacent Yellow group. She then disappeared until August, when she was seen with another group 400 m south of the upland group's home range. In September she became a member of Green group, whose home range was located 2 km from that of the upland group. It would appear then, that juveniles may move from group to group with a minimum of interference.

The integration of new group members, and the maintenance of dominance in the group may at times, however, require overt physical encounters. Epple (1972) observed that the introduction of a strange conspecific into the laboratory group precipitated aggressive behavior, particularly on the part of the alpha animal of the same sex. She also observed that serious fights between alpha animals and their subordinates occurred frequently, and often after the group had been stable for a year or more. In the current study, the "long rasps" (Moynihan, 1970) which accompany aggressive contact were heard frequently, although it was often difficult to determine whether the conflicts were intra- or intergroup in nature. The field observations of Moynihan (1970) indicate that intragroup altercations are more frequent, and, as evidenced by the vocalizations, the more intense. It is possible that high levels of intragroup aggression are the driving force behind the intergroup flow of transient animals.

A group social structure composed of a single dominant pair and a shifting complement of subordinates would have several probable advantages over the traditionally-accepted "extended family" group with an identical dominance system:

1. Gene flow in the population would be greatly increased since individuals from other groups, rather than siblings, would ascend

to dominant, *i.e.* breeding positions. This would limit genetic drift and assist in maintaining the integrity of the species;

2. Immigrants ascending to breeding positions in an open social system would contribute a more varied genotype (*i.e.* heterozygous at more loci), tested over a wider variety of ecological conditions, to the offspring. It follows that offspring exhibiting more variable, more broadly-tested genotypes would be genetically more "fit" for survival under a wider variety of environmental conditions than offspring from isolated social groups subject to a limited range of selective pressures. This consideration is especially important since callitrichids in general are r-selected (as defined by Pianka, 1970) relative to other primate species, and may be thought of as colonizing forms which inhabit widely-scattered, temporally-discrete areas of second growth over a wide range of environmental conditions;
3. Replacement of individuals lost to mortality would be more rapid, thus facilitating the maintenance of group size at optimal levels;
4. The higher incidence of intragroup aggression in non-family groups would favor selection of more aggressive alpha animals. (It might well be argued to the contrary that high levels of aggression might not be adaptive since they might prove to be socially disruptive. However, Bernstein and Gordon (1974) suggested that "Rather than disrupting social relationships, aggression serves to enforce regulated social interactions which maintain primate societies"). It is possible that tamarins which are highly aggressive in intragroup conflicts might also prove highly aggressive in intergroup conflicts. The capacity for

high levels of intergroup aggression would be adaptive in maintaining the large foraging territory necessary to exploit dispersed food resources; and

5. Long distance movements by transient individuals, and high levels of individual aggression fostered in non-family groups might aid in the discovery and colonization of small, widely-separated areas of second growth such as those generated by slash and burn agriculture.

Gartlan (1968) and Eisenberg *et al.* (1972) discussed recent literature in which intraspecific group structure and function were found to vary over environmental gradients. Jolly (1972) found that lemur groups which normally defended fixed territories abandoned these territories and adopted a system of temporal and spatial segregation during a severe dry season. She concluded that "the change may reflect long-term population effects or seasonal food shortage." Social structure, and spatial utilization, then, may vary across both environmental gradients and time, and may even vary within groups over variable environmental conditions.

Anderson (1970), in a consideration of ecological structure and gene flow in small mammal populations, divided potentially-suitable habitats into colonization habitats and survival habitats. In the former, populations capitalized on abundant, temporally discrete resources; the the latter, segments of the population survived in areas which were relatively salubrious at all times. Time-space segregation afforded the *modus operandi* for exploitation of resources in the colonization habitat, while strict territoriality proved to be the energetically feasible alternative in the stable survival habitat.

In Rodman, tamarins occupying lowland areas, which provide a relatively stable food resource throughout the dry season, may be thought of as occupying survival habitats. Their well-defined territories, relatively stable group compositions, and higher rates of infant survival support this contention. Those tamarins occupying upland sites utilize a seasonal resource, and may be thought of as inhabiting colonization habitats. The observed segregation of groups in space and time, the apparent inability of these groups to establish and defend a geographically-fixed territory, and the low rates of infant survival are in agreement with Anderson's (1970) observations on colonizing animals.

At this point, it is necessary to note that a fundamental difference exists between the situation in Anderson's (1970) study and that involving *S. o. geoffroyi* in Panama. Anderson (1970) found it necessary to invoke group selection in explaining the genetic differences found between survival and colonization components of the house mouse, *Mus*, since the colonizing element did not contribute genetic information to the survival populations (*i.e.* there was no direct genetic feedback). As indicated earlier, the colonization element of *S. o. geoffroyi* does have a feedback mechanism - immigration to survival habitats and the rise to sexual dominance by individuals from colonization habitats. Thus the *S. o. geoffroyi* social system allows the transmission of genetic information in the traditional Darwinian manner.

Anderson (1970) characterized the function of the survival component of the population as "maintaining the ongoing population in both the ecological and genetical senses", and the function of the colonization component as "a test of the full range of ecological and genetic variation under all of the accessible variations of the fundamental niche of the species", while at the same time providing for the dissapation of excess animals. It is suggested that populations of *S. o. geoffroyi* follow this pattern, and that the accrued advantages are responsible for their success under environmental conditions which are less than equitable.

Results: Reproduction

A distinct birth peak was evident from late April through early June. Eighteen of the twenty-six groups observed with carried young were seen during this time period. Of the remaining eight, five were seen in March, and single groups with carried young were seen in February, July, and October. Six of the seven well-developed foetuses from the collected sample were from the months of February, March, and April.

Reproductive activity was not, however, limited to the period preceding the annual birth peak. Pregnant females were found in the collected sample from September through May, newly-born young were observed in June and July, and one infant was collected that had been born in August. Moreover, two females collected in April and two females collected in May were found to be in the early stages of pregnancy. This observation, together with the presence of well-developed foetuses in a female collected in September, point to the possibility of a potentially bimodal birth peak, with young being born in April and May, and from September through October. One social group containing infants born in August, and another set of twins which had been born earlier, presumably in March, were actually observed. It appears, however, that the reproductive potential evident from the pregnancies in April and May is rarely realized, for the sightings of infants outside the March to July season of parturition are rare.

Some evidence also exists for a postpartum estrous, or at least a period of estrous relatively soon after parturition. Three lactating females collected during this study were also pregnant and in two of the three, these embryos were well-developed. Also, as indicated above, one group (with one reproductive female) contained two sets of twins which were separated in age by only five or six months. If there is a potentially bimodal birth-peak, as the data suggest, the effect of lactation anestrous, if it exists at all, must be relatively slight.

A trimestral comparison of somatic and reproductive tract measurements for mature males is presented in Table 17. No differences in the size or weight of the reproductive organs were observed. However, body weight differed markedly over trimesters ($F = 3.843$; 2, 52 d.f., $p = .028$). Post-data comparison of the trimestral means for body weight using the Student-Newman-Keuls test (Sokal and Rohlf, 1969) indicates that mature males weighed significantly more during the July to October trimester than during either of the other trimesters ($p < .05$). The average weights of mature males did not differ between the November-February trimester and the March-June trimester ($p > .05$). Gametogenic tissue was evident in the histological examinations of all mature males collected from April to December. Testes of males collected from January to April were not examined.

Table 17. Somatic and reproductive tract measurements of mature male *S. o. geoffroyi*, with a comparison of measurements over trimesters.[1]

	$\overline{X}$	SD	n	F Statistic	Significance Probability of F Statistic
Body weight[2]	481.58	50.05	55	3.843	.028
Body length[3]	231.76	10.85	55	0.190	.827
Suprapubic gland length	31.81	6.27	48	0.144	.866
Suprapubic gland width	20.08	3.09	48	1.545	.224
Suprapubic gland condition	2.37	0.49	46	1.107	.340
Left testis length	11.75	1.52	54	2.248	.116
Left testis width	7.89	1.00	54	1.222	.303
Left testis breadth	6.16	1.23	54	0.274	.762
Left testis weight[4]	3174.78	1146.61	54	0.561	.574
Right testis length	11.83	1.82	56	0.926	.402
Right testis width	7.74	1.38	56	0.277	.759
Right testis breadth	6.10	1.16	56	0.016	.984
Right testis weight	3219.43	1339.74	56	0.084	.919

[1] Trimesters equal: 1. November-February, 2. March-June, and 3. July-October.

[2] Weight to nearest 0.1 g.

[3] All linear measurements in mm.

[4] Testis weights in mg.

The comparison of somatic and reproductive measurements for mature females over trimesters is found in Table 18. Again, no significant differences in reproductive tract measurements were observed among trimesters. However, two measurements, body weight and the width of the suprapubic gland, did differ over trimesters (F = 2.464; 2, 37 d.f., p = .099; and F = 3.752; 2, 39 d.f., p = 0.32, respectively). A post-data comparison of means as described above indicated that mature females were significantly heavier during the July to October trimester (p < .05). Weights did not differ between the other two trimesters (p > .05). The mean width of the suprapubic gland was significantly greater in the March-June trimester (p < .01). No significant differences in suprapubic gland width existed between the other two trimesters (p > .05).

Reproductive females appear to be older than nonreproductive females as evidenced by the criteria of a higher frequency of scarring, especially on the ears and the face, and the higher evidence of damaged canine teeth (7/22 vs. 1/26, $\chi^2 = 5.604$, p < .025, 1 d.f., and 8/22 vs. 3/26, $\chi^2 = 4.433$, p < .05, 1 d.f., respectively). The evidence of a highly developed suprapubic gland was also more prevalent in reproductive females ($\chi^2 = 11.112$, p < .001, 1 d.f.).

The mean number of newborn infants per group (per female) was 2.00 ± .40 S.D. (n = 26). Although social groups usually contained at least two adult females, only one mature female per group was observed to bear young. The number of reproductive females in the collected sample did not differ significantly from the expected number, based on the expectation of one reproductive female per average group size of 6.93 tamarins ($\chi^2 = 1.820$, p > .1, 1 d.f.).

Table 18. Somatic and reproductive tract measurements of mature female *S. o. geoffroyi*, with a comparison of measurements over trimesters.[1]

	$\overline{X}$	SD	n	F Statistic	Significance Probability of F Statistic
Body weight[2]	502.50	54.98	40	2.464	.099
Body length[3]	238.53	16.82	47	0.867	.427
Suprapubic gland length	40.43	6.12	42	2.186	.126
Suprapubic gland width	26.62	4.89	42	3.752	.032
Suprapubic gland condition	2.67	0.48	42	0.722	.492
Left ovary length	7.84	1.28	45	0.055	.947
Left ovary width	5.12	0.97	45	0.908	.411
Left ovary breadth	3.59	0.87	45	0.861	.430
Left ovary weight[4]	855.22	453.16	45	0.779	.465
Right ovary length	7.69	1.13	44	0.029	.971
Right ovary width	5.14	1.16	44	0.271	.764
Right ovary breadth	3.46	0.85	44	1.050	.359
Right ovary weight	789.43	375.92	44	0.797	.458
Uterus weight[5]	2003.29	2247.44	34	1.717	.196
Uterus width[5]	8.80	3.13	36	1.357	.271
Uterus depth[5]	8.02	3.54	36	0.763	.474

[1] Trimesters equal: 1. November-February, 2. March-June, and 3. July-October.

[2] Body weight in grams, pregnant females excluded.

[3] All linear measurements in mm.

[4] Ovary weights in mg.

[5] Pregnant females excluded, weight in mg, linear measurements in mm.

The mortality rate for infant tamarins is quite high -- about 50 percent or more during the first six months of life. Most groups are successful in raising only one infant. It also appears that the site of the group's home range, especially under severe climatic conditions, may affect survival. In this study the lowland group and the surrounding three lowland groups were all successful in raising both of their twins until they were about 3 months of age. Two groups lost an infant at 4 months of age. The others survived until at least 6 months of age. In contrast, Red group, which occupied an intermediately moist range, lost its two young within two months after birth, and in the seasonally dry upland habitat surrounding the home range of the upland group, two groups lost their twin infants within the first two months after birth, and two groups apparently did not produce young.

Discussion: Reproduction

Abundant evidence exists for a definite *S. o. geoffroyi* breeding season in central Panama. Wislocki (1930b, 1939) found small embryos in the uteri of females in January and early February. Given a gestation period of about 140-150 days (Epple, 1970a), these tamarins would have been born in April, May, and June. Enders (1935) observed that a peak season of parturition occurred during these months, and Moynihan (1970) observed that large numbers of infants appeared "quite suddenly" in the Panama City market in May. Fleming (1973) stated, on the basis of Moynihan's (1970) work, that *S. o. geoffroyi* was seasonally monoestrous, with a breeding peak in January and a peak season of parturition in the early wet season. While the dates are accurate, Moynihan (1970) did not suggest that this tamarin is seasonally monoestrous, although the data themselves are suggestive. Information gathered during this study also offer support for the existence of a birth peak. Epple (1970a), in her study of captive *S. o. geoffroyi*, found that births occurred in March, April, May, and August. Her observations suggest that these tamarins are seasonally polyestrous or that a postpartum estrous, or a period of estrous beginning shortly after parturition, occurs. She also observed indications of postpartum estrous in two of three full-term deliveries. Hampton and Hampton (1965) working with the closely related *S. o. oedipus* under captive conditions, observed birth peaks in spring and autumn.

With such a body of evidence pointing to a seasonal birth peak, the presence of pregnant females throughout the year, and the data indicating the possibility of a second birth peak sometime in August or September, are rather surprising. The existence of the primary birth peak in April-June is easily understood since it is correlated with the flush of insects and fruits which occurs at the beginning of the wet season. However, pregnancies leading to the birth of young at other times of the year appear, on the surface, to be wasted reproductive effort, since young born during these less favorable times of the year would be unlikely to survive the rigors of food scarcity in the late wet season and the dry season. Such a strategy would, however, be advantageous during exceptionally favorable years and in the colonization of new habitats. The adaptive advantages of extra birth-peak young under these circumstances may outweigh their apparently maladaptive disadvantages in seasonal habitats at carrying capacity.

The actual fate of most young which are conceived outside the November-February breeding peak leading to the March-June birth peak is unknown. Their scarcity in groups observed after the birth peak implies that either very few are conceived or that those which are conceived are either resorbed, aborted, or must die shortly after birth. In light of the frequency of these extra breeding season pregnancies seen in the collected sample, the latter possibilities are the more likely of the alternatives.

The scarcity of newborn young in August and September is also surprising when one considers the small embryos found in mature females collected during April and May. In August and September insect foods and many of the smaller fruits are fairly abundant. Thus the failure of these pregnancies to contribute young to the population must not be due to inadequate diet for either mother or offspring; but must rather be due to other factors, the majority of which are probably density dependent and behavioral in nature.

The mechanism through which tamarin reproduction is attuned to the seasonally variable environment is unknown. However, one could state unequivocably that the reproductive synchrony responsible for the April-June birth peak is achieved through the perception of proximal environmental stimuli. These must be highly correlated with the ultimate factors that govern the success of reproduction over long periods of time. As Lancaster and Lee (1965) point out, it has been repeatedly demonstrated that "internal rhythm by itself cannot maintain a regular periodicity of birth seasons, but must be triggered and synchronized by stimuli external to the animals." For the sake of convenience the discussion of a possible mechanism for achieving the seasonal effect will be divided into two segments: 1) The various proximal environmental cues which exist, and the probability of their perception by the tamarins, and 2) the actual mechanics of reproduction as suggested by the analysis of reproductive tracts and additional data from the literature.

In a discussion of the factors affecting the physiology of reproduction, Amoroso and Marshall (1960) wrote, "Of the external, or environmental factors, the most important have been found to be light, temperature, and food supply." Changes in humidity and precipitation which presage seasonal peaks of food abundance may be added to this list (*e.g.* Koford, 1965; DuMond and Hutchinson, 1967; Rosenblum, 1968; Vandenbergh and Vessey, 1968; Rudran, 1973; Harrison and Dukelow, 1973). Fleming (1973) discusses the correlative significance of these factors in the reproduction of Panamanian mammals. In the discussion which follows, each of these factors and their probable effects on the reproduction of *S. o. geoffroyi*, will be discussed separately.

As Fleming (1973) indicates, differences in photoperiod at this latitude are slight -- about 63 minutes' difference exists between the longest and shortest days of the year. Because of the barely perceptible changes in day length which occur over the year, he discounts changes in the length of photoperiod as proximal environmental stimuli affecting reproduction in Panamanian mammals. Koford (1965), in his study of the exotic rhesus monkeys (*Macaca mulatta*) on Cayo Santiago Island, which lies far to the north of Panama and experiences daylight changes of about one-half minute per day, also discounts light as a factor affecting the reproduction of these tropical primates.

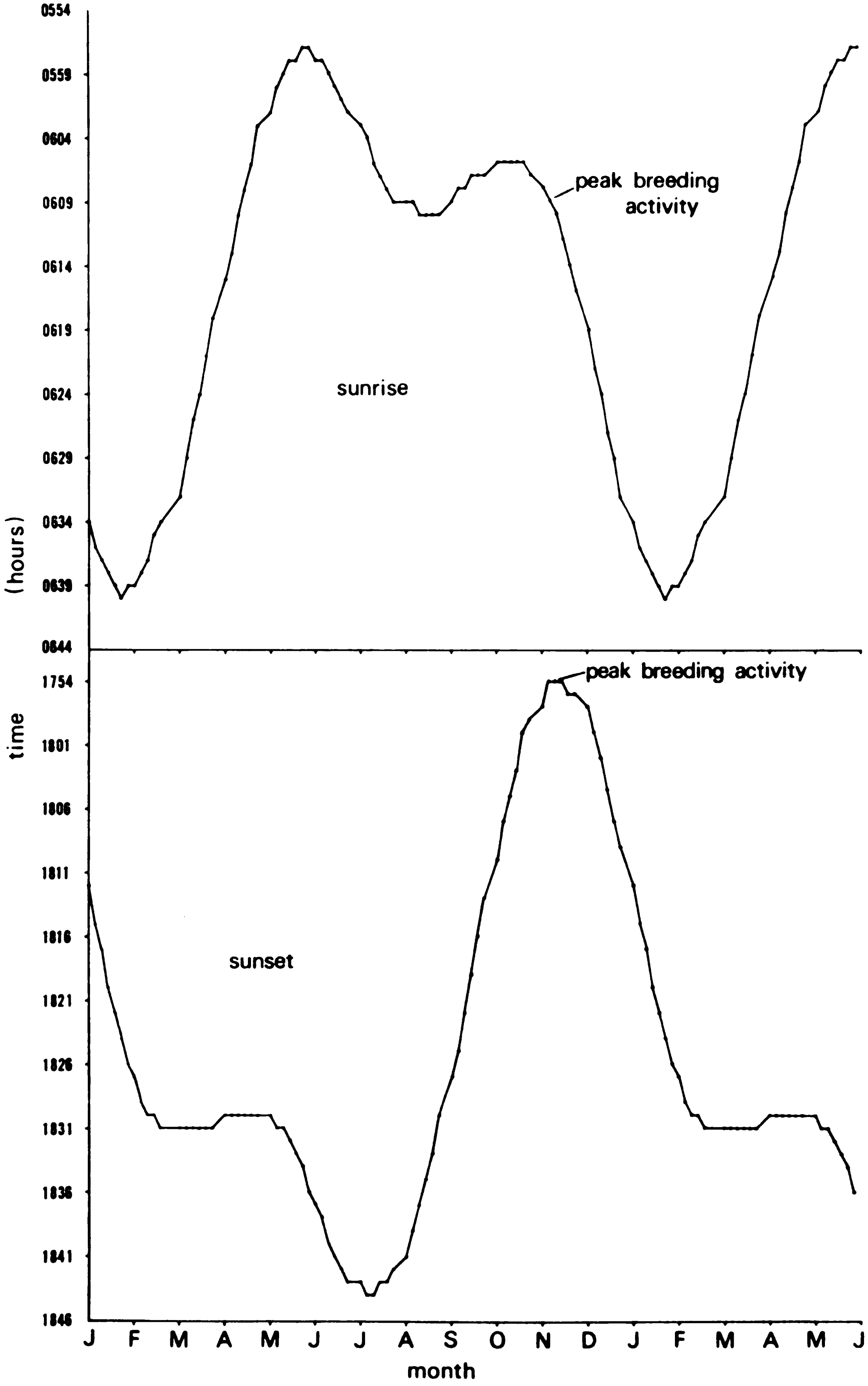
Spinage (1973), in discussing the role of photoperiodism in the reproduction of tropical ungulates, stated that daylight cannot be so easily discarded as a potential environmental cue which triggers reproduction. He observed that while slight changes in daylength might indeed by imperceptible, the sudden shift in the timing of sunrise and sunset which occur at the summer and winter solstices might not be. He observed that even on the equator, where daylength is constant to within two minutes throughout the year, a regular shift of sunset and sunrise times of about 25 minutes occurs over a two month period at the solstice. He also found that several tropical ungulates appeared to utilize photoperiod, rather than the traditionally accepted stimuli of food and water availability and forage quality, as the proximal environmental stimulus in synchronizing reproductive activity.

The sunrise-sunset shift is of greater magnitude in Panama -- about 47 minutes over two months' time (Figure 8). A comparison of the reproductive data in Fleming (1973) for Panamanian mammals with sunset-sunrise times shows that the breeding seasons of many of these mammals coincoide with the shift in sunrise-sunset times. The peak effective *S. o. geoffroyi* breeding activity, based on the parturition peak minus the 140-150 day gestation period (Epple, 1970a), coincides with this shift and the month immediately following it.

This correlation may be fortuitous -- it may be that the climatic changes from wet season to dry season may be the proximal cue, or that reproduction is attuned to quantitative or qualitative changes in the diet which accompany this seasonal change. Perhaps many of the plants, which are themselves synchronized for reproduction in the

Figure 8. Shifts in the time of sunrise and sunset at Balboa, Panama Canal Zone.

Figure 8.


time (hours)
0554
0559
0604
0609
0614
0619
0624
0629
0634
0639
0644
sunrise
peak breeding activity
1754
1801
1806
1811
1816
1821
1826
1831
1836
1841
1846
sunset
peak breeding activity
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
month

dry season (Janzen, 1967), use this shift as an environmental cue for the initiation of their reproductive efforts, and the tamarins might use the condition of the plants as their environmental cue. Plants, whose peculiar estrogens may influence mammal reproduction (*e.g.* Negus and Pinter, 1966), may respond to photoperiodic stimuli which are too subtle to be sensed by mammals.

Temperature may be dismissed as a factor which influences the timing of reproduction. While the mean monthly temperature does reach a low in September and October, and begins to climb during the time that peak tamarin breeding occurs, the differences in mean temperature are so slight as to be imperceptible, and the variation among days of the month, and over years, make temperature changes, at best, a highly undependable cue.

The popularly accepted theory regarding the onset of breeding activity in central Panama is that reproductive activity is triggered by the drop in precipitation and humidity which mark the beginning of the dry season (see Figure 1). For many mammals (see Fleming, 1973), the correlation between the onset of the dry season and the onset of breeding activity is a good one. This correlation, however, does not hold for *S. o. geoffroyi*. While Moynihan (1970), on the basis of his observations and Wislocki's (1930b, 1939) data, concluded that most copulations, or effective copulations occurred in January (the first full month of the dry season), his observations, and his interpretation of Wislocki's data, seem in error. Given the 140-150 day gestation period, young conceived on the first day of January would not be born until the 20th of May at the earliest, and most of the young would not be born until June, after the April-May birth peak which Moynihan (1970) observed. Tamarins born in April and May, and the advanced foetuses in Wislocki's (1930b, 1932, 1939) January and February collections, were conceived in November and December. Those born in March had to have been conceived in October, or even earlier. Wislocki (1939) did, however, encounter pregnant females in his June sample, and these foetuses were, as he suggested, conceived in January and February. From this segment of his sample he incorrectly inferred that the peak breeding season occurred in January and February. This statement was accepted by Moynihan, apparently without reference to Wislocki's other data, or his own good data. The matings which lead to the April-June birth peak, rather than beginning with the onset of the dry season, begin in the wet months of late October, November, and early December, and extend through the beginning of the dry season in late December, January, and February. It appears that the stimulus or stimuli which release the physiological changes and associated behaviors leading to the birth peak antedate the coming of the dry season by at least a month.

Thus, the stimulus, or stimuli, which control the timing of tamarin reproduction, remain unknown. The changes in precipitation and humidity which occur in the transition from the wet to dry season occur after the peak breeding season is well underway, and thus do not trigger tamarin breeding activity, as had been supposed (*e.g.* Moynihan, 1970). Photoperiodic changes, the presence or absence of certain plant foods, the possible existence of plant estrogens which might effect tamarin breeding behavior, and perhaps the low levels of available insects and fruit during the last two months of the wet season and during the dry season, are potential environmental cues which merit further investigation.

Clark (1972) and Chapman (1972) discuss the phenomenon of seasonal breeding in mammals. As the latter author indicates, mammals can be classified into two groups on the basis of the reproductive cycle exhibited by the males: 1) Those species that are fecund and breeding throughout the year, and 2) those species which are fecund during some seasons and sexually quiescent in others. The seasonally breeding species may be further differentiated into two categories -- those which exhibit morphological changes in the testes, whether macroscopic or histological, and those that do not.

Most primate species inhabiting the climatically seasonal Middle American tropics show indications of seasonal breeding *e.g., Aotus trivirgatus* (Wislocki, 1930b); *Cebus capucinus* (Oppenheimer, 1967); *Ateles fusciceps* and *A. geoffroyi* (Eisenberg, 1973); *Saimiri sciureus* (DuMond and Hutchinson, 1967); and *Saguinus oedipus* (Moynihan, 1970, and this study). Detailed reproductive data are available only for the *Saimiri*.

Male *Saimiri* undergo an annual testicular cycle which is accompanied by morphological changes attributable to changes in testosterone levels (DuMond and Hutchinson, 1967). Breeding is highly correlated with low levels of precipitation and humidity (DuMond and Hutchinson, 1967; DuMond, 1968; Rosenblum, 1972). Harrison and Dukelow (1973) found that female *Saimiri* on an ovulation-inducing hormone regime showed optimal breeding response only at low humidities. Thus the *Saimiri,* which are small insectivore-frugivores occupying a niche which is very similar to that of *Saguinus* (Eisenberg *et al.,* 1972), offer a classic example of reproductive cyclicity accompanied by readily visible morphological changes.

In contrast, no apparent seasonal changes in reproductive tract morphology or measurements are evident in the seasonally reproductive *S. o. geoffroyi*. Testis size remains relatively constant, and the testes appear to produce sperm throughout the year. However, as Chapman (1972) points out, the presence of spermatozoa in either the testes themselves or the epididymides does not necessarily indicate fertility. Copulations which Moynihan (1970) observed during every month of the year in his captive, wild-caught *S. o. geoffroyi* appear to be largely ineffective during the non-breeding season(s). The reproductive tracts of nonpregnant females also show no seasonal effects.

It is possible that the cyclicity of the system revolves around the reproductive condition of the reproductive females (as noted earlier, only about one-half of the mature females are actually reproductive at one time). Unfortunately, it was impossible to determine whether or not this group exhibited seasonal cyclicity.

The advantages of maintaining constant reproductive tract parameters and retaining the potential of producing two litters per year, over exhibiting seasonal changes in reproductive tract size and morphology and being limited to one litter per year, can only be surmised. It seems likely that the former strategy would be the most advantageous in situations where the animals live in a habitat that is temporally short-lived and is also influenced by predictable seasonal fluctuations. Using this strategy, animals invading new, temporally discrete habitats (*e.g.* scattered areas of second growth in a seasonal tropical forest) might reproduce more rapidly than they would were they bound to a strictly seasonal cycle. This system would also allow the more rapid replacement of individuals lost to mortality. The latter system would be more advantageous where the animals occupy a more or less permanent, yet seasonal, habitat type and are subject to constant, and relatively lower, mortality rates. The latter system would minimize the energy output for reproduction by limiting this activity to the time of year when reproductive return would be the greatest.

The significantly-greater body weights of both males and females in the third trimester (July-October) appear to be related to the general overall increase in individual condition due to the presence of abundant food during the first half of the trimester and the preceding trimester. These figures may also reflect, in part, the maturation and growth of juveniles which entered the adult population in the first trimester as sexually mature, but smaller, adolescents. The general increase in condition is noticeable, however, even in the older animals. This phenomenon appears to be strictly somatic in nature and unrelated to the "fatted male" condition which accompanies reproduction in *Saimiri* (see DuMond and Hutchinson, 1967).

The significance of the wider suprapubic gland in females during the peak season of parturition (second trimester, March-June) is open to speculation. Pregnant females of the common marmoset (*Callithrix jacchus*) have been observed to scent mark more frequently during the two to three month period preceding parturition (H. Box, pers. comm.). Perhaps the wider gland might reflect increased marking activity. It seems probable that, as Epple (1972) suggests, scent markings plays an important role in communicating reproductive information to other group members. Furthermore, it is not implausible that scent marking by reproductive females in areas of territorial overlap might serve to synchronize reproduction in the population as a whole. The use of pheromones in establishing reproductive synchrony is well known (*e.g.* Michael and Keverne, 1968; Bruce, H. M., 1970).

Social groups were observed to contain only one reproductive female, although the average group contained at least one more sexually-mature female. This phenomenon was also observed by Epple (1970a), who found that only one female, the alpha female, reproduced in captive groups of *S. o. geoffroyi* and *Callithrix jacchus*. While the mechanism underlying this phenomenon has not been elucidated for either callitrichid, current research on the reproduction of *C. jacchus* indicates that dominant behavior on the part of one female may lead to a loss of reproductive cyclicity in the subordinate female(s). J. P. Hearn (pers. comm.) has observed that when two normal, cycling *C. jacchus* females are placed together, one will dominate the other, and the subordinate animal will stop cycling. It is probable that this behaviorally-induced blockage of the endocrine system also occurs in the Panamanian tamarin.

The possible significance of this phenomenon will not be discussed herein. It is worth noting, however, that the actual reproductive potential of mature, free-ranging tamarin females is lower than one would expect on the basis of their reproductive performance in the laboratory, where they may bear two litters of multiple young per year (*e.g.* Deinhardt and Deinhardt, 1966). The importance of individual females to the reproductive effort, and the lower actual reproductive potential per female due to behavioral constraints, must be considered in any scheme to "harvest" these primates.

The high rates of infant mortality evident in populations of the Panamanian tamarin (Moynihan, 1970, and this study) might be expected given this tamarin's small size, its many predators, and an adult population which probably approaches carrying capacity. Within this framework, it also appears that infant mortality may also vary according to habitat type. The limited data comparing the reproductive success of upland vs. lowland groups seem to indicate that upland groups are less successful in raising young than are lowland groups. This information dovetails well with the data presented elsewhere in this work on the differences in group composition, group stability, and the use of time and space found between upland and lowland groups. The apparent differences in reproductive success between groups from these two habitats is predicted in Anderson's (1970) comparison of survival and colonization habitats. As indicated in the other sections dealing with this concept, it must be emphasized that the data are only suggestive, and are inadequate for making definite statements about this apparent phenomenon.

Results and Discussion: Parasites

Helminths: The helminth parasites of *S. o. geoffroyi* have been discussed in detail by Thatcher and Porter (1968). The following information regarding parasites found in the collected sample of 131 tamarins is presented in order to provide additional information pertaining to the incidence of certain parasites in this primate, and to include two forms which are not mentioned in the account by the above authors.

Two nematodes, *Trypanoxyuris callithricis* and *Subulura jacchi* were the most common intestinal helminths encountered. Eighteen tamarins (14 percent) were infected with from 1-19 ($\bar{x} = 6.4$) *S. jacchi*. This infection rate is substantially higher than the 4 percent (7/161) rate recorded by Thatcher and Porter (1968). Only ten (8 percent) were infected with *T. callithricis;* compared to 52/161 (32 percent) in the sample collected by Thatcher and Porter (1968). One to ten *T. callithricis* were observed per infection ($\bar{x} = 4.2$).

Seven tamarins (5 percent) were infected with an acanthocephalan, *Prosthenorchis elegans*. Thatcher and Porter (1968) recorded a similar infection rate (4 percent). However, L. D. Hendricks (pers. comm.) found 18 *P. elegans* infections in a sample of 31 tamarins, an incredibly high infection rate of 58 percent. This rate is comparable with the 57 percent infection rate observed by Porter (1972) in 37 *Saguinus oedipus oedipus*. Infection rate by this important parasite, then, may vary widely. It is possible, however, that the high rates of infection recorded by Hendricks and Porter may result from their animals being maintained in captivity for a time before their examination. Epple (1970a) observed that captive tamarins may become infected by eating cockroaches, an intermediate host of *P. elegans*, found in most monkey facilities.

Two parasites not recorded by Thatcher and Porter (1968) were obtained from the collection. The first, a cestode, *Atriotaenia* sp., was recovered from the small intestines of two tamarins. The second, a pentastomid larva, *Porocephalus* sp., was recovered from the lungs of two individuals.

Filarial worms (*Dipetalonema marmosetae*) were discovered in the scapular and thoracic areas of 4 tamarins. Since these were discovered incidently, the actual incidence of infection, as noted by Thatcher and Porter (1968) is probably much higher.

Ectoparasites: Fairchild *et al.* (1968) state that ticks are seldom found on nonhuman primates in Panama. They found only two ticks on *S. o. geoffroyi* - one *Rhipicephalus sanguineus* and one nymph of the genus *Amblyomma*.

Six of the tamarins in the collection harboured one tick each; two were attached to one monkey. All the ticks, which were immature stages of *Amblyomma*, were attached to the nasal septum. When engorged, they completely occluded the nasal aperture. It appears that only those ticks which adhere to the nasal septum survive the allogrooming and autogrooming behaviors of the tamarins. Ticks, together with large quantities of body hair, were frequently recovered from the stomachs of tamarins, particularly during the dry season.

Two nasal mites were recovered from two monkeys. These have been identified as tritonymphs of an unknown species of the Audycoptidae. Further identification is pending.

No attempt was made to collect chiggers from *S. o. geoffroyi*. Brennan and Yunker (1968) report that three species, *Eutrombicula alfreddugesi*, *E. geoldii*, and *Pseudoschoengastia bulbifera* infest Panamanian tamarins.

Blood parasites: Blood samples from 148 tamarins were examined for blood parasites through direct microscopic examinations of thick and thin blood smears. Trypanosomes were observed in the blood of 122 (88.4 percent) of the tamarins; microfilaria were found in the blood of 108 (73 percent) of the animals examined. Ninety-three (62.8 percent) of the tamarins were determined to have mixed microfilarial and trypanosomal infections. In the total sample, 138 (93.2 percent) of the tamarins harbored at least one of the two types of blood parasites. These infection rates are in close agreement with those found in 408 tamarins from Panama and Colon provinces of Panama by Sousa *et al.* (1974).

Three types of trypanosomes were identified in the sample: *Trypanosoma minasense*, *T. rangeli*, and *T. cruzi*. Direct blood examination revealed that 78 (52.7 percent) of the tamarins were infected with *T. minasense*, 37 (25 percent) were infected with *T. rangeli*, and 2 (1.4 percent) were infected with *T. cruzi*. One animal harbored a mixed *T. cruzi* and *T. minasense* infection; two others harbored mixed infections of *T. rangeli* and *T. minasense*. Nine animals were infected with trypanosomes which could not be identified to species.

The above results, however, are probably incomplete. In a test of the blood of 15 tamarins using the techniques of direct blood examinations, animal inoculation, hemoculture, and xenodiagnosis (described in detail in Sousa *et al.*, 1974), direct blood examinations proved to be 100 percent effective in revealing the presence of *T. minasense*, but only about 60 percent effective for *T. rangeli* and completely ineffective for *T. cruzi*. It thus appears likely that the incidence of infections by *T. rangeli* and *T. cruzi* are much higher.

Trypanosomes were present even in very young tamarins. One individual of one month or less of age was infected with both trypanosomes and microfilaria. Two infants of two months of age, and two of three months of age, harbored trypanosomes. (The ages of infants were determined using data on dental ontogeny in Levy *et al.*, 1972). These infections may have been acquired through triatomine vectors; although Lushbaugh *et al.* (1969), indicates that Chagas' disease (*T. cruzi*) can be transmitted intraplacentally in marmosets.

It seems unlikely, however, that the high incidence of trypanosomal infections in Panamanian tamarins can be attributed to intraplacental transmission. The apparent avoidance of Hemipteran prey by tamarins also renders the possibility of infection by ingestion unlikely. A more probable explanation is that a commensal relationship exists between *S. oedipus* and *Rhodnius paelescens*, the principal triatomine vector of trypanosomiasis in Panama. As mentioned previously, the accumulated debris, or nest pads, found at the customary tamarin roosting sites may serve as refugia for triatomine bugs, particularly during the dry season. The potential verification of this possibility deserves further investigation.

SUMMARY

Estimates of Population Density

A modified version of the strip census method of population estimation was used in an attempt to assess the number of tamarins inhabiting dense, second growth vegetation on the Pacific slope of the Panama Canal Zone. This census method, which is commonly and uncritically used by primatologists, proved unsatisfactory under the existing environmental conditions. The combination of low levels of visibility within the forest and the large size of tamarin home ranges militated against the probability of observer-group contact. Daily estimates of population density were highly variable; on most days, one would conclude that there were no tamarins in the area, while on others estimates as high as 200 tamarins per square kilometer were obtained. When plotted, the distribution of the number of animals seen over censuses was decidedly skewed. Attempts to normalize the distribution and to assess limits of precision for individual estimates by increasing the number of censuses taken or by lengthening the census transects would be impractical under the limitations imposed by the variable tamarin activity pattern and the monetary and temporal considerations present in most field studies. It is suggested that the strip census method be reserved for species living under conditions in which the probabilities of animal-observer contact are much higher.

A second method of density estimation, the mapping of tamarin home ranges and the extrapolation of density estimates from those home ranges to larger areas is more promising, but not devoid of shortcomings. The following factors must be considered in the application of this census technique: 1) It is physically difficult to map tamarin home ranges in the dense vegetation favored by the animal; thus the number of estimates from which extrapolations can be made may be inadequate; 2) the degree of exclusivity in home range usage varies with the group and the habitat; thus one must carefully document home range overlap before assigning density values to the home range; 3) immigration and emigration are common phenomena; one must be certain that the movements of the marked animal followed are representative of group movements; and 4) animal density within habitats may vary seasonally; thus, estimates of ecological density must be adjusted according to season.

Neither of the above methods is sufficient for the formulation of absolute density estimates. The former method should not be used to assess the population density of tamarins living in densely-foliated environments; the latter method, if rigorously and critically applied, will yield valid estimates of population density.

Analysis of the Tamarin Diet

The diet of *S. o. geoffroyi* is diverse and exhibits great seasonal variability. Fruits, flowers, or buds of 108 plant species were used by tamarins during the study. Of these plants, 69 were identified to family, 54 to the generic level, and 26 to species.

Eight orders of the Class Insecta were also represented in the diet, as were members of the Class Arachnida. Vertebrate prey utilized by tamarins included two species of lizards and the eggs of birds.

The animal portion of the diet was found to be substantial - between 36 and 64 percent of the volume, depending on the season. While these figures may be inflated due to the behavioral considerations discussed in the text, they do indicate the importance of animal protein in the dietary requirements of this species. The shift from a preponderance of plant foods during the dry season to insect prey during the early wet season, when both fruit and insects are at their yearly peak of abundance, seems to denote a preference for insects when they are readily available.

Orthopterans, primarily large grasshoppers, were the most important insect prey, comprising over 70 percent (by volume) of the diet's animal component. Lepidopterans (primarily larvae) and Coleopterans together comprised over 20 percent of the remainder. Vertebrate prey items, *i.e.* lizards and bird eggs, are probably relished, but appeared to be relatively unimportant prey items.

Small fruits (< 1.5 cm) were the mainstay of the plant component of this tamarin's diet. The presence of various fruit types in the diet reflect annual and biennial phenological cycles within the plant community. The implications of seasonal differences in fruit utilization are discussed in the text.

The scarcity of both insects and fruits during the dry season and the latter part of the wet season is reflected in the loss of fat reserves and weight by the tamarins. Striking differences in the local availability of food elicit marked changes in tamarin behavior.

Groups inhabiting food-poor upland areas both devote a greater percentage of their time budgets to foraging and increase their spatial range. Seminomadic wanderings occur, with the groups travelling far beyond the boundaries of their wet season home range. Territorial disputes with neighboring groups also become more frequent.

The Use of Time and Space

The activity pattern of this tamarin may be unique in the Platyrrhini. Unlike other members of the suborder, this primate begins its daily activity comparatively late in the morning and generally terminates its activity well before sunset. Thus it does not utilize a one to three hour period in which it might forage. The significance of this activity pattern, together with the assumption of apparent torpor on the part of roosting animals, has been discussed in relation to predation pressures, competition, and the optimal procurement of energy.

Levels of activity were not constant throughout the day, but rather followed a definite pattern. During the early morning hours, the tamarins were active in foraging, travel, and territorial defense. Activity slackened during the heat of the day, when the tamarins alternately loafed and foraged in localized, heavily-shaded areas. Mid-afternoon marked an increase in travel and foraging activity. Activity, in the form of both foraging and travel, increased dramatically just prior to entering the roost tree. The day's activity was often climaxed with rapid, silent, and direct travel of 200 meters or more to a roost tree.

Travels within the home range appeared to be influenced by a number of factors, including: 1) The availability of food resources, 2) the existence of areas of overlap with other groups, 3) the availability of suitable arboreal runways and associated escape cover, 4) the location of suitable roosts and rain shelters, 5) the weather, and 6) the time of day with attendant thermal considerations.

Areas of low brush, vine-enshrouded trees (particularly along forest edges), and areas of vine-covered trees interspersed with emergent palms with favored habitats for foraging and travel. Areas of open forest, whether on xeric or mesic sites, sparsely-forested openings, and areas of grass were avoided. The canopy of the gallery forest, with its associated vines, was used in foraging, travelling, loafing, and roosting.

One tree species, *Anacardium excelsum,* the wild cashew, was particularly important to tamarins in this area. *Anacardium excelsum* is the predominant tree in the gallery forest, where it exceeds 20 m in height. Most of the wet season roosts occurred in tangles of vines in the tops of *A. excelsum;* these tangles of vines were also used as rain shelters. The nondeciduous leaves provided protection from the sun at all times of the year and also served as dry season refugia for the tamarins' insect prey. Finally, the *A. excelsum* fruit and the swollen capsule above the fruit were important food sources during the late dry season when other fruits were scarce. The movements of tamarins throughout the year were affected by the location of *A. excelsum.*

The location of areas of group overlap also influenced patterns of movement within the home range. Most areas of overlap were visited daily; intergroup altercations often occurred at these sites.

The pattern of home range usage employed by the lowland groups in this study differed radically from the usage pattern employed by the upland groups. The home ranges of lowland groups were defended as exclusive territories; in contrast, the home ranges of upland groups overlapped extensively and were not defended as exclusive areas. The difference in utilization patterns may result from behavioral responses to seasonal differences in the carrying capacity of the home ranges. An argument for this viewpoint may be found in the text.

Group Composition and Stability

The size of *S. oedipus* social groups observed was small, averaging six to seven animals per group. The male/female sex ratio appeared to be 1:1. The social groups observed did not appear to be family groups, but rather groups consisting of an adult, presumably alpha female, an adult, presumably alpha male, young of the year, and a complement of transient, subordinate animals (some sexually mature) of both sexes.

Group composition was not stable. One reproductive female and one resident, presumably reproductive male, formed the core of the social groups. Infants and juveniles less than one year of age were also sedentary. The remainder of the group changed frequently through emigration, immigration, and mortality. Of these three mechanisms, emigration and immigration were responsible for most alterations in group composition. Forty-one immigrations and emigrations (considering emigration and subsequent immigration by the same individual as separate events), fourteen disappearances and one death were recorded while observing five groups over a period of 10-15 months per group. While emigration to adjacent groups was common, one emigration of 6.5 km was recorded, and several tamarins travelled more than 2 km from their group of origin. Both mature and immature tamarins of both sexes immigrated and emigrated according to the proportion of their sex-age class in the population. Groups inhabiting upland sites appeared to be less stable than groups occupying lowland sites. The probable evolutionary and behavioral significance of the apparently bisexual dominance system, high rates of group interchange, and differences in group stability are discussed in the text.

Reproduction

Most tamarin births occurred from March through June, with a distinct birth peak from late April to early June. Reproductive activity, however, occurred throughout the year. Pregnant females and/or newly born young were encountered in every month of the year. A number of early pregnancies in April and May, and the presence of well-developed foetuses in a female collected in September point to the possibility of a potentially bimodal birth peak. However, the potential for extra-birth peak reproduction is probably not realized, since sightings of infants outside the March-June birth period were rare.

These observations were supported by the morphological examination of male and female reproductive tracts. No significant differences were apparent in the size or appearance of reproductive tracts collected throughout the year. Histological examination of male testes indicated that gametogenic tissue was present from April to January. Testes of males collected from January to April were not examined, but gametogenesis must occur during that time to account for young born in May and June. Thus while the potential for reproduction is present throughout the year, few young are born, or survive long enough to be observed, outside the March-June period of parturition.

A number of external stimuli which might influence the timing of reproduction have been examined. Changes in photoperiod and temperature were discarded as possible factors since changes in these factors are almost certainly too small to be perceptible. Changes in humidity and rainfall between the wet and dry seasons were also discarded since peak tamarin breeding activity occurs prior to this event. Shifts in the time of sunrise and sunset which coincide with the initiation of breeding activity are suggested as possible external cues, as are plant estrogens.

The data on reproduction also indicate that only one female per social group is reproductively active. This phenomenon is discussed in light of past observations and current research.

Parasites

The incidence of parasites in collected tamarins, and the significance of these parasite loads are briefly discussed with reference to other research and aspects of tamarin ecology.

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