Ecology and Social Organization of the Cotton-Top Tamarin *(Saguinus oedipus)*

By

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[1] INDERENA stands for Instituto de Desarollo de los Recursos Naturales Renovables, Bogota, the equivalent of that portion of the U.S. Department of the Interior which has jurisdiction over renewable natural resources.

INTRODUCTION

F. Fraser Darling (1937) and C.R. Carpenter (1934, 1935, 1940) pioneered the realm of field investigation of undisturbed mammalian groups, showing that it is possible to condition wild groups to the observer's presence and by accompanying them to learn their habits. Although a number of workers applied these methods in the 1950's to North American cervids (e.g., Altmann, 1952, 1956; DeVos, 1960; Harper, 1955; Linsdale and Tomich, 1953), field work on primates did not become fashionable until the 1960's. The number of studies has since multiplied rapidly.

Typical species' group-size and other characteristics were initially linked to gross habitat-based ecological categories and diet (Crook and Gartlan, 1966; Eisenberg, Muckenhirn and Rudran, 1972). As the number of species studied grew, the focus became the variety of population dispersion and group organization patterns that could be found within the suggested ecological groups (Struhsaker, 1969; Clutton-Brock, 1974). However, Clutton-Brock and Harvey's (1977a) recent comprehensive analysis of the extensive literature showed significant differences across gross ecological categories with respect to group size and weight, home range size, day range and population density.

Some nevertheless continue to stress that great differences in social organization within species or between closely related ones can sometimes be linked to relatively fine differences in ecology, especially those affecting foraging strategy, such as proportion of different food types in the diet and density and dispersion of food (e.g., Hladik and Hladik, 1972; Clutton-Brock, 1975, 1977; Durham, 1971; Klein and Klein, 1977). Recent analyses of social organization among ungulates (Jarman, 1974; Geist, 1974), kangaroos (Kaufman, 1974), carnivores (Schaller, 1972; Kruuk, 1975) and bats (Bradbury and Vehrencamp, 1976) have also focused on correlations with ecological parameters. Primate studies have thus converged on a theme which also presently predominates in the heretofore largely separate literature of theoretical ecology.

The intra-specific variation in social structure which has been documented for some primate species suggests however that theories based on one study only for each species being compared could be misleading. Evolutionary trends are not easily untangled from random variation (that is, variation of no adaptive significance): "while ecological factors may determine the upper limit of group size and may favor social rather than 'solitary' living, within these limits group size and sex composition may be arbitrary. Similarly, local differences in the species composition of diet, and in the amount of time spent feeding on particular foods, may reflect arbitrary differences of 'tradition' between groups rather than a real difference in food availability" (Richard, 1974). Studies of various populations of a given species will be required in order to define in what way social systems are directly affected by selection. At present the primate literature suggests that species-modal patterns may be, in many instances, definable only in rather broad terms.

Neotropical primate studies[1]

The New World primates have received relatively little field study

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[1] Spelling and taxonomy used in this work follow Napier and Napier, 1967.

compared to African species. This lag may be related to the methodological difficulties inherent in observing arboreal primates (see, for example, Aldrich-Blake, 1970), and/or to the lesser accessibility of sufficiently undisturbed forests in which to carry out studies.

Hershkovitz's (e.g., 1977) classification of New World primates into three families - Cebidae, Callitrichidae, and Callimicasidae - has until recently been widely accepted and used. His placement of contemporary cebids in seven subfamilies reflects the enormous diversity in diet and morphology encompassed by the group (Table 1). Although only 14 out of the 29 species (representing 7 out of 11 genera) included have received focused field study,[1] information is sufficient to document the fact that their morphological variability is paralleled by striking diversity in social organization and resource relationships (Table 1).

Most species are diurnal, but the group includes _Aotus trivirgatus_, the only nocturnal true primate. In some species, groups are relatively large with one to several adult males and several reproducing adult females (_Ateles_, _Alouatta_, _Cebus_, _Saimiri_) while in others (_Aotus_, _Callicebus_ and probably _Pithecia_) groups probably consist of one reproductive pair plus associated offspring and perhaps other individuals (Moynihan, 1976a). The most recent analyses of platyrrhine relationships, using developmental and reporductive features (Luckett, 1979) and cranial, dental, postcranial and soft tissue morphology (Rosenberger, 1979) emphasize inter-generic relationships and the lack of clear distinctions between the Cebidae and Callitrichidae.

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[1] See Clutton-Brock and Harvey, 1977a, and Baldwin et al., 1977b, for recent bibliographies.

TABLE 1

A comparison of the two primate families, Cebidae and Callitrichidae

	Cebidae	Callitrichidae
No. of genera	11	5
No. of species	21	19
Size range (head plus body)	28-58cm	13-24cm
Weight range	400-10,000gm	50-560gm
Sexual dimorphism:		
-in size	none to moderate	none known
-in color	in 2 species	none known
Locomotion	quadrupedal to semi-brachiating	quadrupedal or vertical leaping
Limb specializations	none to elongated arms	none
Tail specializations	none to prehensile	none
Hand/foot specializations	thumb and hallux opposable nails on all digits	thumb not opposable hallux opposable nail on thumb, hallux claws all other[1]
Number of chromosomes	20-62	44 or 46
Diet	insectivory/frugivory, to mainly herbivory to mainly frugivory	insectivory/frugiv.; exudate-eating
Temperament	quick to lethargic	quick
Group organization	monogamous pairs to single male multi-female to variable group to large age-graded	chiefly small family groups, one breeding female male carries young
Number of young in litter	1	2-3[1]
Recency of radiation between genera	recent to older	recent

Taxonomy follows Napier and Napier, 1967.
References: Hershkovitz, 1972a; Napier and Napier, 1967; Moynihan, 1976a; Boer, 1974; Cronin and Sarich, 1975.

[1] Except Callimico, which in these characters is more cebid-like.

The Callitrichidae constitute a rather uniform group with respect to basic morphology, diet (basically frugivore/insectivores) and, apparently, social organization (Table 1). The range in size in 19 species is minimal. Since size is evidently a key element in resource partitioning among primates (Freese and Heltne, 1978), this may account for the fact that whereas various cebids commonly co-occur this is rare for Callitrichids over most of their geographical distribution. The three Brazilian *Callithrix* species are allopatric to each other as well as the only Callitrichids in the major part of their range, although minor geographical overlap occurs with *Saguinus midas* and *Leontopithecus* (Figure 1). There is no published information regarding the extent of ecological separation between them. The two genera considered to be most closely related based on cranial and dental characteristics (Hershkovitz, 1949) and skin morphology and cyto-chemistry (Perkins, 1975), are *Callithrix* and *Cebuella*, the two genera with non-overlapping distributions. *Cebuella* co-occurs throughout its range, however, with *Saguinus fuscicollis* plus seven other *Saguinus* species with non-overlapping distributions, all sympatric to one or more races of *S. fuscicollis*. Recent field studies suggest basic ecological separation between *Saguinus* and *Cebuella*. The latter is primarily sapivorous, relying on tree sap as the mainstay of its diet, while *Saguinus* species are primarily frugivore/insectivores (Enders, 1930; Fooden, 1964; Hladik, 1967; Hladik, et al., 1971; Dawson, 1976; Izawa, 1976, 1978). To the North of the Amazon-Japura occur five additional *Saguinus* species, including *S. oedipus*, the subject of the present

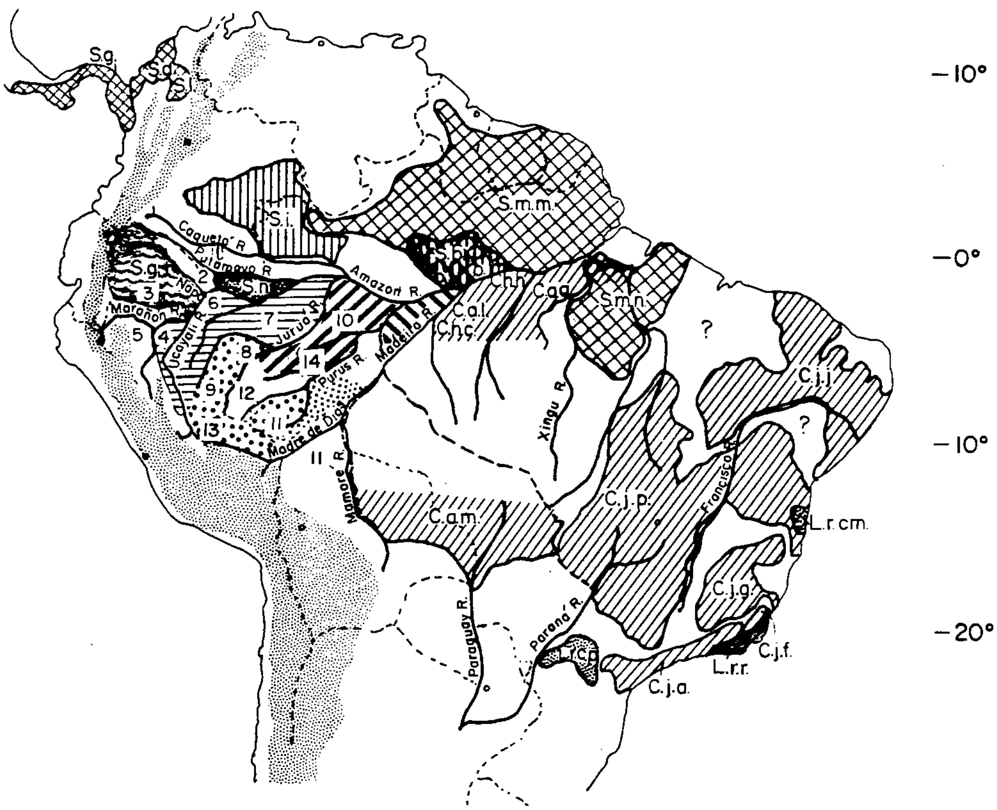

Figure 1

Distribution of the family Callitrichidae

See notes on following page

Footnotes Figure 1

[1] Hershkovitz, 1968

[2] Coimbra-Filho and Mittermeier, 1973

[3] Distribution of Cebuella pygmaea not figured. Occurs within S. fuscicollis range between Purus and Caquetá/Japurá rivers, extending west to the Ucayali, Huellaga, and Pastaza Rivers. (Hershkovitz, 1977)

[4] Hershkovitz, 1966

[5] Hershkovitz, 1977

[6] S. fuscicollis ssp. and limits are as depicted by Hershkovitz, 1977.
1, fuscus; 2, tripartitus; 3, lagonotus; 4, illigeri; 5, leucogenys;
6, nigrifrons; 7, fuscicollis; 8, melanoleucus; 9, acrensis;
10, avilapiresi; 11, weddellii; 12, cruzlimai; 13, crandalli;
14, primitivus

The approximate limits of Callimico goeldii are: Caquetá/Japurá - Javari rivers, then south as far as Madre de Dios from E bank of the Ucayali spreading east. Eastern limit uncertain. (Hershkovitz, 1977) study and the northernmost representative of the family.[1] It is endemic to Colombia.

Previous Work on Callitrichid Biology

The largest body of literature pertaining to Callitrichids derives from captive studies partly as a byproduct of the maintenance of large colonies for research purposes. Their small size, relative tractability compared to larger species, ease of maintenance, and (until recently) the low cost of imported wildcaught animals has made them economical laboratory subjects. They have proved uniquely susceptible to certain diseases affecting humans, for example infectious hepatitis, herpes simplex, human slow viruses and various RNA and DNA tumor viruses (see Wolfe, et al., 1972). High fecundity, similarity of female hormonal cycles to humans, and rapid maturity makes them good subjects for studies of pregnancy, testing of antifertility agents, or studies of physical, behavioral and endocrinological parameters of maturation (Hearn, et al., 1978). They have also been used for testing drugs, in the study of dental disease, and in studies of language acquisition and perception (see contributions in Gengozian and Deinhardt [eds.], 1978).

Captive studies have utilized principally four species: *Callithrix jacchus*, *Saguinus fuscicollis*, *Saguinus oedipus*, and *Leontopithecus rosalia*. They have furnished much information on the care and management of captive colonies, and behavior, anatomy, general physiology, and reproductive physiology and performance under captive conditions. Here

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[1] For purposes of this report I have utilized the Hershkovitz pre-1966 classification, which regarded *Saguinus oedipus* as a separate species from the Panamanian form, *Saguinus geoffroyi*. See also Napier and Napier, 1967, and Hernandez-Camacho and Cooper, 1976.

the findings of principle interest are those pertaining to social organization. Those findings have been strikingly similar in all Callitrichids studied so far, and will be briefly summarized as background for the present study (For recent reviews of this material, see Epple, 1975, 1978; papers in Kleiman (ed), 1977a).

The most stable captive groups are those consisting of one adult reproductive pair plus offspring. Offspring are tolerated often to at least several years of age, that is well past reproductive maturity (which occurs at 1½-2 years). The male participates equally with and often in excess of the female in carrying, retrieving, sharing food with, and otherwise caring for the young. The relative participation of the male and female varies between pairs and in the same pair between litters. Older offspring also help as do any non-related adults which may be present. When serious fighting occurs it invariably involves two individuals of the same sex. It may involve siblings, parent and offspring or - by far the most frequently the case - unrelated adults. Groups containing more than one unrelated adult of the same sex are strikingly less stable than family groups, and fighting usually results eventually in one of the two combatants having to be removed to save its life. Aggression between females seems to be particularly marked. Strangers introduced to any laboratory group are attacked by its members, particularly those of the same sex. Regarding reproduction, it has been found that if a group includes more than one adult female only one produces young. In Callithrix jacchus this has been shown to be due to a cessation of hormonal cycling in the non-reproductives (Hearn, 1977). The mechanism involved has yet to be investigated. Observers discern a dominance hierarchy among group members of the same sex and refer to the reproductive female as the alpha female. If more than one adult male is present, one will form a closer bond with her than the others, as measured by sexual behavior and affiliative measures such as contact and grooming. Subordinate males may copulate with the alpha female (as well as with any other females present), but in Callithrix jacchus at least the copulations of subordinates are apparently seldom complete (Rothe, 1975). If the alpha female is removed from a group, another female begins cycling; if a subordinate female is removed from her group and paired with a male, she conceives almost immediately. There is no evidence of seasonal reproductive quiescence in either sex, although in some species conceptions are more likely in some months than others. Behavioral and endocrinological data suggest an ovarian cycle of about 16 days (Chase, 1967; Hampton and Hampton, 1965, 1977; Hearn, 1977; Kleiman, 1977b; Gengozian, et al., 1978).

Current theory generated from these findings is that the family group is the "natural" group for Callitrichids, and that extreme inter-female aggression is a mechanism for preventing other females from approching the mate, whose help is assumed crucial to her reproductive success (Eisenberg, 1977; Epple, 1978).

It is evident from the foregoing that Callitrichids are of considerable interest from an evolutionary point of view, because they combine several traits which are rare among primates and among mammals in general: group-living, monogamy, extensive paternal care, the presence of "helpers" to the reproductive pair, monomorphism, and territoriality (although, see Discussion). From the standpoint of their ecological niche they are unique among primates. They have no strict Old World primate parallels (Eisenberg, 1977). The New World Callitrichids have occupied niches which in the Old World are largely occupied by members of the family Sciuridae. The presence of Callitrichids may have prevented the late-invading Sciurids (in the Pliocene) from undergoing in the New World a vast radiation similar to that which they experienced in the forested regions of Africa and Southeast Asia (Hershkovitz, 1973; Eisenberg, 1977).

Published field studies on Callitrichids have only recently begun to appear, and still concern only a minority of the family's 19 species: Saguinus geoffroyi (Dawson, 1976, 1977; Moynihan, 1970, 1976a; Muckenhirn, 1967); S. midas (Thorington, 1968; Durham and Durham, in press); S. fuscicollis (Castro and Soini, 1977; Izawa, 1975, 1976); S. imperator (Terborgh, in press); S. nigricollis (Izawa, 1978); S. mystax (Castro and Soini, 1977); Cebuella pygmaea (Ramirez, et al., 1977; Moynihan, 1976b); Leontopithecus r. rosalia (Coimbra-Filho and Mittermeier, 1973; Coimbra-Filho, 1977); and Callithrix jacchus (Stevenson, in press). These studies have yielded information on group size, inter-relations of groups (splitting, merging, etc.) and some basic habitat-use and diet information. Only Dawson's study, initiated at about the same time as the present one, involved an in-depth investigation of marked groups. Izawa (1978) described the ecology and relationships of a number of unmarked S. nigricollis groups which could be approached closely enough to distinguish them with natural markings.

The purpose of this study was to delineate the basic ecology and social organization of Saguinus oedipus, a species about which much was known from captive studies but which had never been studied in the wild.

THE HABITAT OF THE STUDY POPULATION

The forest of approximately 600 hectares was located about 15 km to the east-northeast of Tolu, Sucre, on the Caribbean coast of Colombia (about 9°34'N, 75°27'W) (Figure 2). The terrain constitutes part of an alluvial plain formed from the San Jacinto hills lying just to the east (560 m maximum altitude). The study area elevation is somewhat less than 100 m (Instituto Augustin Codazzi, 1969). The terrain appears level, but after a heavy rain the standing water flows actively along the surface of the ground and drains into a network of channels or "arroyos" 3 to 7 m deep which carry the water seaward. The larger arroyos carry streams which constitute the only source of water during the long dry season.

Because of the relatively low rainfall and its highly seasonal distribution, Espinal and Montenegro (1963), applying the Holdridge classification to Colombia, designated the region as one capable of supporting "very dry tropical forest." Weather records from nearby cities suggest the average annual rainfall in the study area is around 1200 mm.[1] Between December and April when there is practically no precipitation, an estimated 60 percent of trees lose their leaves for part or all of the period.

An examination of the species composition of the forest (Appendix 2) reveals, contrary to predictions based on Holdridge criteria, a notably small proportion of species with xeromorphic adaptations (spines, thorns, leaves with highly reduced surfaces (leptophils, nanophils, microphils)). A considerable number of species with decidedly hydrophilic ecological preferences were in fact present and not concentrated around arroyos,

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[1] See also Appendix 3.

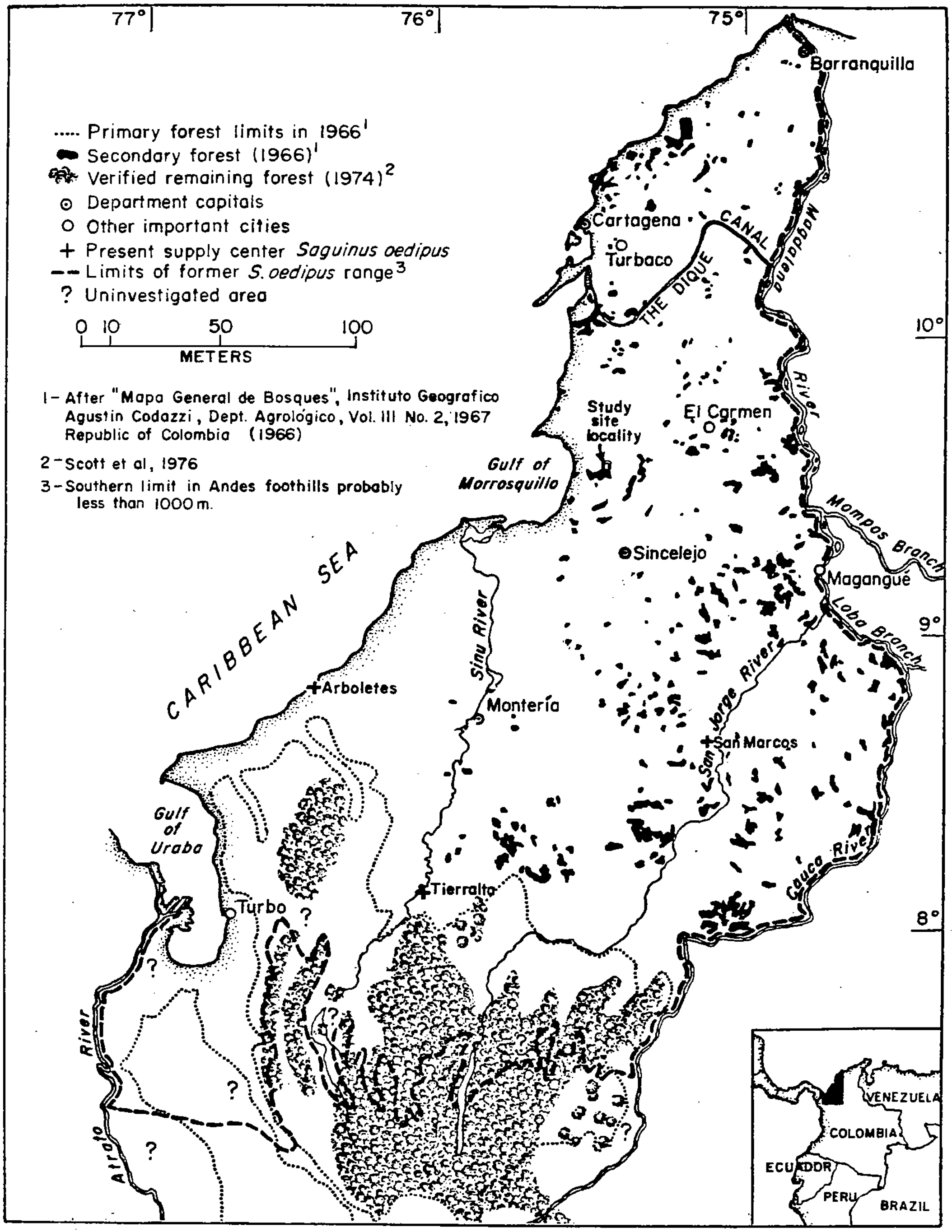

Figure 2

Location of study site and distribution of forest remaining in the original range of Saguinus oedipus for example *Bactris* spp., *Sabal mauritaeformis*, *Lecythis magdalenica*, *Cavanillesia platanifolia*. This may be due to the fact that during the heavy rainfall months of August through November, large areas of the forest become flooded in most years. About 30 percent of the study area was flooded to three feet or less at the worst of one very rainy year (1974). In the preceding very dry year, the forest floor remained nearly dry during the same period. Even during the wet season, three to four days without rain - a not uncommon happening - had a marked effect in drying out the forest floor. A scarcity of epiphytes and climbing vines attested to the relative dryness of the area.

The species composition of the forest, detailed in Appendix 2, is according to my experience typical of secondary forests in Northwestern Colombia. Abundant and easily recognized species include *Luehea* sp., *Bursera simaruba*, *Cavanillesia platanifolia*, *Pseudobombax septenatum*, *Cecropia* spp., *Inga* spp., *Spondias mombin*, *Pithecellobium* (*Samanea*) *saman*, *Lecythis magdalenica*, *Gustavia* sp., *Triplaris* sp., *Calycophyllum candidissimum*, *Guazuma ulmifolia*, *Brosimum* sp., *Muntingia calabura*, *Swartzia* spp., *Garcia nutans*, *Sapium* sp., *Ormosia* sp., *Casearia* spp., *Mayna* sp., *Trichilia* sp., *Urera* sp., *Hybanthus prunifolius*, *Picramnia latifolia*, *Randia* spp., *Quararibea* sp., and various palms including *Sabal mauritiaeformis*, *Astrocaryum malybo*, *Astrocaryum* sp., *Bactris major*, *Bactris pilosa*, *Bactris macana*, *Cryosophila kalbreyeri*, and *Eleais oleifera*. Less abundant are *Ceiba pentandra*, *Bombacopsis quinatum*, *Cedrela* spp., *Enterolobium cyclocarpum*, *Prioria copaifera*, *Sterculia apetala*, *Cochlospermum vitifolium*, *Cordia alliodora*, and *Anacardium excelsum*. The forest floor is dominated in some areas by *Astrocaryum malybo*, a very spiney palm branching from the base. In other areas a mixture of saplings, low palms, and *Heliconia* spp. predominates. Dense 2-3 m tall, *Heliconia* stands occur in areas which receive lots of sun. Ferns occur in some well shaded areas. The relative scarcity of densely vined areas and the openness of the floor in most places, plus the frequency of trees exceeding one or two feet in diameter, suggest a forest of some maturity. Nevertheless, the canopy is quite broken - only infrequently is travel possible at heights exceeding 15 m for more than 50 m in any one direction. Breaks in the canopy are due to both selective logging (see below) and tree falls occurring during seasonal high winds (cf. September-November). In 1973 one such "hurracano" blew over so many trees in one section of the study area that a continuous canopy did not remain at any level (Figure 3). Occasional falls of individual trees due to winds or cutting caused extensive damage to adjacent trees and thereby created openings. Some clearing had also been done previously to facilitate moving logs out of the forest by tractor, and to create work areas at the periphery of the forest where logs could be stacked and sawed. The most recent extensive exploitation of the forest which involved creating clearings occurred in 1970.

This forest is one of the larger remnant forests persisting in what was once a predominantly forested region. It is now surrounded by pasture and contains an essentially isolated population of S. oedipus. Some dispersal by arboreal forms is possible via fence lines which connect to arroyos, since both fence lines and arroyos are often lined with trees. S. oedipus has been seen to cross between forest blocks on the ground also (C.A. Leon, pers. comm., 1973).

Human intervention affecting the forests of Northwestern Colombia probably dates back to at least precolonial times, as Indian remains are common in nearby areas. The pastures surrounding the study forest were cleared less than 15 years ago. The area occupied by the forest was not itself clearcut, but has been subjected to continuing selective cutting.

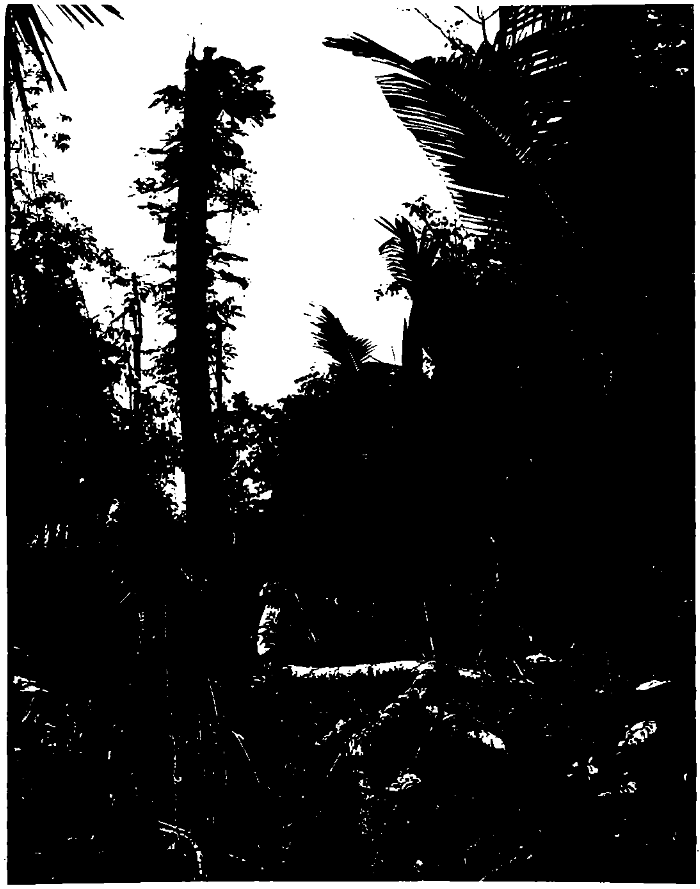

Figure 3

Effects of high seasonal winds on one section of study area

So many canopy trees were downed as to completely destroy continuity at any level. The "hurracano" responsible occurred in October, 1973.

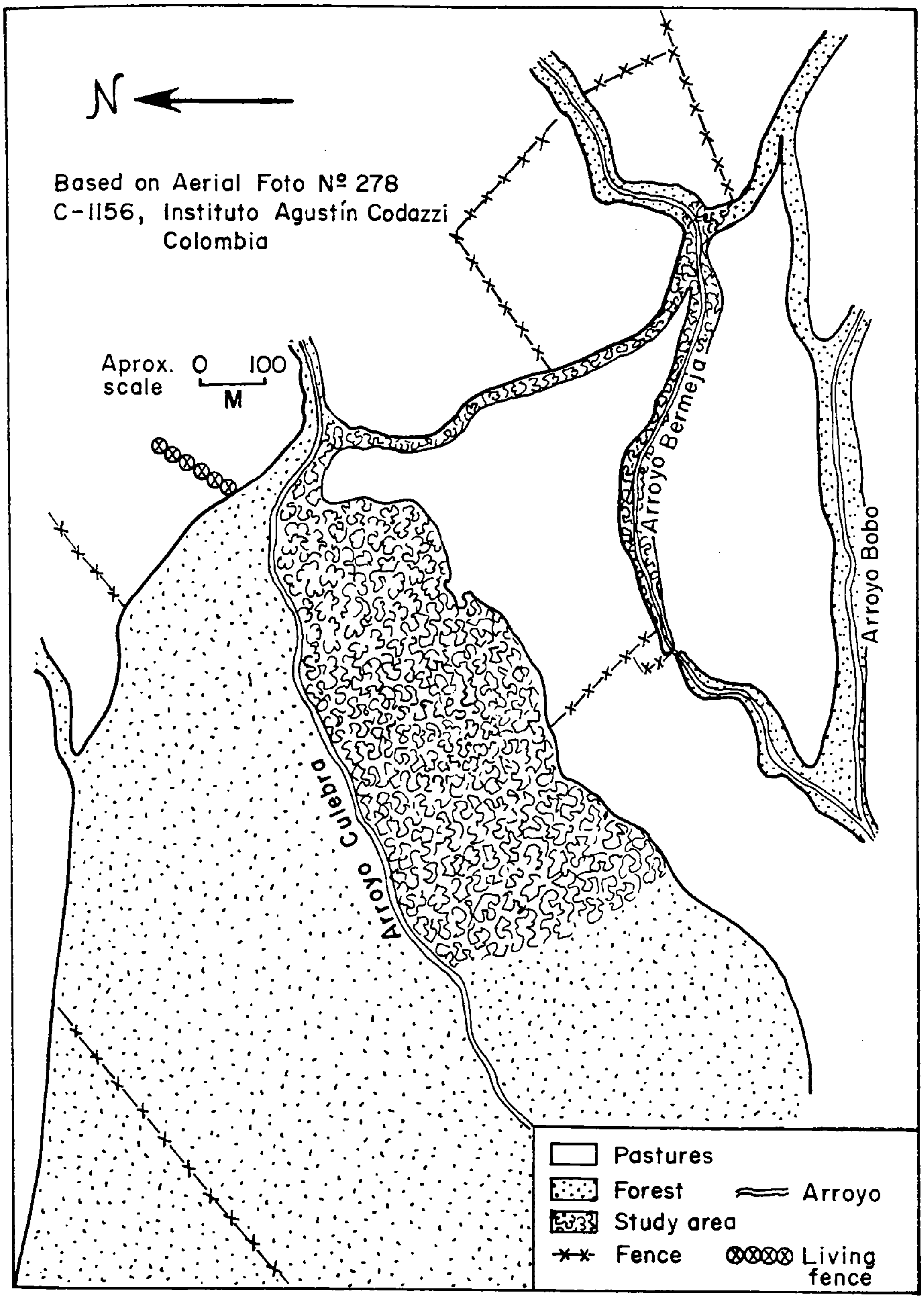

Figure 4

Relation of study area to forest block
and adjacent forested corridors

METHODS

Data were collected continuously between August 1973 and August 1975, and in July-August 1976 and 1977. Trapping was initiated in January 1974 and the first animals marked in May 1974. Prior to that all data collected were on unmarked groups.

Basic procedure consisted of searching for tamarin groups and following them until contact was lost. Success in following was greatest with one group (UB) which frequented the narrow forest-arroyo strip of 7 hectares (Figure 4) and with those groups in which one member was marked with a bell. Over half the approximately 755 hours of total contact time was spent with the UB group.

The three most-followed groups (UB, Ka, Ba) became somewhat conditioned but always showed nervousness if observed intently, especially if binoculars were used. Minimum approach distance was about 20 m. Frequently attempts to observe them as they rested or engaged in feeding or grooming resulted in their moving to more hidden branches or leaving the area completely.

Minimal data were obtained on unmarked groups, as it was not possible except in one case to distinguish individuals or to be certain whether the same group was encountered on different days in a given location. Age and sex composition of groups, often used by field workers to distinguish troops, was not helpful here. Tamarins cannot be sexed at a distance unless one happens to be lucky enough to get a clear look at the genitals - and even then the female's well-developed circumgenital pad can be mistaken for testicles. Age classes are short-lived, as tamarins mature at about 1½ years. The rapid growth of juveniles renders them indistinguishable from adults at a distance after the age of ten months, unless seen immediately adjacent to an adult. Group size was not a useful criterion either. Difficulties in detecting all members of moving groups often rendered group counts questionable. Marked animals were indispensible therefore for group and individual identification as well as for making group counts. Observations on marked groups showed that some individuals were always bolder than others and were seen repeatedly while others, particularly juveniles and adults carrying young, tended to stick to travel routes out of the observer's sight.

The route followed by a group was crudely marked with a machete in order to follow and map it later. Noise was kept to a minimum. The tamarins did not emit alarm vocalizations, make avoidance movements, or show other apparent signs of disturbance during this activity. Alarm was given only when I actually came into view.

Trapping Methods and Results

National Live Traps similar to those successfully used by Dawson (1976) in the capture of *S. geoffroyi* and using the same bait (ripe plantain) proved ineffective. This was probably due to the traps not being encountered by the tamarins in their movements. They were set on branches the tamarins had been seen using. However, there was a greater variety of strata available for the tamarins to utilize in this forest, much of it unreachable without special equipment. Also the area lacked the division into areas separated by roads with predictable crossing routes that was characteristic of Dawson's study site. The National traps also required more labor to set and maintain than the decoy-type traps finally used. The latter were fabricated locally from wire (Figure 5). The trap units were placed on poles tied between trees at a height of about 1 to 1.2 m, in an area with good visibility to approaching tamarins and where vines

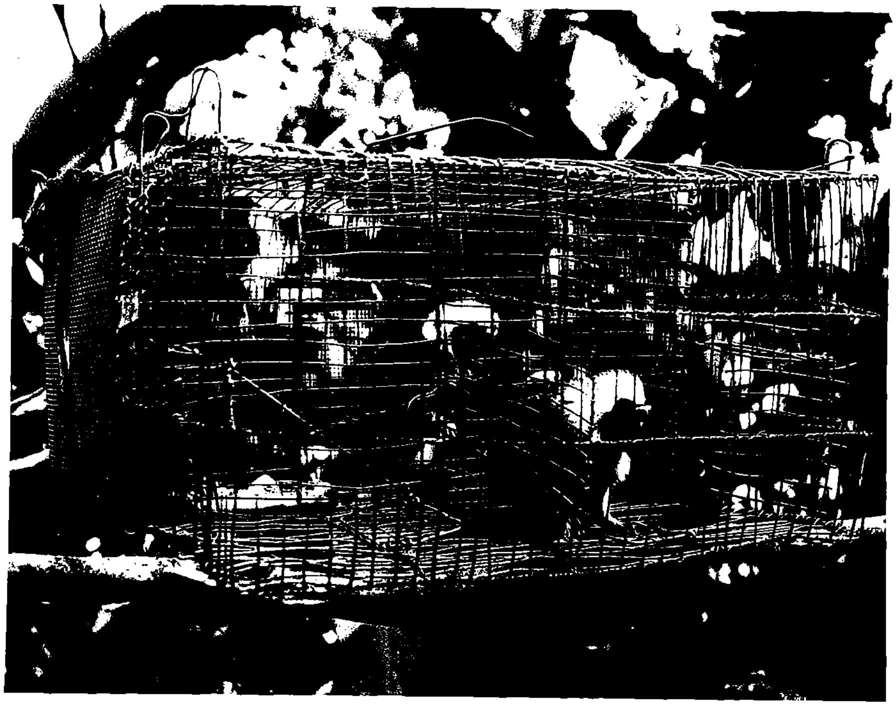

Figure 5

Trap units used for capturing tamarins

or trees provided them easy access to the traps (Figure 6).

A live decoy tamarin was maintained continually in the trap as an attractant. Nearby tamarins would respond to its calls and approach. There were usually only a few days' delay before catching the first animals if the traps were placed in an area where the resident group had recently been seen. Trap success was improved by maintaining them open but not set for several days after a group began visiting them. The first animals caught were often retained in the traps for up to several days because this facilitated the capture of other members of the group. A group with some members in the traps tended to hang around and sleep nearby. Care had to be taken in approaching the traps in order to prevent the group from associating one with them. The captured individuals would vocalize harshly and loudly if stared at from close quarters, or if the traps were touched, and the group would respond by rapidly returning to the scene. Such animals had to be provisioned in the early morning while it was still dark. Some individuals calmed down after a few days and eagerly accepted proffered Musa sp. This post-capture conditioning to a well-liked food plus care taken in approaching and looking at them while encaged may have contributed to the good recapture rate.

With these traps, 165 captures were made in 1181 trap-days (13.9% "success"). One trap compartment (see below) set for one day counted as one trap-day. Thirty two different females and thirty nine males were caught and marked. Thirty five of these (13 females, 22 males) were recaptured. Fifteen (5 females, 10 males) were recaptured once, seven (3 females, 4 males) twice, four (2 females, 2 males) three times, two (2 males) four times, two (2 males) five times, one (female) seven times, and one (male) nine times.

Figure 6

Example of trap setup in forest

Trap Design and Decoy Maintenance

Two types of units were used. One measured 1m x 1m x 0.8m. This was divided with a vertical median partition into two halves, one being reserved for the decoy and the other again divided by a second median partition (perpendicular to the first) into two "trap compartments", each with a trap door. The trap door was held open with an L-shaped wire connected by a second wire to a treadle inside the trap. When released, the door slid shut on wire runners and was held shut by an appropriately placed moveable hook. The efficacy of the hook was variable, but escapes were nonetheless relatively few as the tamarins were usually not persistent or successful in their attempts to wedge under the door.

Later it was found convenient to manufacture the decoy and trap sections separately to facilitate transportation to or through the forest (by mule or foot). Extra trap compartments were also essential for increasing the number of individuals that could be simultaneously captured at the trap site.

Other than transportation from one site to another, the main problems with this type of trap centered around the care and protection of the decoy. An essential feature of a decoy trap is double walls or an extra layer of wire mesh around the decoy's section and the provision of perches so the decoy can get as far from the walls and bottom as possible. This is to prevent injury of the decoy by the visiting tamarins, which often were aggressive toward decoys. The only consistent exceptions were juveniles, which were never attacked. A protected corner was insufficient because rather than retreat to it when surrounded, the decoy jumped back and forth in panic, thus exposing itself to being bitten by one individual while trying to escape from another. The double wall design eliminated actual injuries to the decoy but did not of course reduce the considerable stress involved in the experience.

A further design problem was the protection of the decoy's tail. An open wire floor was used at first, as it conveniently allowed excrements and food residues to drop through, but the decoy's tail often hung outside the cage and was thus vulnerable to mauling by visitors. A solid cage floor was also unsatisfactory, since the tail was then dragged repeatedly through food and excrement. These sticky substances soon were transferred to the rest of the fur. A compromise solution was a solid partition or tray placed a few inches below the wire floor; this reduced the contact of the tail to waste and still mostly protected it from outside attacks.

Openings in the sides of the cage large enough for visitors to reach in had to be eliminated. Otherwise they could grab the decoy and draw it to within biting reach or steal bait or the decoy's food. A protected corner with a small shelf was essential for sleeping and escape quarters from rain.

Three items were critical in the maintenance of decoys: (1) protection from sun, (2) water, and (3) food. When setting the traps it was necessary to choose a spot where the decoy would not be exposed to the sun at midday. It was learned through experience that even a one-hour "sun-spot" at midday can cause tamarin death. Morning sun, on the other hand, is beneficial. Wild tamarins were often observed grooming in the morning sun. The provision of water although seemingly simple presented difficulties. Standard lab-cage water bottles dripped constantly with the movements of the cage as the monkeys jump around; also there was no certainty that the animals used them. In addition, since the bottles were hung on the outside of cages, they were susceptible to perturbation by other visitors such as <u>Cebus</u> monkeys. Open receptacles inside the cage also presented problems, chiefly of volume. No really satisfactory solution to the water supply problem was found. Commonly in a remote location one is limited to utilizing locally available gourds, etc. Water must be supplied not only to decoys, of course, but also to any captured individuals retained in the traps. Insufficiency of water probably accounted for several trap-deaths of captured individuals during one very hot period. It appeared that water deficit was a cumulative phenomenon, since in all cases the individuals in question had been in the traps several days.

Maintaining live decoy tamarins was difficult in a remote area with an irregular and scarce supply of fruit and protein. Obtaining food for them, even such a relatively common item such as plantain, required time-consuming trips to nearby population centers. The lack of refrigeration limited the quantity of supplies that could be bought in any one trip. The exigencies of transport (e.g., the mule trip required, limited space, etc.) as well as seasonality of fruits practically dictated that the staple food for the tamarins was plantain. Local inhabitants claimed to be able to maintain tamarins on the region's human staples - rice, manioc, milk - but I was unsuccessful in getting them to accept these items once accustomed to Musa, which they relished. Only after many months did they show any decline in their interest in it.

One possible strategy for circumventing decoy maintenance problems is the use of broadcast vocalizations plus a stuffed decoy. The necessary equipment to do this was unavailable to me. Another possibility is to use a captured wild individual as a decoy for the neighboring group, returning the former to his own group once some individuals from the new group were caught. I tried this but did not adopt it as the preferable strategy for two reasons. First, it was obviously highly stressful to the encaged wild tamarin to be carried to the new location. Covering the cage during transport helped, but not enough to overcome possible negative effects which might have made it impossible for me to observe that individual once released. A second consideration was the possibility of death or injury of the captured tamarin during its service as a decoy. Every such death represented the loss of a marked animal in which considerable time and effort had been invested. Losses of other decoys were frequent enough. In the process of making the 165 captures, 10 decoys obtained in markets died and 4 wild captured animals died. An additional decoy escaped and two others were left alive with local inhabitants after being used in the traps. Three market animals were in such poor condition when obtained that they were never used as decoys. One animal quit eating after being used for a while in the traps and subsequently died. Only one death involved actual wounding. Five other market animal and 3 wild decoy deaths were thought to have been connected with heat stress. Only one animal was molested by non-tamarin visitors while in a trap. This animal was badly bitten during the day, perhaps while in a moribund state due to heat stress. Cebus monkeys were seen near the traps that day and tooth marks in the bitten individual were large, Cebus sized. They apparently did not molest the traps on any other occasion.

Marking Methods

I drew captured animals into reach from outside the trap using the tail, and then administered the anesthetic ketamine hydrochloride ("Ketaset", Bristol Laboratries, 100 mg per ml.) in the tail or thigh. A dose sufficient for about 20 minutes' unconsciousness was used.(Adult, .02 ml, young juvenile, .01 ml.). Complete recovery and release was possible in about 2 hours.

The tamarins were fitted with a leather collar, or a light neck chain, bearing either a numbered tag (18 mm diameter), or plastic colored "pony" beads or both (Figure 7). Collars were made of leather, about 0.8 cm wide and wrapped with colored fiber-backed plastic tape in different color combinations and designs. They were joined by a twist of wire whose ends were forced down into the leather to hide the sharp surfaces. Tags were attached to the chains or collars via a wire ring, to assure that the tag faced forward. The movement of beads around the chain, which would have disturbed any color-order code of identification, was prevented by placing a chain-link connector on either side of the group of beads. The connector joining the ends of the chain had to be crimped closed with pliers to prevent the chain from being opened by the wearer. The latter was known to have happened in two cases with uncrimped fasteners. Both collars and chains had to be fitted somewhat loosely but not so loosely that they could be forced off over the head or would be caught in vegetation and become a danger to the animal. Animals recaptured up to three years after marking showed no hair loss under their collars or chains. Generally the collar, wire, chain, beads and tags showed no evidence of deterioration, except for occasional slight chewing, or a tendency for the tape to begin unwinding. Some bead colors faded considerably in the course of a year and could have eventually become undistinguishable from other colors at a distance. One captive developed hair loss and lesions under a too-snug collar although exhibiting no signs of distress such as pulling at the collar. Another managed to get the collar in its mouth but could not free its jaw, illustrating a possible danger of a collar that is too loose.

Chains and tags or beads are probably preferable to collars since they appeared more comfortable to the animal. They may be less bothersome to them when they curl up to sleep. Tags, however, have the disadvantage

Figure 7

Captured tamarins marked in different ways
for purposes of identification

of being readable only when the wearer is stationary and facing the observer. The identity of an animal overhead is not ascertainable. Collars are better in this respect but have the disadvantage of rotating about the neck. This means that identifying colors can be hidden unless a wrapping design extends the whole length of the collar. Also, collar colors were sometimes difficult to distinguish. Yellow and white, red and orange, and green, blue and black can be confused in the deep shade frequented by the tamarins. For example, an orange and yellow collar appeared red and white until it was possible (after observing the animal for some time) to see it in the sunlight. Bead or tag colors potentially have the same problem but it seems to be less pronounced because they tend to hang out of the shadow cast by the chin.

One or two animals in each group were marked with a bell as an aid in following the group. The bell with the lowest tone (a falcon bell) doubled the range of detection (normally a maximum of 15 to 25 meters) and facilitated tracking without visual contact. Visual contact was frequently lost when groups moved quickly or when they entered dense viney areas to forage. Radio tracking equipment (used by Dawson) might have been preferable, of course, but was not available to me.

Animals wearing tags, collars, and bells seemed to be accepted normally by group members since they participated in social interactions such as grooming and continued to travel with the same group with which they were observed when captured. There was no evidence from followed groups that collars impeded the activities of the tamarins. I have no experimental evidence regarding bell effects on the predation susceptibility of the wearers. Tamarin predators are unlikely to rely primarily on auditory cues, which may in any case be provided by the tamarins themselves. Their "Long Call" vocalizations are highly localizable, for example. Also, the bells are not as obvious as it might seem. The bells do not ring continuously, but irregularly according to the animal's movements. The sounds of some insects are surprisingly similar. Persons traveling with me were sometimes unable to detect the bells at first, even when I could detect them clearly. Lastly, the most successful and most localizable bell was worn by the animal it was put on for at least two years (1974-July 1976).

Age Estimation

The ability to estimate age is essential to any analysis of group structure, population dynamics, or reproductive strategy. Any investigation of reproductive strategy requires knowledge of when births occurred. In primate groups the occurrence of births can at best be determined within a day by following groups daily. In practice, since it is impossible to follow more than one group simultaneously, monitoring of most groups in a sample is perforce intermittent. Monitoring must also be intermittent when the investigator cannot remain continuously at the study site. The birth date of any newly discovered infant or juvenile can in such cases be designated only by estimating its age.

Possible parameters for estimating age given the limitations of the study were appearance, body measures, weight, tooth eruption, and tooth wear. The first four are potentially useful only during the period of growth. Weight gain is the last of these parameters to level off with age (based on a study of captive-born *S. nigricollis*, Chase and Cooper, 1969), as well as being easily and precisely measurable. A regression line constructed from the age-weight relationship of two sets of twins of known age (Figure 8) was used to estimate ages of other captured juveniles. Their birth dates could then be estimated and those data

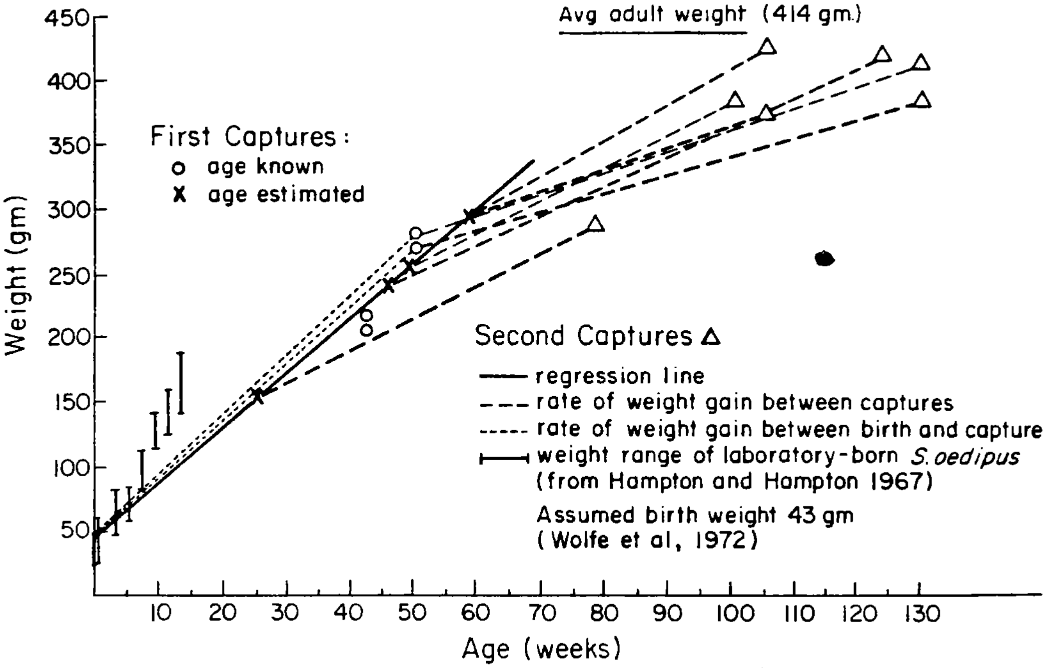

Figure 8

Regression line used for estimating age of captured juveniles; and growth of juveniles between captures.

The regression line intercept of 43 gm was arbitrarily fixed according to the average birth weight of S. oedipus in the laboratory. The slope was estimated using weight data for two sets of twins, whose birth dates were approximately known from observing them with their group shortly after birth, and which were subsequently captured before they were a year old. The dashed lines connect data points for individuals captured twice. Those for K1 and L1 are shown extending back to the origin (birth) because the age of this set of twins was known to within 11 days, and so the age at first capture was also known within those limits. Age at first capture for all other individuals was estimated from the regression line. The horizontal and vertical distances between successive data points are accurate, but the placement of these segments along the horizontal axis is subject to the error inherent in the use of the regression line to estimate age at first capture (see text for discussion). Note, however, that the known data from K1 and L1 agrees well with the remaining individuals.

included in examining the seasonal reproductive pattern (Figure 21). The error in this procedure derives from the variability in the slope of weight gain in different individuals, and from the fact that weight gain is not linearly related to age (Chase and Cooper, 1969). Unfortunately, my data are insufficient to make even a crude estimate of this error. The error estimates shown in Figure 20 were derived from S. nigricollis weight gain data obtained by Chase and Cooper (pers. comm., 1977). I constructed a regression line based on two pairs of S. nigricollis which had reached the same proportion of adult average weight[1] as had the wild S. oedipus which were used to construct the regression line for that species (Figure 8). The error estimates referred to were simply derived from the range of actual data on either side of the S. nigricollis regression line. The error estimate is thus conservative and probably reasonably representative. It increases rapidly with weight. At 40% of adult weight it is about one month (4 weeks). By 60% of adult weight ±10 weeks includes all observed weight values. 60% corresponds to a weight of about 250 gm in the wild S. oedipus.

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[1] Actual weights were not used because the captive adult S. nigricollis were heavier and because juveniles gained weight much faster and attained the average adult weight (464 gm) much sooner (at 69-70 weeks) than the wild S. oedipus. (See Figure 8)

Tooth Wear Observations

The only age determination method tried so far on mammals (cf. Morris, 1972) which is usable on intact adults is tooth wear. For this study, four adult and two juvenile tooth wear or state categories were established (Table 2). Descriptions were at first rather general and later became more detailed. In 1976 and 1977 the canines of all captured animals were measured with calipers. The wear pattern on the upper canines was described and also recorded in many cases as plaster casts or photographs (Figure 9). The wear state of the incisors and molars was also described in general terms.

The focus on canines was dictated by ease of measurement and observation. The molars were more difficult to observe and the wear patterns more complex, less marked in absolute terms, and more difficult to describe adequately without extensive experience and access to multiple specimens.

Measurements turned out to be of limited usefulness. First, although it might seem that the gumline would be a relatively discrete point to measure from, repeatability was poor. Secondly, wear from year to year turned out to be much less than I had anticipated, and in fact, within the limits of error or measurement. Thirdly, gum recession was common on older animals (and especially evident around canines) and actually caused apparent canine height increases between years. Lastly, since the wear face on older animals is actually at an angle to the tip, a canine height measurement is not a very good indicator of canine wear in general, although canines are definitely shorter in aged animals. Also, canine breakage is relatively common in older animals and caused difficulty in judging whether shortening was due to wear.

Table 2

Dental Age-class Criteria

"Dental age" Class	Approx. Age Range	Definition	Example
A4	-	Canines very worn/broken; incisors worn to near gumline	Fig. 9f
A3	Over 5 or 6 years	Canine wear moderate, wear face flat or slanted. Moderately to very discolored	Fig. 9e
A2	2-5 or 6 yrs.	Canines barely worn - tips rounded or very tip flattened. Teeth white.	Fig. 9c,d
A1	1-2 years (subadult)	Canines with tips showing no wear. Teeth very white, sharp.	Fig. 9a,b
J2	About 1 year	Permanent canines growing in	
J1	Under 1 year	Permanent canines not yet erupted	

For purposes of ageing by canine wear, A or "adult" categories encompass all individuals whose canines are fully grown in. Notice that physiological maturity (see definition of "Adult" based on physiological maturity, p. 86) occurs toward the end of the age span during which the individual would be classified as A1.

I decided therefore that the essential instrument for judging age would be a series of descriptions, casts, or enlarged photographs of teeth of tamarins whose age was known. This is the only way that what is essentially a "gestalt" process can be standardized and the standards used be presented in a publishable form. I experimented with making "Jelltrate" molds and plaster casts, and also with photographic recording methods. Both methods have been used by others for tooth-wear studies.[1] I was unable to work out all the problems with the plaster cast technique in order to use it extensively for this study. Photographs of canines from some known-aged animals have been presented (Figure 9) as documentation of the descriptive categories mentioned at the beginning of this section.

The maximum age of these known-aged animals was about 5 years: an individual who was caught as a subadult near the beginning of the study. Descriptions of canines are available for five individuals up to about 3-3½ years. The permanent canines grew in at about 1.0-1.1 years (based on observations on two sets of twins). They are, as in _S. nigricollis_ and _Callithrix jacchus_ (Chase and Cooper, 1969; Johnston, et.al., 1970) the last permanent teeth to appear. The tips are at first very sharp and needlelike. They then become rounded and then flattened. At 3-3½ years only the very tips of the canines are worn flat. Gum receding and canine breakage are rare at this age and height measurement varied from 4.90 to 6.75 mm. Canine wear on the 5 year-old was not distinguishable from that on the 3-3½ year-olds. Although a sample of one could hardly be said to be representative, the slightness of wear on this 5 year-old was surprising. If canine wear continues at the same rate as in the initial four years, it would seem that the "old" animals in this

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[1] See following page

Figure 9

Canine condition of individuals
in the different dental age classes.

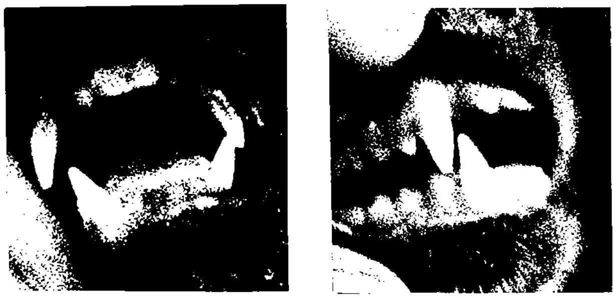
a-Individual designated A1[1]
Estimated age 18 months (Gu)

b-Individual designated A1
Estimated age 23 months (Qa)

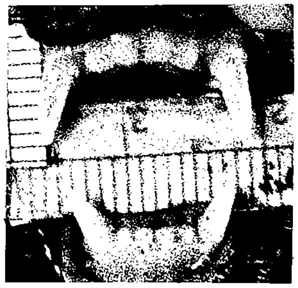
[1] See Table 2, p. 34, for explanation of dental age categories.

Footnote for page 35: Replicas of dental stone, using alginate for the intermediate negative, are finding widespread use in palentological and anthropological studies of bones and teeth, where original material is irreplaceable. Zeimer and Palfrey (1979) demonstrated the precision of this replicating method. Thorington (pers. comm.) and Eisenberg (pers. comm.) have recently been using plaster casts to create aged series for squirrel and howler monkey populations. Moss and Chase (1967) used enlarged photographs of plaster casts of human teeth for taking measurements, taking the magnification factor into account. There were no significant differences between the measurements based on photographs and those made on the casts themselves.

Figure 9, continued



c--Individual designated A2
Estimated age 42 months (Ea)



d-Individual designated A2
Estimated age 5 yrs (Ca)

Figure 9, continued

e-Individual designated A3 (101)

f-Individual designated A4 (Ja)

population may be older than the maximum of ten years thus far observed in captive cotton-tops (Napier and Napier, 1967).

In middle-aged animals a wear face develops which slants upward from the canine tip. The tip remains flat in frontal view as the wear progresses. In the oldest animals the canines were half or less of their original length and very flat, "peglike." The wear face may, in side view, develop a "stepped" appearance. Wear occurs on the frontal areas of the canines also. Gum receding, broken canines, dead (discolored) teeth, missing teeth, and decay are common (see also Hershkovitz, 1970). The initially high pointed cusps of the molars are much higher on the outside than the inside. As the inside cusps are worn down near the gumline the outside cusps begin to approach the same level; the valley or groove that separated the lingual and buccal sides of the molars eventually disappears and the wear surface becomes flat. In such animals the incisors were also worn nearly to the gumline.

Phenological Observations

Phenological data was gathered by three means: (1) periodic survey of marked individual trees; (2) periodic notations by species for a list of easily recognized species, and (3) casual observations. Leaves, flowers, and fruit were noted as being absent, scarce, moderately abundant, or abundant. Fruit or unusual numbers of leaves on the ground were noted, as well as the presence of immature fruit, newly sprouted or yellow leaves, and flower buds. Statements regarding availability of fruits constituting the tamarin diet are based on the above plus observations of tamarin feeding.

Details regarding seasonality of leaf fall, flowering, and fruiting, analyzed by stratum, are presented in Appendix 3. The patterns are shown to be markedly similar to those found in the dry Costa Rican forest studied by Frankie, Baker, and Oppler (1974).

RESULTS

TAMARIN POPULATION DISPERSION

Spatial Configuration

Two types of groups could be distinguished in this population, those whose movements could be circumscribed by a boundary, that is which frequented an established home range, and others which by contrast appeared to lack attachment to a particular area. The former are referred to in this report as "established" groups and the latter as "transient" groups. Transients only remained in the study area for short periods of time (a few days to a few weeks) unless they joined an established group.

The home ranges of eight established groups were included partially (5) or wholly (3) within the 53 Ha study area (Figure10). For the latter three groups, home range sizes were 7.8, 10.0 and 10.0 hectares. Corresponding maximum and minimum group sizes[1] were 13 to 4 (UB area), 6 to 3 (Ka area), and 5 to 3 (Ba area) individuals (Table 3). Neither group size nor composition was stable but home range boundaries were. Figure10 shows the locations of these boundaries. Boundary lines were positioned so as to include almost all movements of groups followed (Figure11) during 1973, 1974 and 1975. The period covered for any one group was 5-18 months. Occasional excursions were observed by the Ka area group into the La area and possibly the reverse (before the La group was marked). On one of these occasions when the Ka group was about 45 m past the boundary shown, the La group appeared, whereupon

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[1] The characteristics of established groups are further discussed under Group Size and in the section Population Characteristics (see Sex Ratio and Age Composition).

Figure 10

Map of study area showing home range boundaries and size range of "established" groups

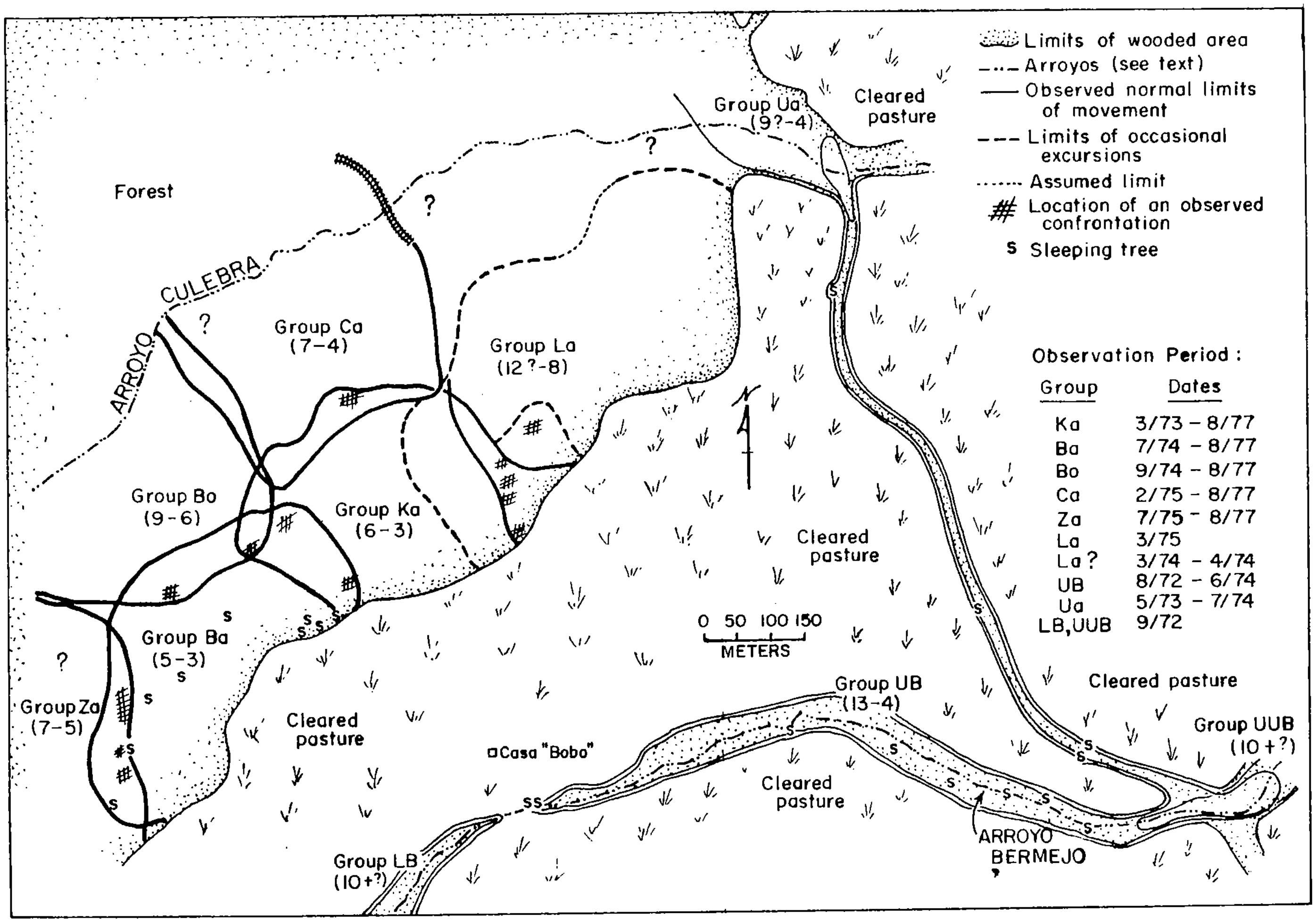

TABLE 3

Group-size maxima and minima, estimated home range, shared area, density, and daily travel distance of three *Saguinus oedipus* groups.

Group	Group Size	Group Range[1] (Hectares)	Shared (Ha)	Portion %	Density[2] Individ/Ha		Approx. Daily Path length[3]	
					Max	Min	Km/day	M/hr
UB	13-4	7.8	1.6	20	1.8	0.7	1.6±0.15(SD)[4]	120-140
Ka	6-3	10.0	2.5	25	0.7	0.3		
Ba	5-3	10.0	4.3	43	0.6	0.4		

Average of maximum and minimum density estimations for these three groups: 0.78 tamarins per hectare.

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[1] As shown in Figure 10.

[2] Density calculations include only half of the area shared with neighboring groups.

[3] Refers to the actual distance over which the group moved.

[4] Sample of 5 complete days in March, April, August and September.

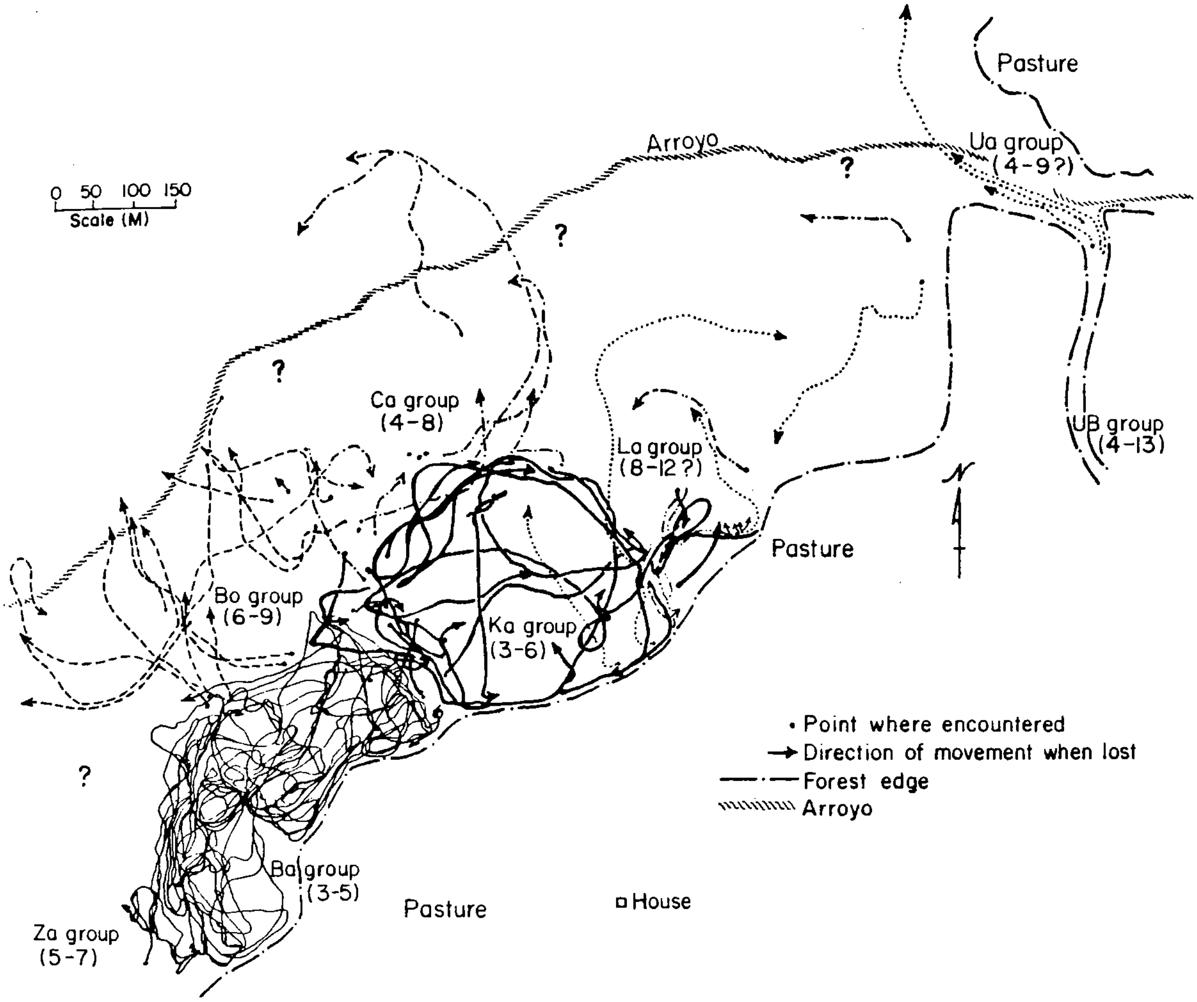


Figure 11

Composite map showing routes taken by followed groups, used to establish home range boundaries as shown in Figure 10 the Ka group retreated precipitously to the more usual limits of their movements.

Evidence of the stability of boundaries is provided by observations made in 1977. Most sightings of a given group fall within the boundaries drawn based on the 1973-1975 observations (Figure 12).

Overlap between home ranges was 20 to 40 percent, not including the occasional excursions mentioned. Including only half of the overlap area in the home range calculation for a particular group, the density for the three groups whose home ranges are cited above was between 0.3 and 1.8 individuals per hectare (Table 3).

Inter-Group Relations:
Maintenance of the Spatial Configuration

Inter-group encounters occurred in home-range overlap areas (Figure 10). Both groups utilized these areas for foraging when the other group was not present. Encounters occurred at irregular intervals about once every few days. Their character varied. On several occasions two groups were observed in auditory contact near a boundary area, but did not exchange calls or move into visual contact.(The observer must assume that if she can detect the presence of a nearby group, the tamarins must also). Groups were also observed to occasionally reverse or change direction of movement, apparently to purposely avoid an encounter. By far the most frequent type of encounter, however, was agonistic in nature, including approach and staring at the other group, chasing, grappling, and the "rasp" vocalization associated with chasing or grappling. Also there was a significantly and strikingly increased incidence of clear whistle-like vocalizations (Table 4). Two types

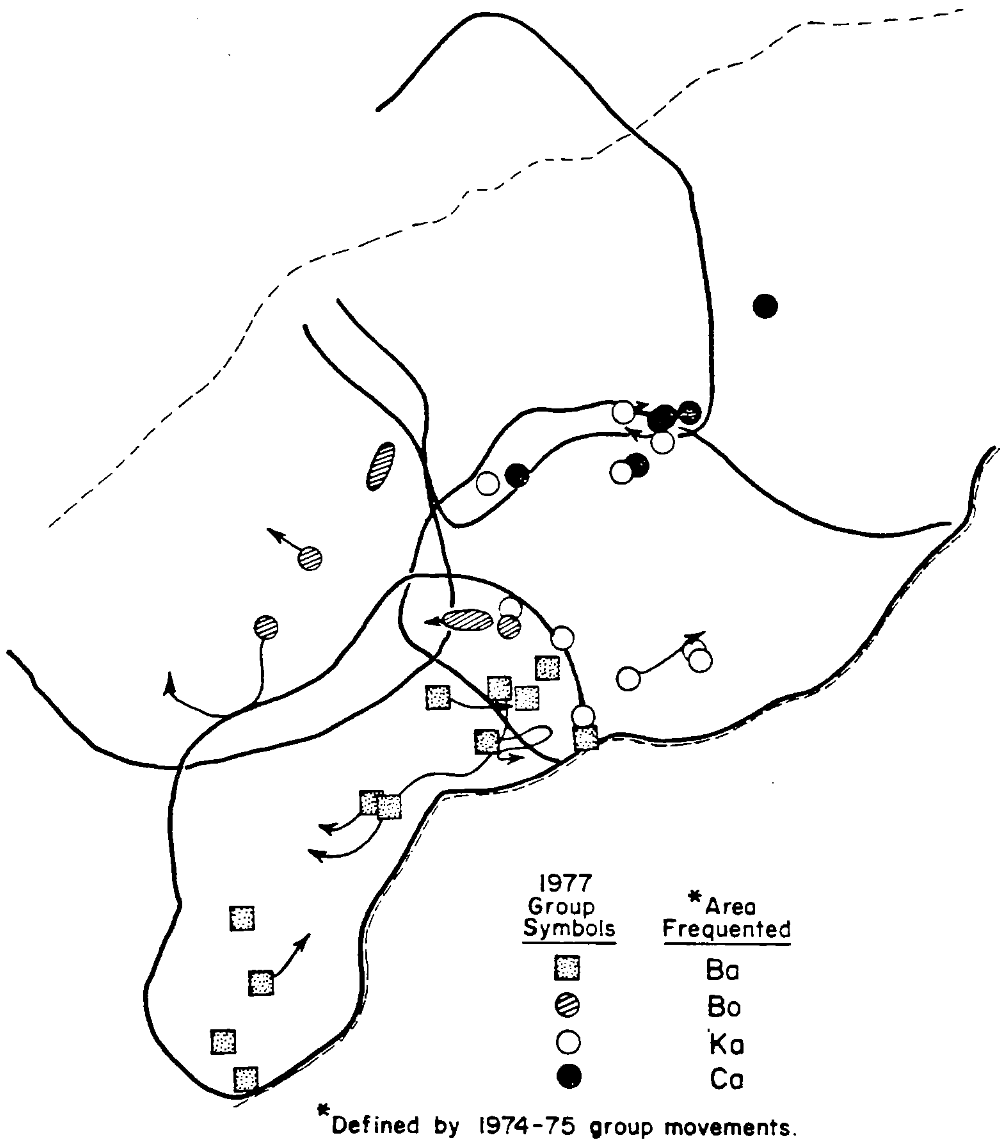


Figure 12

Group sightings in 1977 superimposed
on 1974-75 home range boundaries
(See Figure 10)

TABLE 4

Numerical frequency of vocalizations typical of intergroup encounters, compared with normal activities in *S. oedipus*.

Name of Vocalization	Number Heard in Five Minutes Normal Activity	 Confrontation
Rasp[1]	0-6($\bar{x}$ = .082)	0-10($\bar{x}$ = 4.2)
Long Call[1]	0-22($\bar{x}$ = 1.5)	7-42+ ($\bar{x}$ = 25.4)
Dip[3]	0-32($\bar{x}$ = 2.2)	7-70+ ($\bar{x}$ = 29.4)
Number of samples[2]	98	5

[1] As per Moynihan, 1970 (*Saguinus* (*oedipus*) *geoffroyi*).

[2] Samples were routinely taken at half-hour intervals when possible.

[3] Not mentioned or described by Moynihan (see text).

were especially frequent, "Dips" and "Long Calls." The "Dip" was given singly, sometimes with an introductory chirp. It was about one second long, first decreasing in pitch and then rising immediately and smoothly with no break (Figure 13). This was a vocalization also commonly heard in relaxed foraging situations. The "Long Call" was especially frequent and varied during inter-group encounters. An example of a frequent two syllable type is shown in Figure 13. Two and three syllables were the most common, but the number of rising syllables following the initial descending one increased sometimes to six or more. Breaks between the syllables were clearly discernible. An introductory chirp was sometimes present.

Typically the first indication I had of a group encounter was the alternation of Long Calls from the two groups. A group often called in a not quite synchronous "chorus" as though one member's beginning a Long Call stimulated the others to follow suit. After this initial phase some individuals made contact with members of the other group while others were relatively immobile, emitting frequent Dips and Long Calls. In some cases there was a preliminary phase of approach to within a few meters accompanied with intense staring. Those involved in chases moved around so much that I could only follow events by the vocalizations. "Rasps" suggesting close and agonistic contact were heard over a wide area up to about 40 m^2, implying considerable mixing in space.

In the few encounters which involved marked animals, the most obvious participants were adult males. They were seen chasing, feinting, and grappling. Adult females, however, were (at least in those encounters) more difficult to localize. One of the two Ba group females was once found some 25 m from the focus of a vigorous encounter, foraging quietly,

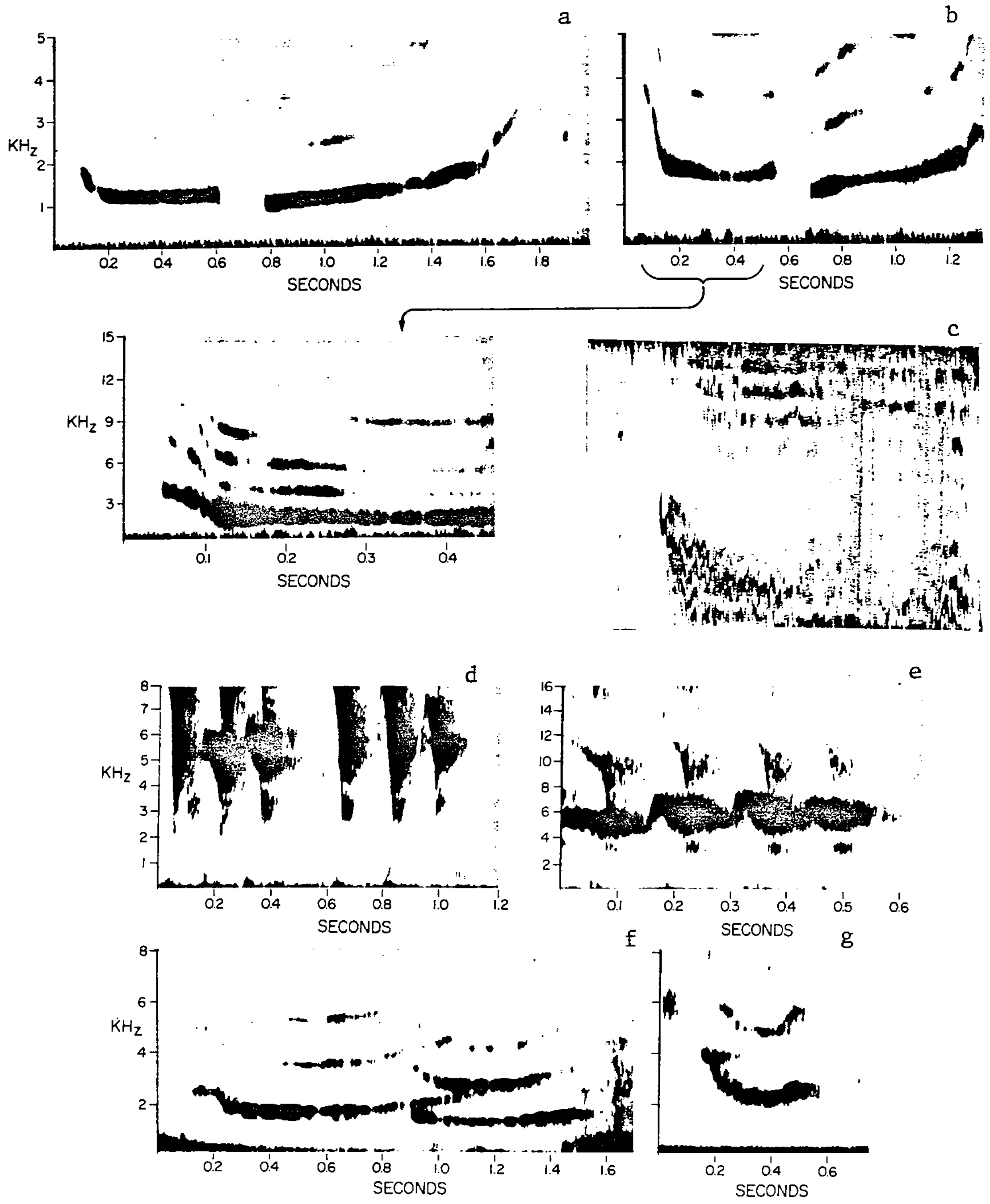


Figure 13

Sound spectographs of *Saguinus oedipus* vocalizations

See notes on Page 47a

Figure 13

Sound spectographs of Saguinus oedipus vocalizations

Recordings were from captive animals of unknown origin.

a,b - Typical (two-part) Long Call vocalization (name applied by Moynihan, 1970, to similar call of S. geoffroyi). Often introduced by a "slide" (top right; Muckenhirn, 1967) or chirp. May consist of up to six syllables (1 to 3 the most common), separated by definite breaks. All syllables except the first usually rise in tone, beginning near the same frequency at which the preceding syllable ended. Much variability is seen, especially during inter-group encounters.

c - Harsh squeal vocalization or "rasp" (Moynihan, 1970).

d,e - Typical Thew vocalization: composed of single notes, often given in rapid succession. With greater intensity a higher proportion of energy is distributed in the higher frequency ranges and notes are run together. Often interspersed with complex chirp series.

f,g - Dip vocalization. Single note which is never repeated and contains an initial descending portion and a final ascending portion; it may be preceded by a short introductory note (right). The "Dip" is variable in length and pattern, but no break occurs between beginning and end. The tonal quality is very similar to that of the Long Call. Calls of two individuals overlap in the left-hand example.

while the males were involved in chases. The second female could not be localized. Adults were observed foraging during other confrontations also.

On all occasions at least some members stayed in the vicinity of the interaction without participating, although their presence was obvious from their frequent vocalizations. Juveniles and infants definitely stayed or were kept out of the area of conflict. Once the Ka group left their twins of about 2 months (semi-independent) in a tree just out of sight of a trap which contained a decoy they were harassing. The adults spent most of an hour at the trap, but periodically one of the three returned to the infants for a few minutes, especially when the latter vocalized loudly. The infants spent most of their time playing. Another time the males of the Ka group interacted with neighbors while the female - carrying both infants - stayed nearby although out of the area of interaction. When those young were about a year old and fully independent they remained relatively immobile during an intergroup encounter while the adults ranged well out of sight.

Encounters usually ended gradually, with each group drifting back into its own area. Nothing resembling the morning calling between groups described for Saguinus midas (Thorington, 1968) or other species of primates such as howlers, colobus, gibbons and titi monkeys was noted in this population.

Movement Patterns of Established Groups

Figure 14 presents an analysis of intensity of use of one home range (Ba group) during three day-length periods late in the 1975 dry season (between March 20-31). These are based on maps on which the travel route of the group was recorded together with exact locations every 15 minutes where possible. Only a few time points were missed. The 10.0 Ha home range was overlain with a grid and so divided into 281 squares about 19 m on a side. Results were as follows:

In the three day period (Figure 14d), 56% (156/281) of the squares were entered. Intensity of use varied greatly:

a) Intensive use - 3.9% (11/281)
   (accounting for 4 to 10 time checks (8/281) or containing a sleeping tree site (3/281))

b) Repeated use - 10% (27/281)
   (accounting for 2-3 time checks, or one time check plus two or more transit records, i.e., group passing through that square)

c) Casual use - 42% (118/281)
   (accounting for one time check, one time check plus one transit record, or two transit records)

Of the eight intensively-used squares used during the day, six were visited on two of the three days in the sample. The large number of time checks in these reflects prolonged periods spent there, accounting for the entire period between 1115 and 1415 on two of the three days. On 3/20 the group spent 0745-0800 in the lowermost block of intensive-use squares and returned there to spend 1115-1430, making a brief visit to the upper block area in the interim. On 3/30 the group spent 1100-1415 in the upper block of intensive-use squares, and briefly visited the lower block the following morning. On the remaining day (3/25) the upper block was visited from 1400-1530 and the lower one not at all. The predominant activities in the intensive-use squares were resting and foraging.

Thirty-seven percent (58/156) of all squares entered were in overlap areas. This is not significantly different from that expected

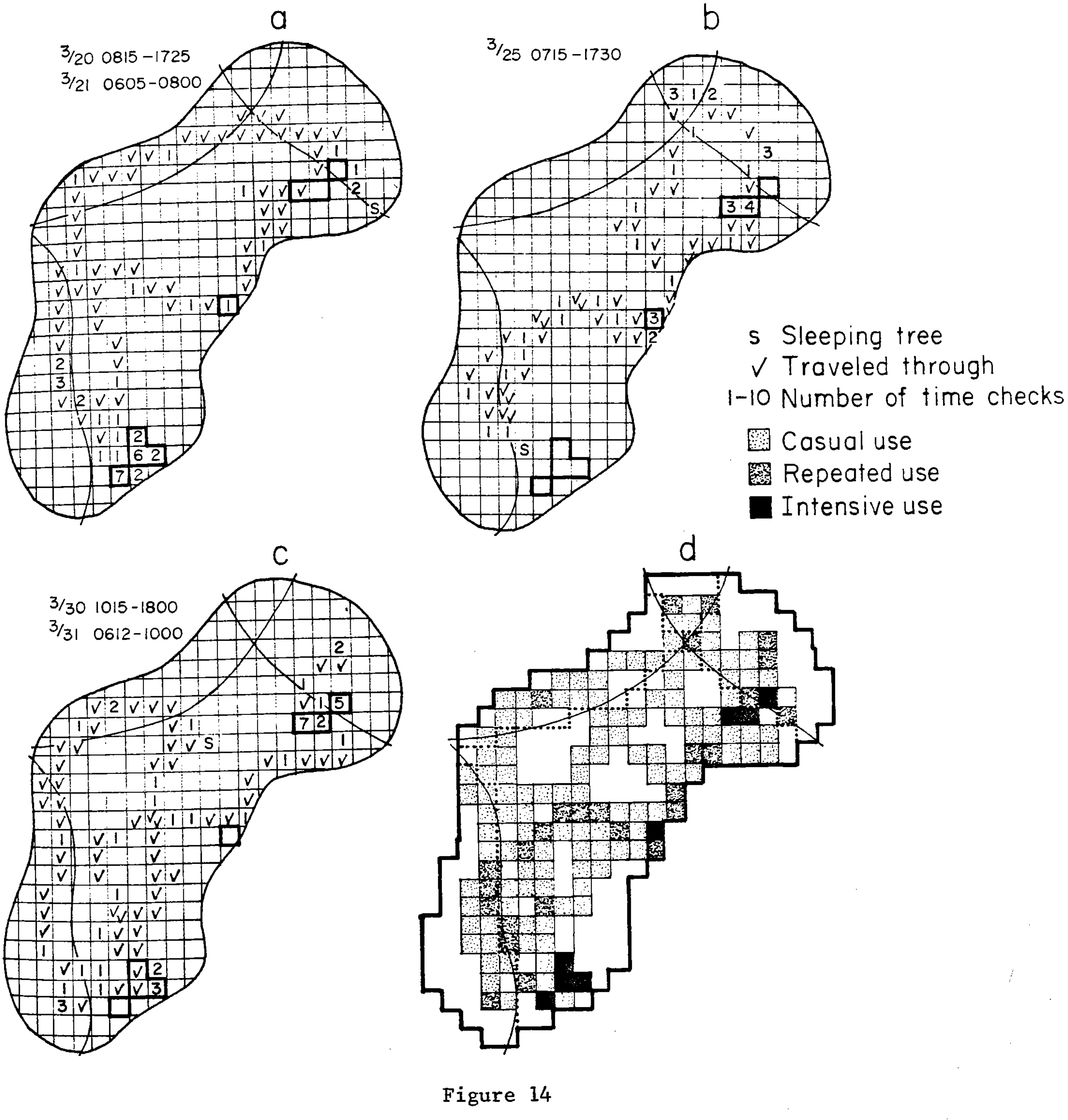


Figure 14

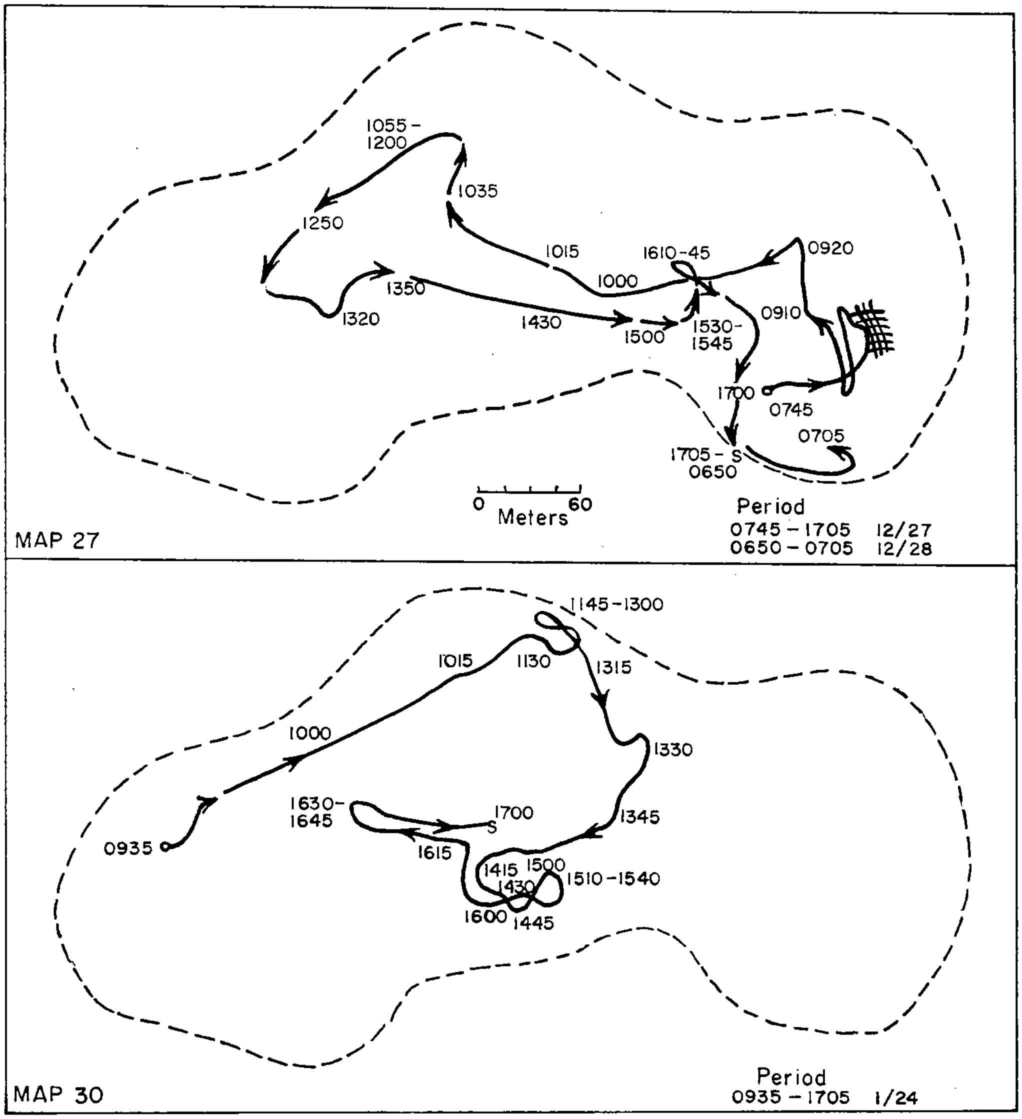
Analysis of intensity of use of Ba group home range
during three day-length periods
(See discussion pp. 48-51)

based on the proportion of the total home range representing overlap areas (110/281 or 39%) ($X^2=0.25$). The proportion of intensively plus repeatedly-used grid squares which lay in overlap areas was 27% (10/37), also not significantly different from expected based on the proportion of the home range lying in overlap areas ($X^2=1.84$). Thus the data do not support the hypothesis that movements in general are directed toward patrolling boundaries with other groups.

Typical 24-hour patterns of movement are shown in Figure 15. The rate of movement (UB and Ba groups) varied between 0.12 and 0.24 Km/hr and total daily travel distance (sensu Mason, 1968) was about 1.6±0.15 (SD) Km. The latter figure is from a sample of 5 complete days on the UB group in the months of March, April, August and September (Table 3). It can be seen that, despite the tendency (shown above) to concentrate activity in certain areas of the home range, daily movement patterns result in much of the home range having been visited in the course of a few days. During their movements between intensively-used areas the tamarins visited fruit trees and foraged for insects and other substances (for further discussion see section on Food Resources).

Intra-Group Relations

The following statements refer to my observations on groups UB, Ka and Ba. Groups were cohesive. Daily group splitting or coalescing such as reported for Saguinus fuscicollis (Castro and Soini, 1977), S. nigricollis (Izawa, 1978), and S. midas (Thorington, 1968) did not occur in the groups studied. In over 300 hours of contact with group UB, no instance of prolonged splitting or joining of subgroups was seen. Two cases of temporary splitting were observed. In both cases



s = sleeping tree location
o = initiation of observation
# = contact with neighboring group

Figure 15

Typical daily movement patterns of Ba group

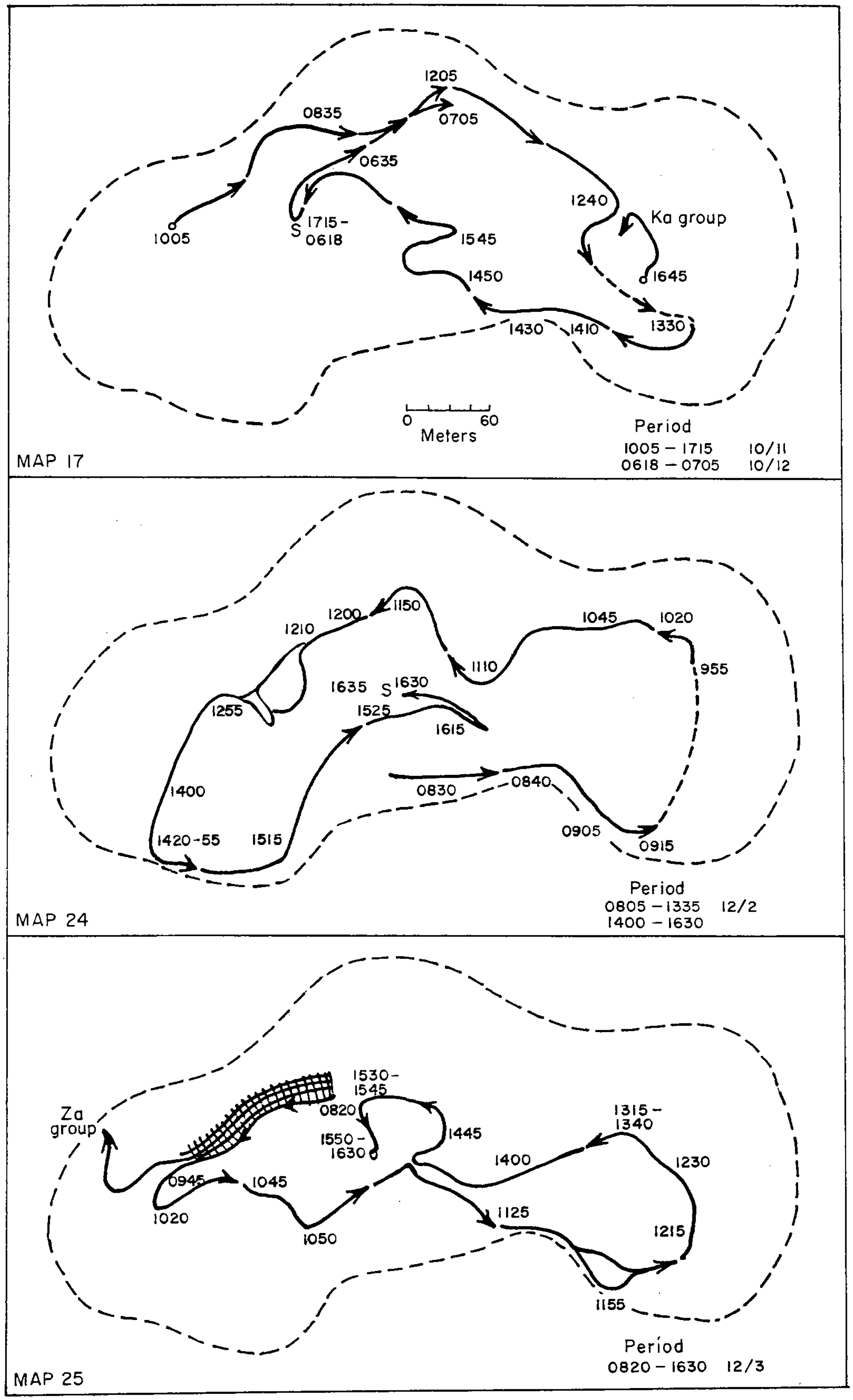


Figure 15 (con't.)

the separated subgroups exchanged contact vocalizations (Dips, Long Calls; see page 46) until one moved to join the other.

Individuals separated from their group typically ran back and forth through the trees giving loud Long Calls. Frequently (but not invariably) one or more group members would respond with a Long Call. The isolated animal(s) would then move toward the group, the exchange of calls ceasing as soon as it (they) rejoined the group. Long Calls were audible to the observer on occasion up to at least 250 m away, and in fact often provided a means of rapidly locating groups.

There was no obvious leader in either of the two best-studied marked groups (Ka and Ba). Foraging was individualistic, with individuals following devious paths during foraging. The group as a whole, however, traveled in a seemingly definite direction and tended to repeat previous routes. Contact was maintained visually and through vocalizations (Dips and Long Calls or parts thereof).

There was no food announcement vocalization, or other means of advertising a favorable food source, except in one possible case. On this occasion, a juvenile spotted a favored and scarce food (Herrania sp.) but hesitated to approach due to my presence and the low height of the tree, about 1.5 m. Meanwhile the other group members had begun to leave the vicinity. The juvenile then uttered a series of distinct loud chirps, upon which the group immediately returned and approached the food (I had moved further away in the meanwhile also).

Most social interaction occurred around concentrated food sources (fruiting trees, scarce favorite foods), during rest periods and probably in the sleeping tree, which usually was entered well before dark. The frequency of "Rasp" vocalizations was noticeably greater around favored foods, especially in trees where fruits were few in number, large, and sparsely distributed. Rests often occurred in open trees on wide branches, although they occasionally rested in dense vine entanglements (I sometimes suspected this was less by choice than in order to avoid me.). During rests individuals lay alone or in pairs or trios within a few feet of each other, often lying along a wide branch with legs hanging down. Allogrooming and autogrooming was common. Some group members might continue foraging nearby or interrupt their rest with a short foraging bout. "Dips" and "Long Calls" were emitted occasionally during rest periods.

Transients

Transients were a common phenomenon in the tamarin population observed. They were occasionally alone (5/14 cases) but were more often in groups of two (5 cases), three (1 case), four (2 cases) or five (1 case).[1]

Transient groups consisted of immigrants to the area and/or emigrants from established groups. During 1974-1975 nine such groups of tamarins were observed in the study area which were not part of any established group. All but three of these groups consisted of individuals which had never been part of any established group in the study area. In two of the remaining three cases the individuals involved had left a group in the study area and were never observed again in the area. In the last case an adult male previously seen with the Bo group (Ia), along with a second male (Pa) of unknown origin, formed a group with two females

---

[1] The characteristics of transient groups or the transient sector of the population are further discussed under Group Size and Population Characteristics (see Sex Ratio and Age Composition).

(Ho, Jo) apparently from outside the study area. This group was seen various times during a three-week period, usually near the edge of the home range of the Ba group, neighbors of the Bo group (Figure 10). The Ba group was observed twice to chase them vigorously on encountering them. The two males subsequently (re-)joined the Bo group while the two females were observed or trapped several times elsewhere in the study area over a 3½ month period. They were not observed again during the remaining 5 months of the study.

Some immigrants succeeded in attaching themselves to an established group temporarily or permanently (see below). In addition, individuals which left one group in the study area and joined another (2 cases) must also be included as part of the transient sector. There were many other disappearances of marked animals from groups which could have been due to emigration but since the individuals in question were not observed after leaving their groups, mortality could not be ruled out.

Established groups showed on some occasions marked aggression toward transient groups. The encounters between the Ba group and the transient group frequenting their home range for several weeks were marked by extensive and prolonged chasing. Three out of four captured individuals of one transient group, consisting of five animals, had fresh slash wounds which probably resulted from the aggression of resident animals. These were the only tamarins caught with fresh wounds, although scars were very common (see Mortality). The limited extent of the woods in that area and its conformation - a narrow strip (one end of the UB group's range) - might have prevented the intruding group from escaping or leaving the residents' home range as normally must occur.

By contrast there was no apparent aggression shown toward extra-group individuals on two other occasions. One female (Mo) was observed to join the Ba group temporarily. One hour before joining with them, Mo (who had been trapped and marked in another part of the study area two days previously) had been moving with three unmarked individuals, which were not seen again after she approached the Ba group. Mo's approach to the Ba group occurred on an open branch and was clearly observed. A grooming session lasting over an hour was immediately initiated between Mo and three (two males, one female) of the four members of the Ba group. During the grooming bout, the various partners alternated. Mo traveled with the group for some days, but her association with the group ended shortly thereafter, and she was later observed alone in the Ba group's area. On two of three subsequent sightings, she was observed to approach the Ba group, but not to stay with them except perhaps for a short period. During the last observation of Mo, an adult male from the Ba group appeared to chase her for a short distance. She was not seen again.

The Ka group was joined by an old male, Oa. I did not observe Oa joining the group but he remained with it for at least 2 years while various individuals present when he joined disappeared from the group (see also Appendix 1).

Some transient groups resulted from the simultaneous exit of the individuals involved from an area-attached group, as for example in the instance where an adult female (Fl), a subadult female (He), and a juvenile (Gl) about a year old disappeared simultaneously from an established group (Ca). The adult female was identified with certainty in an adjoining area and the subadult female tentatively; thus I believe that the three left the group together. Another pair of tamarins (an older [A3] male and a subadult or young adult [A1-2] male) moved from one established group (Bo) to another (Ka) which occupied the adjoining home range (Figure 4). This occurred sometime during my 1976-1977 absence from the area. Some transient groups, however, were composites. For example, in one case a female from one group (Ba) joined with a male from the neighboring group (Bo). The two were seen together and separate from their groups on two occasions, both times in the Ba group's home range. After that they were not observed again in the study area. A second case, where two males from an established group temporarily joined a pair of immigrant females, has already been cited above.

Size Fluctuation in Established Groups

Established groups varied in size from three to thirteen. Table 5 summarizes this data and analyzes the causes of group size changes. Figure 16 presents size profiles of eight groups. Appendix 1 details changes in groups over time.

Fluctuations in numbers prevent the calculation of an "average"

Table 5

Summary of changes in established group size and causes thereof

					Sources of Increase			Sources of Decrease		
Area	Dates[1]	Size Range	Total Assoc.[2]	Assoc. Entire Period[3,5]	Birth[4]	Immigration[5]	Reimmigration	Verified Emigration[6]	Capture or Death	Disappearance[5]
UB	8/72-8/75	4-13	min. 17	?	4				2	10
Ka	3/73-8/77	3-6	11-12	0	4	4-5				3-7
Ba	7/74-8/77	3-5	11	0	2	4		3		3
Bo	11/74-8/77	6-9	13-15	3	3	2-4	2	4-5		1-3
Ca	2/75-8/77	4-8	11-13	3-4	4			3		
Za	7/75-8/77	5-7	7	4	2					1

[1] Dates represent beginning and end of observations and include periods of non-observation or absence from study area (e.g., Aug. 1975-76 and Aug. 1976-77).

[2] Total number of tamarins observed in association with group over period indicated (min=minimum). Uncertainties in cases of Ka, Bo and Ca groups due to presence of unmarked animals in 1976 and 1977 which could or could not have been the same individual.

[3] Number of tamarins present in group for entire period of observation. Uncertainties in Ca group due to possible identity of unmarked individual in 1976 and 1977.

[4] All individuals of subadult age or younger were considered to have been born in to group. (For definition of "adult" see Methods.)

[5] Uncertainties due to presence of unmarked animals (see above) or possibility that some individuals not seen in 1977 due to insufficient observation.

[6] Verified emigrators were individuals seen alive elsewhere after leaving the group.

Figure 16

Sizes and age-class profiles of eight "established" tamarin groups.[1]

	1973	May 1974	Mar 1975	Aug 1975	Aug 1976	Aug 1977
A?	FMM	FMM	M	M	F	F
A4			M	M	M	M(M)[2]
A3						
A2					FM	FMM
A1				FM		M
J2			FM			
J1		FM			MU	
Totals	3	5	4	6	6	6
Tot A	3	3	2	6	4	6
Tot J	0	2	2	0	2	0

Group occupying Ka area

	Aug 1975	Aug 1976	Aug 1977
A?			
A4			
A3	FM	FM	M(F)
A2	M	M	FFM
A1		FF	FM
J2			
J1	FF	FF	
Totals	5	7	6
Tot A	3	5	6
Tot J	2	2	0

Za area

	Sept 1974	Jan 1975	Aug 1975	Aug 1976	Aug 1977
A?	F	F			
A4					
A3	FM	FM	FM	FM	MM
A2	M	M	M	M	F
A1					MM
J2					
J1	U			MM	
Totals	5	4	3	5	5
Tot A	4	4	3	3	5
Tot J	10	0	0	2	0

Ba area

	Feb 1975	Aug 1975	Aug 1976	Aug 1977
A?	M		U	U
A4	FMMM	FMMM	FMMM	F(M)M
A3				F
A2	F	F	F	MM(F)
A1	M	M	MM	M
J2				
J1		MU	M	
Totals	7	8	9	7-9
Tot A	7	6	8	7-9
Tot J	0	2	1	0

Bo area

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[1] For definitions of age-classes, see Table 2 . For details on group changes over time see Appendix 1.

[2] M, male; F, female; U, sex unknown; parentheses indicate uncertainty as to presence this individual due to insufficient opportunity for observation of the group.

Figure 16

	Feb 1975	Aug 1975	Aug 1976	Aug 1976
A?	U	U	F	
A4	M	M	M	FM
A3	FM	M	M	M
A2			M	M
A1	FM	M		MU
J2				
J1	F		MU	MM
Totals	7	4	6	8
Tot A	6	4	4	6
Tot J	1	0	2	2

Ca area

	Mar-Aug 1975
A?	
A4	F
A3	M
A2	FMM
A1	F
J2	FM
J1	
Totals	8
Tot A	6
Tot J	2

La area

	May 1973	July 1975
A?	6	4
A4		
A3		
A2		
A1		
J2		
J1	2	1
Totals	8	5
Tot A	6	4
Tot J	2	1

Ua area

	Aug-Nov 1972	Feb-Apr 1973	Oct 1973	Feb-Apr 1974	June 1974	Jan 1975	July 1975
A?	10-15	9-11	7	5-7	4	MM	UUU
A4						F	F
A3							
A2							
A1						F	F
J2	0	0	0	0	1?	0	0
J1	0	2	0	0	2	0	0
Totals	10-15	9-13	7	5-7	7	4	5

Ub area

group size, since any method of selecting data from the varying time periods that the different groups were under observation is arbitrary and does not give a sample from which a central tendency can legitimately be derived. Nor can data from study area groups be combined with that of unmarked infrequently observed peripheral groups (Figure 10).

Causes for changes in group size were designated by the following categories: births, emigration, immigration and re-immigration events (movements out of and into groups), captures, deaths, and disappearances (Table 5). Disappearances include all cases in which an individual was not sighted subsequent to its disappearance from a group. Some of these were probably actually emigrations into other parts of the forest adjacent to the study area. Only one case of mortality was actually observed (see Mortality).

One capture from the UB group by local residents was known to have occurred. If other such captures occurred, this would account in part for its decrease in size from 13 when I first began observing it (August 1972) to 7 in the succeeding eleven months. The forest occupied by the UB group was different from most groups for various reasons all related to its striplike conformation. The group inhabiting it probably came into contact regularly with locals utilizing an adjacent footpath in order to reach the main forest block to which it connected (cf. Figure 4). Nevertheless, I consider the probability of captures by such visitors to be rather small because on several occasions when I was following the tamarins and someone passed by unaware of my presence, the tamarins were not noticed by them. The capture referred to was made in March 1973 during a period when laborers were employed for brush clean-up and plowing of the adjacent pastures. From their vantage point in the fields the workers were able to observe the tamarins traversing the strip of forest adjacent and to trap it in one sector where most of the trees had been felled. The tamarins were only vulnerable to capture in this area, which they could traverse only by descending to the fence or to a few remaining low trees. The workers chased the group and by throwing something at one of the tamarins, stunned it then captured it by hand. This shows that captures were possible but I consider mortality or dispersal to be the more probable causes of the decrease in the UB group's size.

Mortality in such a forest strip could be disproportionately higher than in a forest block of the same area and similar physiognomy just because of the greater proportion of edge and therefore sites vulnerable to predator detection and attack.

The home range in question was also unique in that it formed part of a nexus of continuing forest strips lining fence lines and arroyos that could be viewed as corridors for dispersal, except for the fact that their continuity is variable. Also there exist no other large forests in the area aside from the one in which the study was carried out. A more apt designation might be dispersal "sinks" into which emigrators are likely to wander and perhaps attach themselves to a resident group for a period of time. This would account for the unusually large size of the UB group (13 members for a period of at least several months) compared to the main forest block. All groups of 10 or more that were observed in this study in fact occurred in similar forest corridors (see Figure 10) except for one. The latter (La) however occupied the far end of the forest block adjacent to the point where it was joined by three corridors, an area through which dispersers would have had to pass to reach them. Possible distant disturbances such as forest destruction in these forested corridors could have increased the frequency of dispersers in them also.

An alternate possibility is that the large size of corridor-inhabiting groups could represent unusually good reproduction and/or survival. This, in turn, could reflect some aspect of the habitat such as perhaps unusually good productivity. One brief survey was carried out comparing the arroyo vegetation with that of the main forest block. Individual trees over 2 m in height in a strip $1\frac{1}{2}$ m to the left of the established trail were identified or samples thereof taken for comparison. In the arroyo forest 1210 m^2 was a sufficient area to find 100 different species, while in the main forest block 1500 m^2 were required. Although trees and vines were greater in absolute number and density in the main forest, the variety (based on one transect in each area) appeared to be greater on the arroyo. This was despite the fact that cattle have access to the latter and not to the main forest block. The identifiable species in the two areas were common to both, but the brief survey carried out indicated a difference in the proportional species representation. The resource base in the forested strip could well be correspondingly different. The UB group did produce a set of infants in each of the two years I observed it adequately (Figure 20). Survivorship of both litters was poor compared to many other groups (see Survivorship).

There was no evidence that group size changes in the main forest block could be attributed to human interference. Groups could not be isolated and chased there, nor was any trapping activity observed other than my own. In most cases the number of individuals known to have been associated with the group was far greater than the maximum group size (Table 5).

RESOURCE USE

Food Resources Utilized

The cotton-top tamarin diet included fruits, newly sprouted leaves, buds, leaves, leaf stems, insects, and small vertebrates. They also licked nectar or gathered pollen or insects from certain flowers or fruits, and extracted unidentified material from the surfaces of branches and trunks of some trees.

It was not possible to determine what proportion of the diet each type of food represented, since both insects or small fruits may have been taken during long periods when the monkeys were foraging in dense vegetation. The shooting of monkeys to obtain stomach samples was impractical and undesirable. Nevertheless some general comments can be made.

A highly salient aspect of the movements of tamarin groups was their visits to fruiting trees. Frequent long relatively direct progressions ending with a visit of 10 minutes or longer to a fruiting tree in which all or most group members fed gave the impression that the group knew the location of the trees in question and moved through the forest with the intention of visiting them. Also an analysis by species of trees sequentially visited would undoubtedly show that trees (or vines) of one or two preferred species were at any given time being visited with a frequency significantly higher than expected based on their abundance in the forest. Thus the basic foraging pattern in this species involved moving from tree to tree bearing preferred fruits, or with vines bearing preferred fruits. The implication is that the tamarins knew the locations of available foods. Foraging routes tended to be repeated, but movement patterns varied in detail from day to day. Foraging for insects and

Table 6

Types and heights of food-resource species

Type and stratum or strata	Number of Species	Proportion (of tree species used)
Tree		
Low (height 4.5 m and below)	5	.11
Low to medium	3	.07
Medium (4.5 to 13.5 m)	27	.60
Medium to high	1	.02
High (over 13.5 m)	9	.20
Epiphyte	1	
Vine	10	

other items occurred en route, and their abundance may have also influenced movements.

The tamarins were observed foraging feeding on the ground (fallen Psidium guajava fruits) and in all strata. However, the majority of identified fruit resources were middle-canopy (4.5-13.5 m) species (Table 6). The types of fruit utilized varied from berries to fleshy fruits several cm in diameter to fruits enclosed in a pod, with small fruits in the majority (Table 7). Evidence that the tamarins were highly selective in their choice is that many fruits with apparently appropriate location, fruiting pattern, and morphology (e.g., juicy berries) were not utilized by the tamarins. Examples are Bursera simaruba, Picramnia latifolia and Rauvolfia litoralis, all of which were abundant. Palm fruits were another abundant resource that was ignored by the tamarins. Some fruits were visited but not eaten. The tamarins visited Pithecellobium saman and Sterculia apelata fruits, both of which are rather woody. I was not able to verify that they were opening or removing any part of these fruits when contacting them with their mouth and suspected they may have been eating the exudate of the former or removing insects from them.

While many of the fruits relied on by the tamarins could be characterized as having a gradually ripening crop with few ripe fruits available at any one time, mass-fruiting species were also important in their diet (Table 8). With the data available it is impossible to assess the exact proportion of the diet that these fruits constituted or how much it varied according to the overall supply pattern. Figs, for example, appeared to be a reliable food supply given the annual fruiting pattern for the population as a whole (Table 8). Actually the seemingly prolonged

Table 7

Sizes of Fruits Utilized[2]

Size[1]	Number of Species Heavy Use (One or more years)	Occasional Use (A few observations)	Infreq. Use (One observ.)	Totals
5 mm	11	3	7	21
6-15 mm	10	3	5	16
16-25 mm	4	4	3	12
over 25 mm	1	0	2	4
Totals	26	10	17	53

[1] Diameter of fruit unit (seed plus arel) excluding woody capsule or pod.

[2] As per Table 8.

Table 8

Availability of non-animal food resources used by *S. oedipus* in this study area

E	F	M	A	M	J	J	A	S	O	N	D	Use Index	Scientific Name	Local Common Name
●	●	X	●	X	X	●		●	●	●	X	*	*Ficus* sp.	Higo
X								X	X	●	●	+	? (Cucurbitaceae)	
X	X	X	●	X	X					?	X	+	*Hirtella* sp.	
	X	●	●									*	*Anacardium excelsum*	Caracoli
?	o	o										*	*Pithecellobium saman*	Campano
	=											+	*Cavanillesia platanifolia*	Volandero
?	●	●	●					●	●	●	?	*	?	
?	●		X	●	●	X			●	●	?	*	*Genipa americana*	
?	●								●	?	?	*	*Ficus palmicida*	Abrazopalo
?	X	X	X	●	●	X	X	●	X	?	?	*	*Muntingia calabura*	Niguito
?	X	X	X	●	X	X						+	*Capparis* sp.	
?	X	●	X	X	X	X	X	X	?	?	?	+	*Ardisia* sp.	
?	X	●	X	X	X	●						*	? (Amaranthaceae)	
?	●	X	X	X								+	*Guazuma ulmifolia*	Guacimo
?		X					●	●	?			*	*Quararibea* sp.	Palo de Leon
		●	●	●							●	*	?	Manao
		o	o		X	X					X	+	*Sterculia apetala*	Camajon
		●	●	X	X	X						*	*Trichostigma octandrum*	
		●	X									*	*Trichilia* sp.	Mangle
		X	X	X	●							+	*Hasseltia floribunda*	
	▲	●	●	X	●	●	X	●	●			*	*Spondias mombin*	Hobo
		●	●									+	*Tournefortia* sp.	
		●	X	X	X	X						+	*Piper* sp.	
		●								?	●	*	*Stylogyne turbacensis*	Pie paloma
		●	●	●	●	?	X	X	?	?	X	*	*Inga punctata*	Guamo de mico
		●	X	X	o	X	X	X	?			o	? (Apocynaceae)	Tomate de monte
			●	●	●							o	*Monstera* sp.	
			X	X	X	●	X	●				*	? (Euphorbiaceae)	Mangle
			X	●	X	X	X	●	●	?		*	*Brosimum* sp.	Caucho
			●	X	X							o	? (Urticaceae)	
			●	X								*	*Casearia* sp.	
			▲									+	*Pseudobombax septenatum*	Majagua
					X	●	X	X				+	*Sapium* sp.	Nipi-nipi
					X	●	X	●				*	*Cecropia* spp.	Guarumo
					●	X	X	X	X			*	*Mayna* sp.	
							●	●	?			*	*Pittoniotis trichanthera*	Lomo de Caiman
							X	●				*	*Casearia*	
							●	X	?			*	?	Yaya
								X	?			+	*Pisonia* sp. ?	
								●	?	●	?	o	*Zizyphus* sp.	
								X	X	●	X	*	*Psychotria* (*grandis*?)	
			X						●	X	●	*	*Paullinia* sp.	
									?	●	●	+	? (Gesneriaceae)	
?										?	=	o	*Bignonia*	
		(5	2		3			2		2)		o	Miscellaneous	
													Total (fruits only) available	
													Total other	

Table 8

Legend

X - Available in the month indicated during some year (1972-1975)

? - Possibly available (insufficient observations)

o - Tamarins observed visiting fruits (but not consuming the fruits themselves

● - Tamarins eating fruits in the month indicated during some year (1972-1975)

= - Visiting flowers (licking nectar or eating pollen or insects?)

▬ - Eating flowers

▲ - Eating new leaves or buds

Use Index symbols: relative proportion of diet

* Very important - multiple observations of use

\+ Two to various observations

o One observation

fruiting season reflects the asynchrony of fruiting by individual trees (see also Hladik and Hladik, 1971). Since a home range may include only one or two large figs this means that their importance to a given group would depend on the overall food supply situation at the time a fig came into fruit. It might vary annually and from group to group. This could explain why the UB and Ba groups utilized the fig trees in their home ranges whereas the Ka group repeatedly passed by figs loaded with ripe fruit in their home range. It could explain also why the UB group sometimes utilized available ripe _Spondias mombin_ fruits and sometimes did not.

Tamarin fruit-eating appeared to be highly selective with regard to not only species but also individual fruits in a tree visited. Occasional agonistic encounters around particular fruits (in species with larger fruits, such as _Genipa americana_) might be another indication of selectivity. Many small fruits were swallowed whole. Bites were taken from others. The latter fruits were typically not consumed totally. One to several bites would be taken and the remainder dropped, i.e., "wasted." This happened even with highly preferred species, e.g., _Inga punctata_. The amount of time spent in a given tree was usually relatively short, on the order of 10 minutes, and when a visit ended there often appeared to be ripe utilizable fruit still present.

The following extracts from my notes document the above points and also show how the tamarins reached and manipulated fruits:

> (Feeding in Unidentified species ("Yaya") bearing seeds covered with arel in a woody receptacle): "clung on nearby thin branches with hind feet and grabbed fruit with front feet, extracted seed with mouth, then with one hand still on fruit used other to hold seed while eating it. Took 1 or 2 bites, obviously didn't eat all the arel, then dropped them. Nor did any one animal eat all the seeds in any one fruit."

"They move around a lot. Don't take more than 1 or 2 fruits from a bunch. Grab the fruit off with the mouth, then get back up - right on the branch to eat it, manipulating it with the hands."

(Feeding in Genipa americana) "There was much interest in one particular fruit. It seems that one animal was trying to keep the others from it. When one would approach the fruit, this animal would give a prolonged screech...saw several others eat from the fruit. Other fruits were ignored."

(Feeding on Brosimum) "This fruit is on the lower surface of slender branches - reach it by sitting on more substantial branches and picking them off, or hanging upside down to eat (the latter mostly)."

(Feeding on Paullina) "It was noted that there are still quite a few of these fruits - red and therefore presumably ripe - on the vines, but the animals (as noted before) moved on without exhausting the supply."

"They grab off the fruit with their mouth, then sit on a solid branch to eat it, often moving several feet from where the fruit was gotten, holding it in the paw, and take bits from it, dropping the remains."

(Feeding on Ficus palmicida) "goes from branch to branch, stopping to take a fig here and there...definitely taking figs, can see it clearly, but never eats more than 1-2 from any one stalk."

(In Unidentified, highly favored species, "Manao") "Saw one case of apparent conflict over fruit in which 2 animals grappled, one gave a harsh squeal after which retreated."

(Feeding in Ficus palmicida) "Appear to be eating only the ripe ones (at least, they are highly specific about which individual fruit they pick). They chew them up and spit part (seems like a large part) out."

(Feeding in Inga punctata, a highly favored species) "surprising how many seeds that were dropped - well over half - have most of arel still on them."

(In Cecropia) "... hanging by hind legs, tail draped over branch, for as long as 5 minutes, feeding. Two shared same fruit without any vocalization exchanges."

"Saw a cotton-top suspend his body by his hind legs and, hanging down, grab a branch with his hands, pull it up to his mouth and feed on something there. No doubt that his hind legs were bearing his entire weight."

Insect foraging took two forms. When moving through the forest slowly tamarins would typically move for a short distance, then stop and look around, crouching on a tree limb, turning the head in all directions as though searching (similar movements occurred when tamarins were visiting a fruiting tree). A direct movement to some food item might follow or the animal might simply move on.

> "I watched one for about 10 minutes consecutively. Prominent in his behavior was looking all around, above and below."
> "I clearly saw him approach a bunch of leaves and turn over one leaf. Also prominent in his behavior was frequent change of position, rapidly, and once he dropped from about 25 feet to about 5 and climbed back up again."

The tamarins would also enter dense viney areas and remain there for prolonged periods. Some of this time was undoubtedly spent foraging for insects. I was occasionally able to observe a tamarin with a captured orthopteran, and one time a frog was eaten. Other small vertebrates and birds' eggs may well figure in the diet. Captive tamarins will eat eggs, mice, and birds (Epple, 1970).

The tamarins were observed visiting flowers of *Bignonia* sp. (yellow). They appeared to be licking or eating something at the base, after removing the corolla. Flowers of the third unidentified species were also visited. Nectar, pollen, or insects (or some combination of these) were probably obtained during visits to flowers.

Vegetative parts constituted a minor proportion of the cotton-top diet. They were most important during the end of the December to April/May dry season when fruit is scarce and trees in this highly deciduous forest were flowering and leafing out. The vegetative parts eaten and corresponding months observed were:

Newly sprouting leaves (March)

Terminal ends of vines or twigs (April, May)

Buds? - Something located at leaf bases on terminal, i.e., newly sprouting branches (*Spondias mombin*, *Pseudobombax septenatum*, a third unidentified species) (April, May)

Leaf stems (young *Ceiba pentandra*, 2nd unidentified species) (May)

Leaves of vine (May)

These observations were about evenly divided between 1973 and 1974.

A final source of food was unidentified material obtained from the surfaces of branches and trunk of some trees. In some trees the same sites were visited by a succession of individuals. Such spots were frequently but not always decaying. Fungi, sap, resin or insects are four obvious possible items which could have been present there. At least one African primate has been observed eating tree mushrooms (T. Rowell, pers. com., 1979). Sap constitutes an important part of the diet of at least 2 Callitrichids, *Cebuella pygmaea* and *Callithrix jacchus*. They dig holes in trunks and branches, utilizing their projecting incisors, and lick the sap that gathers in the holes (Coimbra-Filho and Mittermeier, 1977). *Saguinus*, however, lack the appropriate dentition and the behavior I observed did not correspond to what I would expect to be involved in digging such holes; nor were the holes I did observe (see below) similar to those described for sap-lickers. Both *Saguinus fuscicollis* and *S. nigricollis* have been observed consuming tree exudates (Izawa, 1978).[1] The descriptions below do in some cases suggest that some kind of exudate was available at the sites visited. In one case, caterpillars were found on the trunk surface at about 2 m, suggesting that these, if present on the higher parts of the tree the tamarins were visiting, could have

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[1] He reported resin to be a major food source for *S. fuscicollis* (1975, 1976) but modified this view in his 1978 publication.

been the prey. Some of the behavior observed suggests that larvae were perhaps being pulled out of their holes. The following note excerpts will illustrate the behaviors involved:

> "... picking something from bark surface and chewing it. Kept putting mouth to bark at precise points and could see mouth moving afterwards."
>
> "Two animals were seen to pick at something on the trunk, but had to be something attached to or exuded by the bark, because, judging from the body movements, it required some force to detach whatever it was. They were biting and tugging and when came loose their body would jerk." Seen in three trees, one "a branchless old cedar," another a "40-foot tree which had holes spread on the trunk, about ¼ inch in diameter, with apparently some liquid (?) exuding out."
>
> "Four animals were feeding on something in a certain area - pressing mouths to bark. In part but not all of that area there was a small amount of exudate."
>
> "Keep pressing mouth to bark. Healthy tree, so not termites. Ants? Or are they eating bark? In one spot I definitely saw an animal tearing bark from edges of an already-clear space. Have seen different animals go to same place."
> "The animal stops at _a_ spot, it is very defined, and procedes to put its mouth to it. Will raise head momentarily from time to time...and may change orientation. Sometimes various animals are seen to go in turn to the same spot. Also, I have noted in trees with no visible fruit, that sometimes there is a good deal of squealing heard, and in these trees one often sees a high frequency of the behavior described. Also, these 'spots' are not always on the upper side of the branch."
>
> "In old _Spondias_ _mombin_ riddled with insect holes, spend about 15 minutes foraging all over trunk, both with and without bark, pulling - at times - or picking something from surface and chewing it. Did not seem to pick just where there were holes."

My notes show a total of twelve such entries for the UB group, in somewhat over 300 hours of contact, between August 1972 and July 1973, all recorded in April and May of 1973. A few entries were made for other groups. The differential might reflect a real frequency difference, the fewer hours of contact with other groups, and/or their resulting lesser conditioning somewhat from year to year. Nevertheless it is clear that availability in terms of number of species fruiting rises sharply toward the end of the dry season, starting in February and reaching a maximum in April just as precipitation takes a sharp upswing following three very dry months (See Figure 21, p. 101). The same fruiting pattern is evident in the forest as a whole (Appendix 3). The consumption of vegetative parts during the months of March, April, and May (p. 72) coincides with this upswing in fruit availability. Thus the use of these items seems attributable not to scarcity of other foods, but rather to some other factor such as needed mutrients or high protein content.

November through February - the end of the heaviest rainy season and the beginning of the driest season - are the months of lowest fruit availability. These months probably represent or include a critical period for the tamarins in some or all years, particularly since insect availability probably follows roughly the same pattern (Dawson, 1976, 1977).

Quantitative differences complicate interpretation of the availability figures shown in Table 8. One mass-fruiting species could, for example, provide a greater quantity of food at a given time than many slow-ripening species combined. With the data available it is not possible to assess the exact proportion of intake provided by such mass-fruiting species, although in some cases they were obviously important since the tamarins visited them repeatedly. Outstanding examples are: Ficus sp. (bearing figs about 1½ cm diameter), Ficus palmicida (ca. ½ cm diameter), Anacardium excelsum, Quararibea sp. (fruits), and Spondias mombin. All were also utilized heavily by other primates and non-primates (see Appendix 2). Ficus sp. appears at first glance to have a prolonged fruiting season, but individual trees actually bear fruit for only a few weeks. The seemingly prolonged fruiting season actually reflects an asynchrony of fruiting by individual trees (See also Hladik and Hladik, 1971). Tamarin home ranges included only one to a few figs or other mass fruiting species. Thus their importance in terms of total intake would depend greatly on the overall food situation at the time they came into fruit. It also might vary annually and from group to group in a given year. This could explain why the UB and Ba groups utilized the fig trees in their home range whereas the Ka group repeatedly passed by figs loaded with ripe fruit in their home range. It could also explain why the UB group sometimes utilized *Spondias mombin* fruits and sometimes did not.

Water

Tamarins were not seen to come to the ground for water. Many home ranges in fact lacked any arroyo which might form a source of permanent water. The tamarins probably obtained necessary water from their food and/or leaf surfaces and small pools in branch or trunk cavities. One group was observed licking water from leaf surfaces after a rain. During the dry season water condensation on vegetation from frequent heavy fogs may constitute an essential source of water, since in at least some years no rain falls for several months.

Sleeping Trees

Between 1630 and 1830 hours, usually well before dark, a tamarin group entered one of various sleeping trees in its home range. Sixteen such trees were located in the UB group's home range and 8 in the Ba group's (Figure 17). The trees used were scattered in various parts of the two home ranges. Two other tamarin groups accounted for one sighting each, making a total of 26 sleeping trees observed. Many of these were upper strata (13.5-20 m) trees, for example *Lecythis magdalenica* (9 sites), *Ceiba* sp. (1 often-used site), *Pseudobombax septenatum* (3 sites), *Samana samanea* (1 site), and *Prioria copaifera* (1 site). In all cases the trees could be entered via adjacent trees; i.e., they were not emergent trees. In some cases the tops had been broken off.

In contrast to the Callitrichid *Leontopithecus rosalia* (Coimbra-Filho, 1977), cotton-tops did not utilize holes for sleeping, although

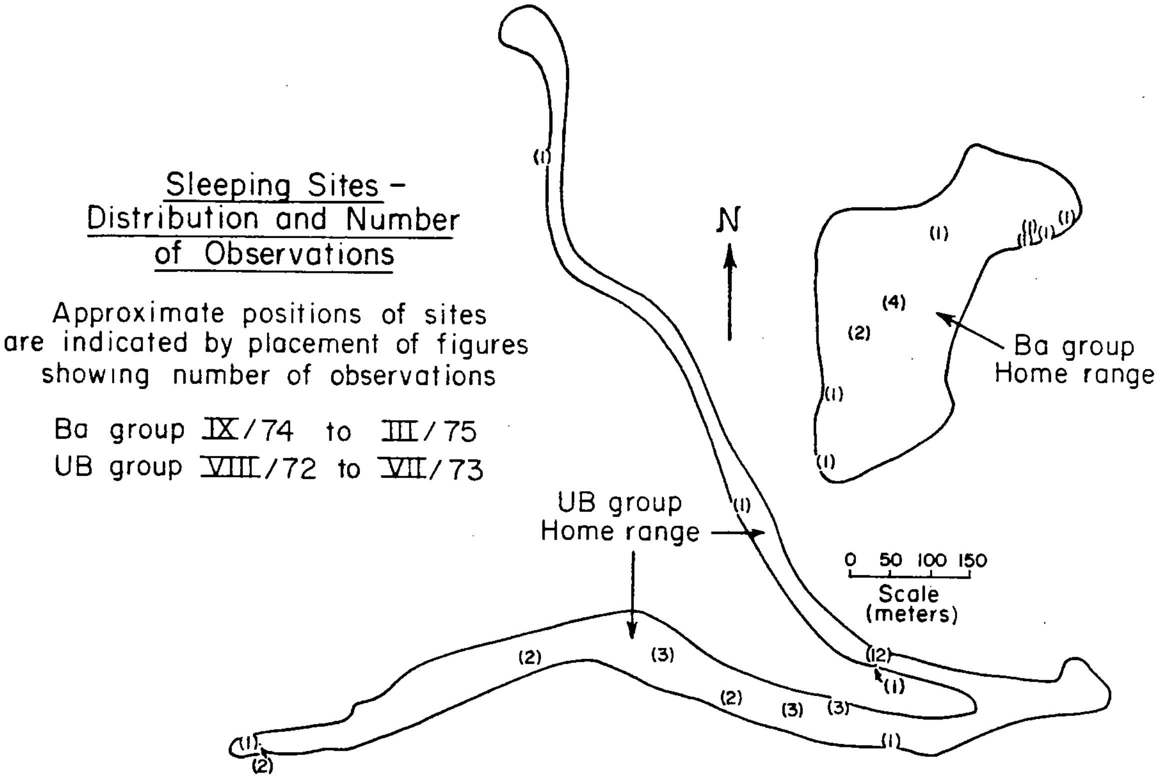
Sleeping Sites - Distribution and Number of Observations
Approximate positions of sites are indicated by placement of figures showing number of observations
Ba group IX/74 to III/75
UB group VIII/72 to VII/73
N
Ba group Home range
UB group Home range
0 50 100 150
Scale (meters)
(1)
(1)
(1)
(1)
(4)
(2)
(1)
(1)
(1)
(12)
(1)
(2)
(3)
(2)
(3)
(3)
(1)
(1)
(2)

Figure 17

Figure 18

Examples of trees used for sleeping by *Saguinus oedipus*.
Site where tamarins slept is circled in each case.
Group is present in left-hand example

they were available. *Aotus trivirgatus* and *Eira barbara* were seen using tree holes. In eighteen of the 26 sleeping trees the group chose a wide main fork or a broad branch at 10-22 m for sleeping. In some of these sites, very little cover was present and the animals were in fact visible from the ground (Figure 18). In others they were hidden by vines to a greater or lesser degree. In four cases they slept among the bases of the grown-out leafy branches of a broken-off tree, at 13-20 m from the ground. In three cases low trees with dense crowns were chosen (3-7 m tall), and I was unable to determine the exact sleeping location. In one case the UB group slept near the end of a branch among a dense viney mass, at about 17 m from the ground. In the latter four cases I suspected the group was trying to avoid my seeing them bed down. The tamarins may have moved after I hurriedly left to reach camp before dark. Their presence the next morning was not verified as it was in most other cases.

In one instance the tamarins bedded down in the same tree with a group of howlers (*Alouatta seniculus*) which had arrived beforehand. The howlers occupied forks well out on the branches, while the tamarins settled in two crotches close to the trunk. The latter was also one of the two only cases in which a group was seen to split up to sleep. During the periods that this occurred the group involved (UB) had 13 and 10 members. This seems rather a large number of animals to fit on one branch or fork. The splitting up may have been related to this rather than social factors.

Around 1630 hours the tamarins' behavior acquired a characteristic pattern: the group became more cohesive and often traveled quickly and quietly, though foraging still sometimes occurred. Vocalizations became noticeably subdued. The group appeared to be trying to get away from me. If they saw me near a sleeping tree as they approached (e.g., one they had used in the past which I had approached expecting them to enter it), they would not enter it. They would pass it by and keep traveling. This behavior was effective in "losing" me and may function similarly with predators. When they entered the tree they would do so in quick succession.

The above describes the behavior of groups which were aware of my presence. On several occasions due to the fact that one member of the Ba group was wearing a bell I was able to stay out of the group's sight and still follow it. On these occasions they gradually approached the sleeping site and foraged sporadically near it for about an hour. They spent long periods sitting quietly and looking around between progressions, which were very short. Then, one by one, they gradually entered the sleeping tree.

Shade Trees

Shade-providing trees are probably an essential resource for tamarins. Although they frequently groomed in the early morning sun, rest periods during the remainder of the day were spent in the shade. At midday the tamarins often rested for an hour or more in the shade, lying on wide branches with the legs draped on either side. This is the position taken by captive animals under heat stress (Hampton, Hampton and Landwehr, 1966).

Structural Aspects of the Niche

Tamarins share with other primates the use of larger tree branches permitting a quadrupedal gait during rapid forward progression. However, tamarins have capabilities not possessed by the larger monkeys.

Since they possess claws they can utilize vertical surfaces with great ease and can in fact jump from one vertical surface to another. Due to their small size they can traverse gaps by jumping from one thin branch to another. They often jumped onto single branches no more than 1 cm in diameter and crossed open spaces on vines of similar dimensions (Figure 19). This permits them to go into areas of new secondary vegetation where trees may be widely spaced and may lack substantial branches. Their small size permits them to utilize densely vined areas which would be difficult for the larger monkeys to negotiate. Size differential may also be the basis for partitioning of resources used by the tamarins in common with the larger monkeys, as shown by the following observations of tamarins and howlers feeding on the berries of the vine Trichostigma octandrum occurring in the upper levels of the canopy:

> "Howlers get at the berries of the thinnest branches by hanging onto one or more substantial ones - in one case I saw an animal clinging by his tail to a branch about 1 inch in diameter, with one foot on a similar branch and the other foot on a mass of smaller branches; suspended like this reaching out and drawing the tendrils to its mouth. Thus it would seem that there could be considerable overlap with Saguinus." "Much of the time it seems that the howlers, especially the younger ones, could also reach the berries the Saguinus are feeding on, especially with the help of the (prehensile) tail." "Where the Saguinus would appear to have an advantage is on thin branches that aren't close to the main vine mass - that howlers can't reach by drawing them in - because a very thin branch of 1 inch diameter or less will support a Saguinus easily, whereas a howler (large one anyway) will need several of these."

The tamarins can reach the thin fruit-bearing branches by sitting on the tops of branches, distributing their weight among several thin ones, and using the tail pressed against one for balance. Alternately they may hang by under a branch with all four feet or just with the hind feet while manipulating the fruit. Fruit is plucked with the mouth or (in the case of large fruits) bitten into. It may be drawn

Figure 19

Tamarin crossing open space on
vine one inch in diameter

into reach with the forelimbs. After plucking the fruit, they often sit back on a solid branch to eat it.

Travel routes occasionally incorporated palms, including the spineless top surface of the very spiny *Astrocaryum*, but only when other movement routes were restricted. They never foraged in palms.

The tamarins did not manipulate the environment while foraging the way *Cebus* monkeys did. I did not observe them unrolling leaves, digging into accumulations of leaves, etc.

Inter-specific Competition

Cotton-top tamarins clearly compete in this forest with squirrels, (*Sciurus granatensis*), other diurnal primate species (*Cebus capucinus*, *Alouatta seniculus*), and various frugivorous birds, as evidenced by repeated observations of dietary overlap (Appendix 2). Nocturnal competitors include *Aotus trivirgatus*, *Didelphis marsupialis*, *Marmosa cinerea*, *Caluromys* sp., and other frugivorous species. Insect-gleaning birds and mammals (including *C. capucinus*) also probably overlap in diet with the tamarins.

Squirrels relied heavily on some items utilized lightly or not at all by the tamarins. Examples are the flowers and leaf stem bases of *Lecythis magdalenica*, the ripe or green fruits of *Guazuma ulmifolia*, and the nuts of *Astrocaryum malybo* and a second unidentified *Astrocaryum* (possibly *standleyanum*) palms. The latter were obviously staple foods for the squirrel population for at least four or five months out of the year.

The *Cebus capucinus* were not observed eating palm nuts. During the fruiting season of *Lecythis magdalenica* they could frequently be heard pounding the large thick pods of that species. No other primate in the forest was apparently capable of opening these fruits.

Most interspecific contacts observed were neutral. Both squirrels and howler monkeys were observed on various occasions in the vicinity of tamarins, including feeding in the same tree, without evident interaction. No polyspecific associations between primates were observed as reported for some South American sites (Klein and Klein, 1973; Castro and Soini, 1977; Izawa, 1976; Terborgh, in press). In fact, two primate species were rarely seen within sight of each other. There were also no associations between any of the diurnal primates and birds, such as those described for *Saimiri* (Klein and Klein, 1973).

The only cases of aggressive interspecific interaction observed were the following:

1. On one occasion a tamarin chased a squirrel from a tree.
2. A toucan (*Pteroglossus torquatus*) was observed to fly away twice when a cotton-top moved as though to approach it.
3. A *Cebus* chased a tamarin for a few meters when it entered a fruiting *Ficus* where the *Cebus* were feeding. The tamarin left the tree immediately. The *Cebus* clearly dominated the larger *Alouatta* - howlers were twice observed to rapidly vacate trees where they were feeding when a *Cebus* group approached. Several times I had the clear impression that tamarins also avoided *Cebus* (which move very noisily through the forest) when they were heard approaching.

Time Budget

The tamarin day begins between 0550 and 0650, and ends when it enters the sleeping tree at 1630-1830. Like S. geoffroyi (Moynihan, 1970) the cotton-top begins moving and feeding relatively late in the morning compared to most primates, up to an hour and 20 minutes after dawn.

Foraging might occur at any time of the day, but inactive periods of a few minutes to 30-60 minutes might be seen as early as 0900. Early morning rests often occurred in the sun. Grooming often accompanied rests. The longest rests, occasionally up to two hours when the tamarins often appeared to go to sleep, occurred in the shade around midday.

Long rests were only observed in well-conditioned groups or those which could be followed at a distance due to one member's being marked with a bell. Unmarked groups were hard to detect as they were settling down, with the result that I was frequently within their range of flight before I realized they had stopped moving. This probably accounts for the fact that I initially had the impression that the tamarins were active all day and did not rest at midday as do other primates (see also Moynihan, 1970).

POPULATION CHARACTERISTICS

Sexual Dimorphism

Adult[1] males and females were indistinguishable with regard to pelage, average weight, or head and body length (Table 9). The maximum (unworn) upper canine height for both sexes was about the same, 6.5 mm.

Growth

Growth data were available from seven juveniles captured once under a year of age and again as young adults (Figure 8). The minimum adult[1] weight (334 gm) was probably reached at about 1½ years. Average adult weight (414 gm) would have been reached at about 2 years of age by some individuals, but most gained weight more slowly. It appears that the growth rate was slower in this population than in captivity (Figure 8).

Annual Variation in Weight

Weight did not vary significantly between trimesters (Table 10), although for both sexes the average weight was slightly higher in the March-June trimester. This is the trimester in which food availability was greatest, as indicated by the fact that there was a maximal number of species bearing fruit eaten by the tamarins (Table 8). Dawson (1976) found a significant weight increase in Panamanian tamarins during the July-October trimester.

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[1] Any female with well elevated, pigmented circumgenital and suprapubic glands was considered an adult, as was any male with descended, normal-sized testicles (measuring approximately 1.3 to 1.5 cm x 0.9 to 1.1 cm).

Table 9

Weights and Measurements of 54 Adult *Saguinus oedipus*

		Weight (gm)				Head and Body Length (cm)[3]	
	n	Average[1]	(SD)	Range[2]	Median	n	Range
Males	28	411	37	334-500	410	26	21-24
Females	26	416	34	350-480	414	24	21-24
All	54	414	35	334-500	414	50	21-24

[1] One to 4 measurements per individual; used average where more than one. Weighted means: males, 417; females, 415; all, 416 gm.

[2] Range of above averaged values where more than one weight per individual. Range of individual values: 334-520.

[3] Variability in length measurements was great.

Confidence limit for total length (2 measurements each): for 5 females: ±1.0-5.0 cm; for 8 males: ±0.5-6.4 cm.

For 7 adult males, 2 adult females, 2 measurements each, maximum 95% confidence limit was ±2.0 cm:

	Total L	Tail L
$\bar{\bar{x}}(M)=$	58.4	35.9
$\bar{\bar{x}}(F)=$	56.9	34.9

[4] See text for definition of "Adult."

Table 10

Adult[1] Weights by Sex and Trimester

	Males			Females		
	Mar-Jun	Jly-Oct	Nov-Feb	Mar-Jun	Jly-Oct	Nov-Feb
$\bar{x}$	423 ±50[2]	413 ±36	414 ±31	426 ±32	415 ±36	412 ±30
n	9	33	7	5	26	9
F		0.262 ns[3]			0.280 ns	

[1] For definition of adult see footnote, p. 86

[2] Standard deviation, weights in gms.

[3] $p > .05$

Sex Ratios

The sex ratio M:F for the whole population sample observed was 1.2:1, but this was not significantly different from 1:1 (Chi^2 test, Table 11). In five established groups in Jan-Mar 1975 and six groups in July 1975 the sex ratios were 1.7:1 and 2.1:1 respectively. The latter figure just approaches significance ($p=0.10$) (Table11).

The sex ratio (1:1.4) of all transients, including animals passing through the area, those joining or leaving groups, and those changing groups within the study area, is not significantly different from 1:1 (Table 11). It is, however, biased in the opposite direction from the established group sex ratio.

Age Structure

Age-class profiles for established tamarin groups show that the maximum number of juveniles present was two (Figure 16). They were accompanied by three to seven adults of varying ages. In all cases the number of potentially reproductive individuals (2 years or older) exceeded two. Many of these individuals accompanying the presumed reproductive pair fell into the older age classes. This pattern was fairly consistent over a three-year period (Table 12).

Turning to the transient age-class profile (Table 13): of a total of 31 individuals observed (not counting disappearances), all but one were adults. The exception was a juvenile of about 1 year of age which disappeared from her group (Ca) simultaneously with an older parous female which could have been her mother (F1). Nineteen transients were examined for tooth wear. Three were subadults (A1), 5 young adults (A2) and the remaining 11 were older adults over 5 or 6 years old (6 were

Table 11

Adult Sex Ratios

	M	F	Unk[1]	M:F	Chi2[3]	p
Overall (all tamarins seen in area)	39	33	18	1.2:1	0.50	>.10
5 Groups Jan-Mar 1975	15	9	1	1.7:1	1.50	>.10
6 Groups July 1975	15	7	1	2.1:1	2.91	.10
All transient animals[2]	11	15	4	1:1.4	0.62	>.10

[1] Adults of unknown sex, excluded from calculations.

[2] Includes both those immigrating/emigrating to/from the study area and those changing groups within the study area.

[3] Comparison to 1:1

Table 12

Summary of age-class composition of five *Saguinus oedipus* groups over three years

Age Class	Est. Age			Five Groups: Ka, Ba, Bo, Ca, Za areas Number M,F and (Sex Undetermined)						
		Aug 1975			Aug 1976			Aug 1977		
			T	(%)		T	(%)		T	(%)
A?	Undet.	1,0 (2)	3		0,1 (2)	3		0,0 (2)	2	
A4	Over 5	5,1 (0)	6	(27)	5,1 (0)	6	(20)	5,2 (0)	7	(23)
A3	or 6 yrs.	3,2 (0)	5	(23)	3,2 (0)	5	(17)	4,1 (0)	5	(16)
A2	2-5 or 6 yrs.	2,1 (0)	3	(14)	4,2 (0)	6	(20)	5,4 (0)	9	(29)
A1	1-2 yrs. (subadult)	3,1 (0)	4	(18)	2,2 (0)	4	(13)	4,2 (2)	8	(26)
Juv	Under 1 yr.	1,2 (1)	4	(18)	4,2 (3)	9	(30)	2,0 (0)	2	(6)
			25	100		33	100		33	100

Table 13

Age-class Composition of Transient Sector

	Joining or Leaving Established Groups						
	Immigrants	Emigrants	Changers[1]	Temporary[2]	Uncertain[5]	Total[3]	%
A?	2	3		6		11	
A4	3	(1)[4]	(1)	1	1	5	25
A3	2	2		1	1	6	30
A2	1			2	2	5	25
A1	1	1	1			3	15
Juv		1				1	5
						31	100

[1] Individuals moving from one established group to another.

[2] Remaining in area only a few days to a few weeks; in one case temporary joining of an established group.

[3] Total number of individuals. Note that this table excludes possible emigrants, i.e., individuals which "disappeared" for unknown reasons.

[4] Parentheses denotes events by an individual already listed.

[5] No chance to observe area (UB group) subsequent to discovery.

A3, 5 were A4). The percent of subadult and young adult individuals together, that is ages about 1 to 5 or 6 years, was thus about equal to that in the two older age categories, which cover an equivalent or perhaps a few more years. The evidence from this small sample is, therefore, that older animals are quite likely to leave their groups, perhaps as likely as younger ones. Some of these older animals may also have been part of a reproducing pair. This is suggested by the fact that judging from nipple condition, three parous females were included among the transients (Fl, Yo, Go). A fourth parous female disappeared from her (Ka) group and so may have become a transient. The juveniles she had produced were about 6 months old at the time of her disappearance. They remained in the group accompanied by 2 males.

Mortality and Possible Causes Thereof

Important predators could be arboreal or aerial. The tamarins used different alarm vocalizations for the two. *Eira barbara*, a mustelid with marked arboreal tendencies, reported to prey on *Saguinus geoffroyi* (Moynihan, 1970), was sighted seven times near tamarin groups. In one instance the *Eira* began feeding in the same large fig tree as the tamarins. In each case the tamarins reacted with long series of piercing calls. Mnemonically the sound produced could be described as theeeeeew, descending somewhat in pitch ("Thew" call, Figure 13). This call may be equivalent to the "Loud Sharp Notes" of *S. geoffroyi* described by Moynihan, 1970. Loud chirps in varying combinations may be mixed in between thews. As in that species, this type of alarm response tended to be contagious although individuals out of sight would often continue foraging.[1] Vocalizing individuals would stop frequently and look around at or for other group members. The Eira appeared to ignore them completely. The same vocalization was elicited by two other potential terrestrial predators, humans and dogs. Initially, this was the predominant reaction by any group I tried to follow which was not accustomed to me. As long as I stood still the alarm would gradually cease, with some individuals noticeably more persistent than others while others drifted away. Anytime I began moving the alarm would be renewed. This could go on for an hour or two until the group gave up giving alarm and fled without it.

Birds flying overhead elicited a series of 5 to 10 loud short chirps, of approximately the same tone, given very close together, i.e., a "Chirp Burst." This vocalization was never repeated. It was commonly, although not invariably (see Table 14) given to hawks. Once the hawk alighted, even if relatively close to the group (e.g., in one instance, 3 m away) no further alarm was given until it flew again. The alarm may then be repeated, even though the hawk may be simply changing perches. An unsuccessful predation attempt on Saguinus by a hawk was seen.

Tamarins were observed to fall eight times. Twice intruders dropped to the ground while being chased by residents. The drops were so abrupt and in such unlikely places as to seem deliberately evasive rather than

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[1] During alarm calling there is a strong impression that all group members are visible, especially since the alarm response often continues for 15 minutes or more. From personal experience, I would rarely count more than 5 to 7 individuals in a group actually composed of 10 to 12 during such an alarm (or even after hours of following) except under unusual conditions or where there was exceptionally open vegetation. With smaller groups invariably one or two individuals were missed. Since a group often renews the alarm when the observer begins to follow, repeated low group counts may be obtained. I believe that some published estimates of callitrichid group size may be low, because group counts are often made under such conditions.

Table 14

Stimuli evoking the aerial predator call ("Chirp Burst") over a period of several months (UB group)

Stimulus	Number of instances
Hawks (various species)	10
Buzzards (2 species)	6
Toucan	2
Parrot (Macaw)	2
Ibis	1
Hawks flying overhead without eliciting the response	3

accidental (Similar behavior has been described in gibbons [Tenaza, 1975]). In both cases the animals involved moved along the ground after dropping rather than immediately ascending, and were not followed by their pursuers. In a third case connected with agonistic interactions, one of two grappling animals fell and caught itself on vegetation below. Falling was also observed during normal activity. Twice adults fell to the ground during foraging (from 3 and 27 m, respectively) and once an adult fell from 13 meters but caught itself on vegetation below. All immediately ascended again. Twice juveniles fell to the ground (ages 1½ months and 2 months, from heights of 12 and 17 m) and were retrieved by adults. In both cases, the juvenile moved along the ground vocalizing until picked up. One of these may have died as a result of the fall since a dead juvenile was observed the following day being carried by a group member. However, there were two juveniles in the group at the time, so identification could not be certain. The animal died during the night and was carried for about two hours in the morning, then was left in a tree when the group moved on.

Two captured tamarins showed signs of extensive recent hair loss due perhaps to some kind of skin infection or perhaps a mite infection. Mites were found localized behind the ears on three additional individuals, on the arm of a fourth and in an unstated location on a fifth. The fur of all other captured animals appeared luxuriant and healthy.

Scars were relatively frequent. The most frequent location was the bottoms of the feet (22 cases noted, often more than one scar on a single individual; not all scars on bottoms of feet were noted because they were so common). Scars around the head were next in frequency, around the temples and topknot (8 cases), around the mouth (heavy tears or missing parts of lips) (7 cases), other parts of the face (6 cases). Scars on the legs, ears, circumgenital area, back, and tail totaled 10 cases. Two animals had a damaged or missing toe joint. Three had an enlarged tail joint causing a kink in the tail. Twelve individuals had more than one scar or wound: the maximum was five (one case), one had four; three scars were found on six individuals, and two on four. No sign of serious infection was found. This accords with laboratory observations on the extreme rapidity of healing in this species (Hampton, Hampton and Landwehr, 1966).

Survivorship

Discussion of survivorship is limited by the fact that except in the case of juveniles the disappearance of a marked individual could be due to either of two factors: mortality, or its having left the study area. (The study area, it will be recalled, constituted only about 45 hectares of a forest totalling over 600 hectares.)

Juveniles however, can be assumed to leave the parental group very rarely, if at all, under a year old. Any disappearance can therefore be interpreted as due to mortality. One death was in fact witnessed (see Mortality). The data concerning juveniles are summarized in Table 15.

Analysis is complicated by varying periods of observation and in one case by a possible identity confusion. The six-month survivorship was 75% (18/24 minimum born), while the one-year survivorship was about the same, 75% (15/20 observable). For older tamarins the sample decreases drastically in size. One case of a 1-2 year old leaving the natal group was observed while 7 in four other groups remained with their groups. Five of these at least (the other two were not observable) continued in

Their natal groups for another year, passing their third birthdays.

Table 15

Survivorship of Young

Group & Year	Min.[1] No. Born	Age Reached 6 mo.	1 yr.	2 yr.	3 yr.	Observations
UB-1973	2					Death at ca 1 1/2 mo. Disappearance at ca 2 mo.
-1974	2					Both disappeared
Ka-1974	2	2	2	2	1	Other possibly present
-1975	2	1	--------	--------	--------	
Ba-1974	1					Disappeared ca 5 mo.
-1975	2	2	2	2	---	Assuming unmarked subadult seen 1977 corresponded to unmarked juvenile of 1976.
Bo-1974	1	1	1	1	1	
-1975	1	1	1	--------	--------	
Ca-1975	1	1	1			Left group at about 13 mos. with two older females.
-1976	2	2	2	--------	--------	
-1977	2	2	--------	--------	--------	
Za-1974	2	2	2	2	2	
-1976	2	2	2	--------	--------	
La-1974	2	2	2	--------	--------	

[1] Actual number could be somewhat greater since early natality not witnessed. Captive *Saguinus oedipus* are reported to have 69-74% twins, 11-19% singles, and 10-15% triplets (Neyman, in prep., and Gengozian et.al., 1978).

Note: -------- indicates no observation possible.

Summary of Survivorship of Juveniles

Age	Potential No. Observable/No. Present	%
6 mo.	18/24	75
1 yr.	15/20	75

REPRODUCTION

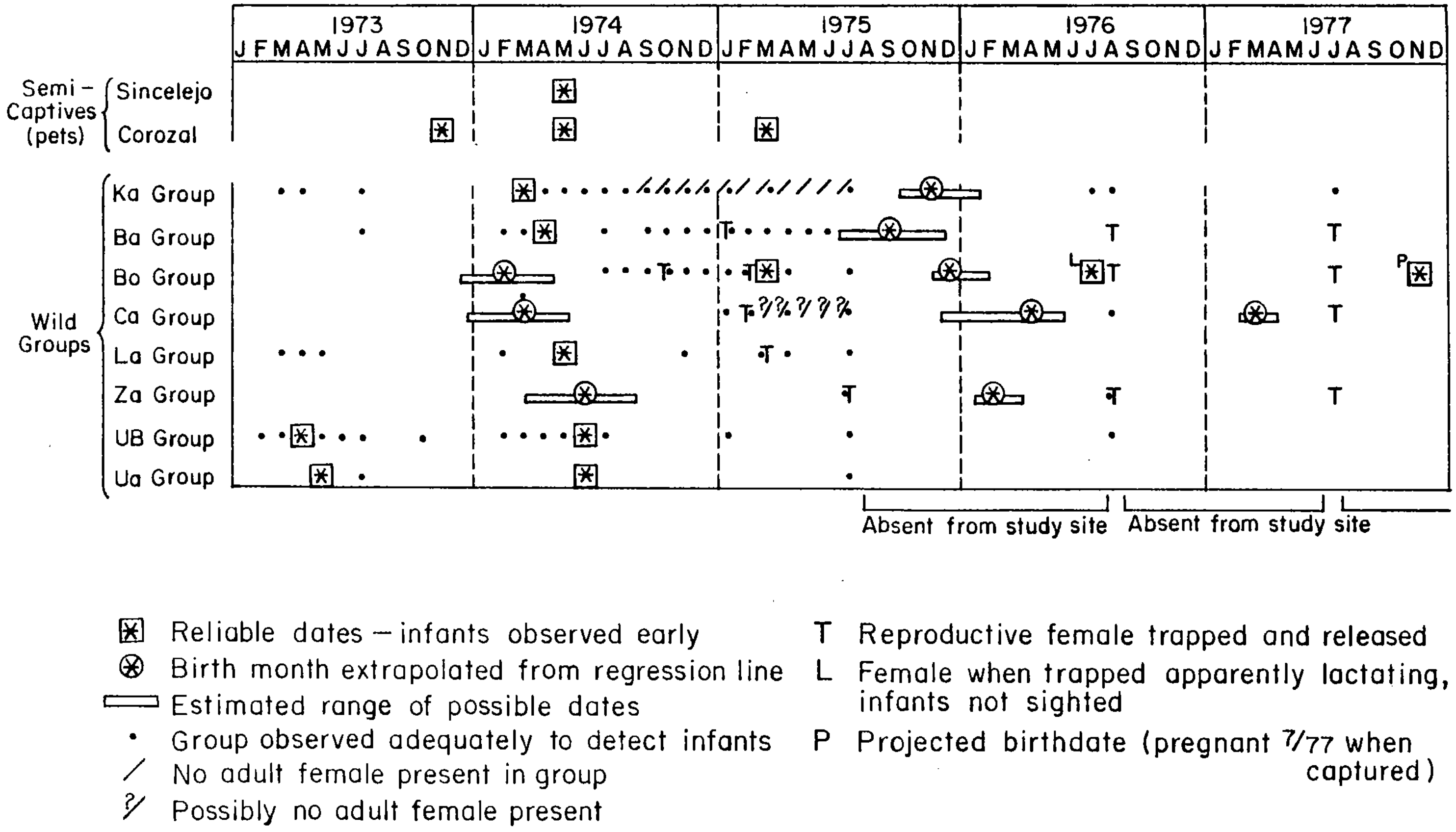
Litter Size

Of 17 litters observed, 13 or 76% were twins and the rest singles. Since these were first seen at ages varying from one week to several months, that is after early mortality had already taken its toll, it is likely that the actual percentage of twins born was higher. In captive S. oedipus (Gengozian, et. al., 1978) the percentage of twins has been reported to be 69% (n=83 deliveries), with 19% singles and 10% triplets. T. Rowell's Berkeley colony of S. oedipus produced 74% twins (n=27 deliveries), 11% singles and 15% triplets (unpublished). Dawson (1976) observed a set of triplets in wild S. geoffroyi. Since females only have 2 mammae, however, it is unlikely that more than two members of a triplet litter often survive in the wild. Even under the presumably optimal diet conditions in captivity, one triplet usually dies.

Frequency

Information on the timing of births in the population I observed is summarized in Figures 20&21. Births (and therefore conceptions) occurred in most months. However, 17/22 or 77% of births over five years occurred in the first 6 months of the year. Three out of the 5 cases of later births coincide with a lack of observed births earlier in that year.

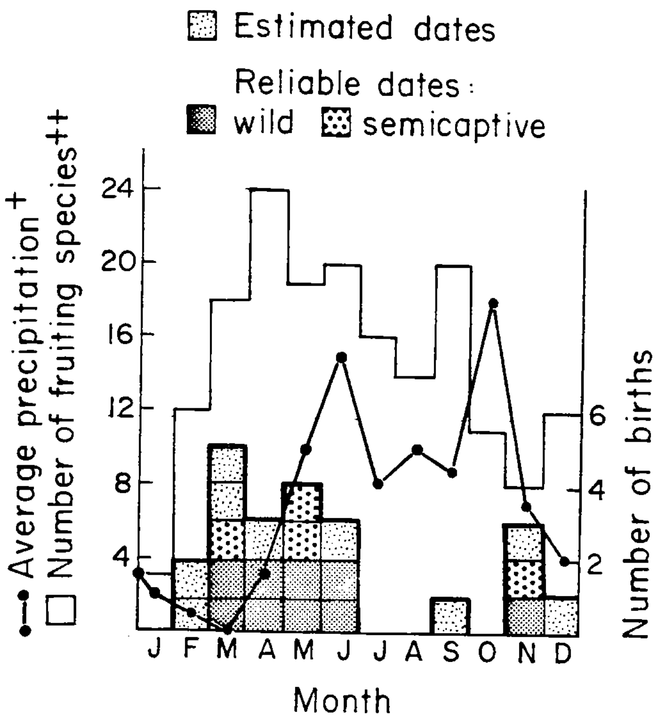
Delineation of the pattern for individual females was complicated by turnover of females in groups. One old obviously parous and therefore most likely the sole reproductive female in her group (of two adult females present), was present from 1974 to 1977 in the Bo group. Inter-birth intervals were about 8,6, and 15 months for the four births attrib-



*See p. 32 for explanation of how these ranges were determined.

Figure 20

Births observed in "established"
and semi-captive groups of S. oedipus



+Toluviejo, 1950–1957
(Instituto Augustin Codazzi, 1969)

++Species used by the tamarins (1972-75)
with available ripe fruit (1974-75)

Figure 21

Seasonal birth pattern compared with
rainfall and fruit availability patterns

utable to her. In another (Ca) group the same female could have been present in 1976 and 1977 during which she was the only adult female. Two births occurred, separated by about 10 months. Lastly, in a third group (Za) where Zo was the only adult female present in 1975 and 1976, the inter-birth interval was about 20 months. The inter-birth intervals stated must remain rough estimates, due to uncertainty in estimating birth dates (see Methods-Age Estimation), and to other considerations discussed below. However, the data do indicate that only one birth per year occurred in most groups. This result was unexpected, since captive Callitrichids, including Saguinus oedipus, do frequently conceive while still lactating and are in fact capable of births every five to six months.

In some cases the lack of births in the groups I was observing could be attributed to the absence of a female in the group. This was true for the Ka group from about September 1974 to completion of the initial phase of the study in August 1975, and also for the Ca group from about February 1975 until at least August 1975 (Figure 20). By the time I returned in August 1976 both groups had females and juveniles present. In both areas the males remained throughout.

Turnover of females is not the only possible explanation for the long intervals between appearances of infants in groups, as is shown by the data on individual female inter-birth intervals already discussed. For those cases in which females were present and group composition remained stable there are two possible explanations. One is that the length of the interval is more apparent than real, that births actually did occur but I just never saw the infants before they died. This possibility cannot be entirely discounted since intervals between observations of a given group were at times irregular (Appendix 1). It is possible that infants may have in some cases been present but not seen, since adults carrying infants sometimes tended to be particularly shy of being seen by me. This may have happened in 1976 with the Bo group, since Lo appeared to be lactating but infants were not sighted. (Of course, the infants may also have been lost early.)

Despite what has just been said, I do not feel that the lack of observed infants born in the first 6 months of 1975 is attributable to observational parameters. Since there had been a concentration of births in the first half of 1974 I was expecting the same in 1975 and looked particularly for infants and juveniles whenever I encountered groups. Repeated encounters of groups rules out in most cases the possibility of simply missing infants. Also I trapped most groups during that period and so examined a great number of tamarins in hand and from close distances[1] without finding a pregnant or lactating female, or observing juveniles or infants. Another possibility to consider (relative to whether the long and variable intervals between births were more apparent than real) is that my trapping of the reproductive females in early 1975 (see Figure 20) caused abortions. Abortion is a frequent response to manipulations of captive S. oedipus (Hampton, Hampton and Landwehr, 1966). Unfortunately I lacked the expertise at the time to detect early tamarin pregnancies. One female (Lo) was, however, in an advanced stage of pregnancy at the time of capture and gave birth anyway. No infants appeared either that year in two groups which were

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[1] When one group member is captured the rest of the group tends to stay in the vicinity of the trap for some time, and to return rapidly to it when the captive squeals at the observer on close approach.

not trapped (UB, Ua - Figure 20). Lastly, the phenomenon of the missing 1974 birth peak seems to have recurred in 1976 and 1977 when trapping was not a factor.

Having eliminated the observational artefact explanation, a second possibility suggests itself, namely that the timing of production of young is variable and is linked somehow to climate or resource variability (see Discussion).

Number of Young/Lifetime

All captured females with elongated nipples and judged therefore to be parous females, fell into the older dental-age categories A3 and A4. It appears then that females may not begin reproducing until they are more than five or six years old.

The maximum lifespan for captive tamarins so far reported is 9 years 10 months (Napier and Napier, 1967). I have commented already (see Tooth Wear) that the relatively slight degree of canine wear evident in the oldest (5 years) individual of known age in this population suggested the maximum lifespan could well be longer; the average lifespan can, however, only be guessed at. At most it is likely that a female's reproductive lifespan could not exceed 6 years. Her maximum output is probably thus around 24 offspring given 2 births per year and an effective litter size of two. The data on frequency of reproduction presented above suggest, however, that output in this population was on the order of one litter per year or slightly more. Mortality and uncertainties of securing a mate and territory would further reduce the number. The final number of offspring reaching sexual maturity per female per lifetime cannot be determined with the data available, but certainly would be fewer than ten if the observed pattern persisted.

Life history parameters for males are probably similar to those for females, given the lack of sexual dimorphism and relative equality of investment in group and home range defense. For males the possession of a mate and a territory may be critical to sireing offspring, although there is no information on opportunities for fertilization by itinerant males. It was notable, however, that in two groups where the reproductive females disappeared or left (Ka, Ca) the males present at the time stayed on. In a third group (Ba) the two adult males disappeared and the adult female left (was seen in the area of an adjacent group), while the male subadult stayed on. Males were known to leave and enter groups; however, in every case more than one male was present and it was not known which was the reproductive.

Parental Investment

Parental care involved lactation, carrying the young, retrieving them from danger, and sharing food with them. Adapting group movements to accomodate infant-carriers and juveniles, and probably also near-term pregnant females, might be considered a form of parental investment. Lastly, since no transient group had infants it seems that reproduction is linked to attachment to a defended area. Thus the cost of that defense might also be considered in part as parental investment.

Both females and males participate in infant-care activities. In many laboratory groups the male's contribution to carrying and retrieving considerably exceeds that of the female, who may in the most extreme cases take the infants only for nursing. There is great variability between pairs and between litters of the same pair (Epple, 1975;

Stevenson, 1976; Hoage, 1977). Carrying is probably a considerable burden on tamarins since a set of twins can weigh 60-80 gm at birth (Wolfe et. al., 1972; Chase and Cooper, 1969; Kleiman, 1977b; Eisenberg, 1977), or 14-19% of the average adult body weight.

The infants are at first carried constantly but rapidly become mobile, first crawling all over the back of the carrier. Gradually they venture onto the substrate for increasing distances. I had the opportunity to observe extensively the development of one set of infants from the age of about a week (UB) until one died at 1½ months and the other disappeared shortly afterward. I observed a second set (Ka) at intervals throughout the juvenile period. The following remarks are based on these observations. The first brief contacts with the substrate were observed on days 11-22.[1] At 22-33 days, separation to about 8 inches from the carrier was observed, but the carrier quickly gathered the infant back up. Starting around 31-42 days carriers began forcing the infants off their backs and leaving them while they foraged nearby. In order to rid themselves of the infants, carriers would rub the back against a branch while reaching back with the forepaws. The infants would move about on the back trying to avoid being rubbed off. The infants I observed vocalized constantly after being left, until picked up again. The separations were at first only on the order of a few minutes, so the infants or juveniles were still being carried most of the time. Also they were retrieved at any disturbance. By 2-2½ months of age juveniles were moving independently except when the group traversed difficult areas. They were still being picked up if

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[1] Range in age is due to the fact that the infants were 1-11 days old when first observed.

alarmed by me or a visiting group. Although by this age the combined weight of two juveniles was on the order of 160 gm, or 39% of the average adult weight (Table 9), both might on occasion still be carried by one adult. Active playing was observed between twins about this age, including running, jumping, chasing and grappling, accompanied by constant chirping vocalization. By about 4-4½ months the juveniles were locomoting completely independently. I did see, however, one case in which a juvenile about this age was retrieved. She could not traverse a gap which the group had apparently crossed and was apparently inhibited by my presence from venturing lower in order to cross. After she had vocalized continuously for some minutes an adult finally returned to get her.

My notes on semi-independent juveniles (2-2½ months old) show that commonly heard at this age were long series, many minutes long, of characteristic and very distinctive infantile vocalizations. Observation conditions were such that I was never able to get a clear view of what was going on during these incidents. J. Terborgh (pers.com., 1978) was able in his observations on Peruvian S. fuscicollis and S. imperator to ascertain that these long vocalization bouts occurred when a group member had captured a juicy insect. Juveniles by these tactics were often successful in getting other group members to give them the item. The frequency with which I observed the vocalization bouts described leads me to believe this "food-sharing" (Hoage, 1978) is probably an exceedingly important element in care-taking. Captive juveniles have been observed to starve to death when food-sharing was inadequate; captive juveniles do not at first take more than minimal food for themselves from the feeding dish even though perfectly capable of doing so (Epple, 1970). Inadequate food-sharing could be due either to lack of response by other group members or to weakness of the juvenile and consequent inability to stimulate group members to give it food. Weaning occurs in the laboratory at 60-80 days[1] (Epple, 1970; Fess, 1975). Timing is probably similar in wild tamarins and thus the 2-2½ month period may be a particularly critical one.

"Helpers"

All groups contained one to several adults in addition to the reproductive pair. In the Ka group all three adults, including both males, carried the infants.[2] In the UB group at least three individuals carried infants. The exact number was uncertain since group members were not marked. The UB group infants were definitely the center of attention. The carriers were frequently approached by other group members.

Who are these extra adults? The data were contradictory. In many cases they were undoubtedly offspring from previous years. Five cases were known (three groups) in which offspring were still in their groups as of their third birthday (Table 15). The extent of immigration and emigration seen, however, suggests they could at times have been unrelated individuals.

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[1] The first solid food is taken at about 30-40 days (Epple, 1970).

[2] Other groups were marked too late in the study to catch a birth and also were not habituated to me.

DISCUSSION

Use of Space

A salient feature of the space-use pattern by groups in this tamarin population was the constancy of home range limits which obtained despite considerable fluctuation in group size and membership, and seasonal fluctuation of resources. This constancy was due to the infrequency of excursions outside of normal boundaries plus the fact that those which did occur did not result in permanent home range extensions. Some may have been exploratory in nature (Burt, 1943). Another object could have been the procurement of particular resources available at that time. These occasional excursions have not been included as part of the home range, which I have defined as the area normally used by a group (Burt, 1943; Brown and Orians, 1970). As Figure 15 shows (p. 52), several daily ranges are sufficient to give an excellent approximation of home range size (compare with Figure 11, p. 42).

The relative infrequency of trespass could have been the result of agonistic interactions between groups, which were observed many times. The direction of separation of groups after an interaction was not random. Each group tended to move from the overlap zone toward the more central parts of its home range. This fact, along with the infrequency of intrusion when neighbors were not present, reinforced the impression of a mutually recognized boundary area. So did the observation that when once intercepted unusually far within the La group's area, the Ka group immediately moved back to the more usual boundary area. There is no evidence that the tamarins patrolled boundary areas - that is, they did not visit grid squares near boundaries significantly more often than expected (p. 51).

Approximately 60-80% of the home ranges of the three intensively studied S. oedipus groups (UB, Ka, Ba) was exclusively used by the residents, apart from the abovementioned occasional intrusions. The pattern observed was similar to that exhibited by a Panamanian S. geoffroyi group in riverine habitat, and contrasts with a second group in nearby deciduous uplands (Dawson, 1976). The former maintained 85% exclusive use and inter-group encounters were similar to those described here. Avoidance perhaps based on vocal exchange was occasionally seen, but agonistic inter-group interactions involving chasing were frequent and were interpreted to involve boundary defense. The upland group by contrast maintained only 17% exclusive use. Home range boundaries were not stable for this group, since it expanded considerably the area it used during the dry season when food was scarcest. This group seemingly did not defend boundaries but only the area around itself. Food resource abundance was inferred to be relatively stable in the case of the riverine group. In the uplands it fluctuated widely from scarce to superabundant relative to nearby areas. When the latter obtained, intrusions by neighboring groups became more extensive, thus accounting for the relatively small proportion of exclusively used home range area for this group. This instability of resources, together with greater turnover and evidence of lowered reproductive success of the upland relative to the lowland group, led Dawson (1976) to suggest that the uplands constituted marginal habitat for Panamanian tamarins. The much larger home range needed by the upland compared to the lowland group supported this contention, since group size was nearly identical (Table 16).

The space-use pattern shown by this study's Cotton-top groups was

TABLE 16

Comparison of space use by *Saguinus oedipus* and *S. geoffroyi*

	No. grps Studied	Grp. Size	Home Range Size (Ha)	Density Ind/Ha	Daily Path Length (Km)
S. oedipus	3	4-13	8	0.7-1.8	
		3- 6	10	0.3-0.7	1.6 ± 0.15 (SD)
		3- 5	10	0.4-0.6	
S. geoffroyi					
lowland	1	6.1 ± 0.3*	26	ca 0.27	2.06 ± 0.40 (SD)
upland	1	6.3 ± 0.5*	32-43+	ca 0.36	

* Standard error Data from the present study and Dawson, 1976.

very similar to that seen in the Panamanian lowland group. Both maintained exclusive use of a large proportion of their home ranges, evidently through defense of boundaries all year around. The seemingly greater proportion of exclusively-used area in Dawson's lowland group could be an artifact attributable to differing definitions of home range (e.g. to what extent "occasional excursions outside normal boundaries" were included), and/or the longer sampling period in the present study.

Dawson (1976) linked differing degrees of deciduousness with stability of fruit and insect resources. The degree of deciduousness was least in the lowland group's home range (10%) and approximated 30% in the upland group's area. I estimated about 27% of tree species were deciduous in the present study area (Appendix 3), and that about 60% of all trees were leafless during part or all of the dry season (p. 11). No gradient in leaflessness was detectable at different distances from the arroyo which formed one boundary of the study area, even though it constituted the only water source during the dry season. Thus, my study area in terms of deciduousness most nearly resembled the home range occupied by Dawson's upland group, but nevertheless the Cotton-tops exhibited a space-use pattern more similar to his lowland group. Here it may be significant that the forest constituting my study area contained a higher proportion of species with decidedly hygrophilic ecological preferences than expected based on Holdridge criteria (p. 11; Appendix 2). The combination of annual flooding plus a long dry season has probably produced a different vegetational complex than that of the Panamanian hills, despite rather similar climates. Also deciduousness tended to affect mainly upper-strata trees in this forest (Appendix 3), while as we have seen (Table 6, p. 66) middle-stratum trees provided the bulk of the fruit portion of the Cotton-top diet. Since Dawson's upland forest was rather young it mainly lacked an upper stratum. The effect of the dry season on the food resources of his upland group may thus have been more drastic than in the more protected lower strata of my study area forest even though the number of deciduous species was less.

Reproductive success and degree of turnover were about equal in all Cotton-top groups studied (Table 5, p. 59), excepting the UB group, which occupied the remnant fence-line-arroyo forest strip. That group had an unusually high turnover compared to other groups and none of the infants born to it survived past a few months old (Table 15, p. 98). It did not expand its home range seasonally as Dawson's upland group, nor were intrusions by other groups observed.

The results of this study contrast with those of the Panamanian study (Dawson, 1976) in other important ways. The Panamanian lowland group's home range was 2½ - 3½ times the area of the three intensively-studied Cotton-top groups. The upland group's home range was 3 - 5½ times the area used by Cotton-top groups. Daily path length was also much greater for the Panamanian groups. Density on the other hand was not significantly different. The Panamanian tamarin density fell within the range of maximum and minimum densities for the three intensively-studied Cotton-top groups. A contributing factor to the larger home range size may have been a greater degree of insectivory or carnivory in Dawson's population. Primates spending a considerable portion of their time feeding on insects tend to occupy larger home ranges in relation to their population group weight (Clutton-Brock and Harvey, 1977a). My impression is that the relative importance of insects was less for the Cotton-top population. Alternate possibilities are greater competition in the Panamanian study area from other frugivores or insectivores (mammals, birds), or less overall productivity. Also since the Panamanian study area forest was much younger it probably was less diverse in composition and therefore provided fewer alternate food resources during critical seasons.

Could the _S. oedipus_ groups studied be considered "territorial"? Their space-use pattern fits the ecological definition of territoriality: Because each group maintained exclusive use of a certain fixed area, groups were spaced out in a manner departing from random towards regular (Pitelka, 1959; Davies, 1978). Groups also engaged in aggressive interactions with neighboring groups at home-range edges. Thus, whether ecological or behavioral criteria are applied, most observers would answer affirmatively the question posed above.

What ecological characteristics do Cotton-tops and other "territorial" species or populations share which might indicate selective or proximate factors operating to produce "territoriality"? This question is of particular interest, since the conclusion by other authors that few primates are territorial (Bates, 1970; Clutton-Brock and Harvey, 1977) suggests its occurrence could perhaps be linked to infrequently-occurring ecological conditions.

My literature search revealed quite a few primate species in which one or more groups or populations have been described as "territorial" (Table 17). In most cases at least some aggression between groups was observed and in all some part of the home range was exclusively used. Further generalizations are more difficult. The striking feature of the table is the variability in space-use patterns and behaviors between groups that have been subsumed under the term "territorial". Some of this owes itself to the already much-commented-on lack of consensus concerning definitions (e.g. Carpenter, 1958; Klopfer, 1969; Emlen, 1957; Kaufman, 1971; Leyhausen, 1971; Owen-Smith, 1977). Another factor in the case of Presbytis, especially in short studies where observers were not well acquainted with the study animals, could have been the confusing of confrontations between reproductive groups with confrontations between all-male and reproductive groups (N. Muckenhirn, pers. com.). Certainly with all other factors equal the percent of home range that was exclusively used showed tremendous variation within and between species, as did the extent and type of participation by the two sexes. Also it is evident that spatially-oriented aggression is not strictly correlated with any gross habitat feature or diet type, or with any particular type of social organization. In short, those variegated patterns which have been referred to as "territoriality"

TABLE 17

Character of Intergroup Relations in Some Primates Described as "Territorial"

	Character of Intergroup Relations	Ref.
Cercopithecidae		
Cercopithecus aethiops	Not stated. % HR overlap[1] for 4 groups: 11, 12, 22, 42%. HR size: .071 - 0.37 mi^2.	1
Cercopithecus mitis	Non-overlap but did not see conflicts.	2
Papio anubis	Variability in outcome of encounters between different groups.	3
Macaca mulatta	Temple troops had 80-90% HR overlap, usually avoiding contact - same pattern as seen on Cayo Santiago. Contacts usually agonistic, direction of outcome varied with identity of group and location. Some unexplained instances of nonaggressive contacts. Avoidance depended on visual cues, not vocs.	4
Presbytis cristatus	HR overlap only "a few trees". Of 90 instances of visual contact, 27 involved fighting/chasing among males. Other troop members agitated, but sometimes embraced or moved between troops. Intruders to "territory" chased out.	5
Presbytis johnii	Spacing-out due to extensive use of core areas. Loud morning vocs and male voc/display on contact. Female participated only once in 84 encounters, w/facial threats. Rest males - all males in multiple male troop with involvement decreasing according to rank. Behavior during confrontations: 80% voc, gestures; chases 18%; contact 2%. Peaceful withdrawal by one group in 4/84 cases; feeding in proximity, 10/84; rest	6

	Character of Intergroup Relations	Ref.
	ended in encounters. Males maintained constant vigil, would move long distances (often more than 500 yds.) to challenge other male. HR size: 1/4 - 1 mi^2.	
Presbytis entellus (Dharwar)	Overlap small. Confrontations involved cf. leader males - stares, threat gestures, display jumping. Other adult group members "assume indifferent attitude."	7
Colobus guereza	HR and "territory" "virtually coincide". Roaring by (dominant) male at distance; penile erection and jumping display at close range. No contact ever seen. Females not participating. Territory size: .036 - .084 mi^2.	8
Hylobatidae		
Hylobates lar	% HR exclusive stated to be 80-90% (p. 23); looks to be 50-80% from map (p. 30) (2 groups studied). Overlap 24-75 yds. wide. Both sexes participate in morning calling (F "great call", M series loud hooots), both display (swing around). Encounters marked by M "conflict hooos", much swinging, staring, and chasing. Saw contact and fighting only once in 126 conflicts. Females may vocalize, offer support to M (grooming), occasionally join M in chasing; generally stay away. Avg. HR size (his & Carpenter's (1940) data), 40 Ha.	9
Hylobates klossi	Overlap zone 25-50 m wide. Aggression cf. between members of same sex: intra-M singing at 150-500 m apart, intra-F singing 10-50 m apart, i.e. at the very boundary, plus vigorous brachiation and other locomotory displays. Meetings of males quiet and hard to detect. Avg. territory size, 6.7 Ha.	10

	Character of Intergroup Relations	Ref.
Symphylagus syndactylus	Home range overlap about 30%. Had difficulty defining limit of "defended" area (i.e. of "territory"), suggest there may be a gradient of probability of outcome of encounters at different locations. Exclusion cf. by long-range signals: Contacts relatively infrequent - Markedly less "territorial calling" and boundary display than in *H. lar*. (Also more folivorous, less frugivorous, and with markedly smaller HR area relative to biomass.)	11
Cebidae		
Callicebus moloch	Overlap probably less than 20%; groups engaged in elaborate and extended displays when meeting - calling, rushing and chasing prominent. Brief contact occasionally. Both sexes participate.	12
Callitrichidae		
Saguinus geoffroyi	HR overlap 15-85%. Only group with relatively dependable food supply "detended" its area. Confrontations similar to present study: peaceful withdrawal occas. seen but aggressive interaction frequent. Relative role of sexes not known. HR size, 26-43 Ha.	13
Indriidae		
Indri indri	..."is territorial in that groups use a large central portion of their ranging area exclusively". Only 6 meetings between groups in over 2000 hrs. observation (cf. on 3 groups). In each case one group had intruded just inside area of neighbor, and a "singing" battle ensued. No malefighting seen. Marking frequent - but also seen other parts HR. Inhabit hilly area, each group on own hill.	14, 15

	Character of Intergroup Relations	Ref.
Propithecus verreauxi	Two groups in rich semi-deciduous forest had approx. 50% overlap with neighbors & avoidance predominated over aggressive encounters; two groups in arid forest had only about 10-15% overlap & inter-group battles frequent. Termed the latter "territorial". HR 6.7-8.5 Ha.	17
Lemuridae		
Lemur macaco	Long exchanges of vocalizations, visual display (leaping, rubbing) by both sexes. Chases and attacks.	15
Lemur catta	Territory primarily defended by females: running at each other with vocalizations. Physical contact rare. Males and juveniles remained in background as observers.	16

References:

1-Struhsaker, 1967
2-DeVos and Omar, 1971
3-Hamilton et al., 1975
4-Southwick et al., 1965
5-Bernstein, 1968
6-Poirier, 1968a, b
7-Sugiyama et al., 1965
8-Marler, 1969
9-Ellefson, 1974
10-Tenaza, 1975
11-Chivers et al., 1975; Chivers, 1974
12-Mason, 1968
13-Dawson, 1976
14-Pollock, 1975
15-Petter, 1965
16-Budnitz and Dainis, 1975
17-Richard, 1974

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[1] HR = home range

reflect a variety of selective pressures, undoubtedly combined with flexibility in response to proximate stimuli. In order to go further in delineating ecological or evolutionary correlates study must be oriented toward those proximate stimuli. Intra-species flexibility is a question that particularly needs addressing. Studies on groups other than primates tend to discuss territoriality as though it were a species characteristic (e.g. Owen-Smith, 1977; Jarman, 1974). Various primate studies, including that on Saguinus geoffroyi discussed in detail above, have shown that different populations or groups of the same species can vary radically in their space-use patterns (Dawson, 1977; Hamilton et al., 1976; Gartlan and Brain, 1968; Yoshiba, 1968). This suggests caution in developing evolutionary arguments concerning the occurrence of territoriality in a species in the absence of replicated studies under varying ecological conditions.

The critical determinant of Cotton-top space-use pattern is probably the availability and dispersion of food resources. Scarcity of water holes and sleeping sites have been linked to variation in grouping patterns in desert and savannah-dwelling primates (e.g. Kummer, 1968). Tenaza (1975) considered sleeping sites a critical determinant of home-range boundaries in Kloss' gibbons. However in this Cotton-top population movements were not oriented toward access to water, and sleeping sites appeared to be plentiful. Shade trees enabling monkeys to escape the potentially lethal effects of the midday tropical sun could constitute a critical resource. In this area however suitable trees for noon resting were plentiful and widely distributed. Mineral sites could constitute critical resources much as do watering holes in the desert. Izawa (1975) observed several species of

Amazonian Colombian primates utilizing mineral licks; but no such sites were noted for this population. The remaining possible critical resources are food and mates. The aggression seen between *oedipus* groups could serve the purpose of mate protection, as suggested by Epple (1977) based on laboratory observations. However mate protection alone would not account for the space-use pattern seen, since it would require only the driving off of any potential competitors from the vicinity of the group, not the exclusive use of a large portion of the home range. Nevertheless any behavior favored because it assured exclusive use of food resources would also give the benefit of mate protection with no additional energy expenditure.

The distribution of fruit resources used by *S. oedipus* conformed to the condition described by Brown (1974) and Altmann (1974) as conducive to territoriality. Fruits were obtained largely from small-crowned understory trees which were in general visited for only short periods of time, usually five to 20 minutes. The trees visited on a given day were scattered and the monkeys moved between them often in a direct and seemingly purposeful manner. Their direct movement from long distances toward fruiting trees visible only at close range gave the distinct impression that they knew the locations of the fruiting trees in their home range and arranged their movement pattern so as to visit them. Because they tended to visit in succession different trees of the same species, the tamarins utilized at a given time relatively few fruits compared to what was available.

Brown (1974) and Altmann (1974) couched in energetic terms their explanation of the suggested correlation between territoriality and the distribution of food resources in small dispersed packets. The essence of the idea is that it must be more energetically economical in such a situation to keep intruders out entirely by defending a boundary than to defend individual resource packets. As the primate space-use data amply shows (Table 17), even in the so-called territorial species, groups are not separated by discrete sharp boundaries but rather show varying degrees of home range overlap (Table 18). Their idea could be expanded to explain the variability in percent of exclusively used home range in different groups and home ranges, if one assumes that the probability of defensive aggression by residents always varies inversely with distance from a currently productive resource. Where the food distribution pattern is characterized by scattered resources, each providing a small proportion of the necessary daily intake, the distance to a resource currently in use would always be relatively short. One might postulate a "circle of worthwhile defense" around each resource packet. The area of exclusive use is that where those circles of worthwhile defense converge on one another, that is, an area where there are no lacunae which residents would not defend if they encountered intruders there. A necessary correlate is that neighbors do not bother to intrude because they "know" that the residents' predisposition to defend would be too great to make it worthwhile.

The risk involved in inter-group encounters could be considerable. Carpenter (1940) observed a much greater incidence of scarring, torn ears, etc., among gibbon males compared to females. Even though the percent incidence of actual fights was rather low, the gibbons devoted a sufficiently high proportion of their time to inter-group confrontations that a male could expect to engage in many potentially damaging fights during his lifetime (Ellefson, 1974).

Variability in percent overlap between home ranges of any two groups must reflect varying balance between (1) What is risked in an encounter with neighbors and (2) What is to be gained by seeking resources in an area also frequented by others utilizing the same diet, relative to that gained by investing the same energy in search within an area which others of the same species do not frequent. The balance would be affected by overall availability of food, diet flexibility, the size of the resource packet to be gained by intrusion, and the average distance to the next currently available packet. The smaller the individual packet the less to be gained and therefore the less likely intrusion, given vigor and effectiveness of defense by residents. Given equal size, the farther apart the packets, the more likely intrusion since detection is less likely. Mitani and Rodman (1979) suggested that defendability of territory by primates depends on the relationship between perimeters and the daily range. The extreme situation, where home range is small enough to allow continuous surveillance of perimeters and therefore where intrusion does not occur at all, has not been documented yet in primates.

Social Organization

The immigration/emigration patterns and upper size limit of groups observed in this study were unexpected given that previous field and laboratory workers had predicted the basic callitrichid social unit in the wild would probably turn out to be the nuclear family group: one monogamous reproducing pair plus associated subadult offspring (J.K. Hampton, et al., 1966; Epple, 1972, 1975; Eisenberg, et al., 1972; Moynihan, 1966; Kleiman, 1977c). *Hylobates* is consistently cited as illustrating the nuclear family group type of social organization. Offspring are peripheralized as they approach maturity, thus maintaining group size below six, with a mean usually between three and four (Table 18). Monogamous primates other than callitrichids seem to fit the hylobatid pattern in terms of group size mean and range. Early reports of small group size in wild callitrichids (Table 19) plus reports of monogamous tendencies in captive groups suggested at first a similar pattern for callitrichids. This study provides more evidence of greater differences than at first were suspected.

Group size has turned out to be much more variable than early workers would admit (Tables 17, 18 and 19). They suggested that reports of large groups (over that expected for a monogamous primate) were erroneous or reflected temporary aggregations around food resources (Moynihan, 1970; Coimbra-Filho and Mittermeier, 1973). I have argued that due to observation conditions large groups may be even more common than the extant data suggest (Neyman, 1977). Four groups of ten or more individuals were observed in this study area (Figure 10). The largest of these (UB), with 13 members, was followed regularly for several months and shown to be stable and cohesive during this period. It was, in short, not a temporary feeding aggregate or merging of two groups. Repeated observations and some following of the other large groups suggested they were of a similar nature.

Groups larger than the six maximum of other monogamous primates could in some cases probably be attributed to the larger litter size (1-3), shorter gestation period (5 months) and faster maturation schedule (1½ - 2 years in laboratory) of callitrichids. One pair could potentially produce 12 offspring in two years and thus theoretically a

TABLE 18

Primates Reported to be Monogamous (Field Studies)

	Group Size				
	Mean	Range	N	Inter-group Relations	Ref.
Indriidae					
Indri indri					1
Cercopithecidae					
Presbytis potenziani		2-6	21	Both sexes participate in long distance visual, vocal displays. Encounters: males approach, vocs, then retreat - no chasing or fighting seen.	2
Nasalis concolor	3.5	2-5	15	Males approached each other rapidly to about 25 m, each gave "single loud vocalization", turned & ran back into respective home ranges, followed by group.	3
Hylobatidae					
Hylobates lar	4.4	2-6	21	Table 17.	4
	3	2-6			5,7
Hylobates concolor		2-6	6		6
Hylobates klossi	3.6	3-5	11	Table 17.	8
Symphylagus syndactylus		2-6	8	Table 17.	6
	4	4,4	2		7
	3-	3-5	1		9
		1-3	1		
Cebidae					
Callicebus moloch	3.3	2-4	8	Both sexes participate. Inter-group calls from nest tree, later "actively	10

	Group Size				
	Mean	Range	N	Inter-group Relations	Ref.
				converge" toward each other & usually meet in same areas at boundaries of their territories day after day.	
Callicebus torquatus	3	2-4	8		11
Pithecia monachus	3	1-6	5		12
Callitrichidae					
Saguinus midas	3.4	2-6	8		13
Saguinus fuscicollis, and *nigricollis*	Table 19			Form coalesced groups in Colombian Amazon.	14
Saguinus geoffroyi, and *oedipus*	Table 19			Inter-group contacts vary in character, from avoidance to chasing/fighting, with the latter frequent. Both sexes probably participate.	15

References:

1-Pollock, 1975
2-Tilson and Tenaza, 1976
3-Tilson, 1977
4-Carpenter, 1940 (Thailand)
5-Ellefson, 1967 (Malayan peninsula)
6-Carpenter, 1940 (Sumatra)
7-Ellefson, 1974 (Malayan peninsula)
8-Tenaza, 1975 (Siberut Island)
9-Chivers et al., 1975
10-Mason, 1966
11-Kinzey
12-Izawa, 1976
13-Thorington, 1968
14-Izawa, 1978
15-This report; Neyman, 1977; Dawson, 1976, 1977

TABLE 19

Reported Group Size in Free-ranging Callitrichids

Species	Duration of study[5]	Group Size[1] Range	Group Size[1] Approx. Median	N	Splitting coalescing observed	Location	Reference
S. midas	1 wk (i)	1-7		8	yes[2]	Brazil	Thorington, 1968
S. midas		5-20				Surinam	Geijesko, in Husson, 1957
S. midas	9 wks (W)	2-17		11	C,S[3]	Surinam, French Guiana	Durham and Durham in press
S. mystax	months	2-6[6]		12		Peruvian Amazon	Castro and Soini, 1977
S. fuscicollis	months	2-10[7]		25	yes	Peruvian Amazon	Castro and Soini, 1977
S. fuscicollis	months	2-10	4	4	no	Manu River, Peru	Terborgh, et al., in prep.
S. fuscicollis	months (W)	20-40+		46		Colombian Amazon	Izawa, 1976
S. fuscicollis	months (D)	to 12				Colombian Amazon	Izawa, 1976
S. nigricollis	months (i)	5-8 to 30 (coalesced groups)		10	yes	Colombian Amazon	Izawa, 1978
S. geoffroyi	intermit.	1-9	3	28	C	Panama	Moynihan, 1970
S. geoffroyi	1 year (m)	1-19	7	71[9]	C[4]	Panama	Dawson, 1976, 1977
S. oedipus	years (m)	1-13	6	25[9]	no	Colombia	Neyman, this study

Species	Duration of study[5]	Group Size[1] Range	Group Size[1] Approx. Median	N	Splitting coalescing observed	Location	Reference
Cebuella pygmaea		1-10		9		Colombian Amazon	Izawa, 1976
						Peruvian Amazon	Ramirez, et al., 1977
C. pygmaea	weeks	4-8		2	no	Manu River, Peru	Janson, pers com; Gazzo, pers com.
Leontopithecus r. rosalia		2-8[8]			poss.[8]	Brazil	Coimbra-Filho and Mittermeier, 1973

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[1] Includes carried infants. N means number of units observed (in some data the same group may have been counted more than once).

[2] Coalescing for travel and defense.

[3] Coalescing during travel.

[4] Two largest groups (14 and 19) around concentrated food sources.

[5] W = "wet" season; D = "dry" season; m = marked animals; i = animals individually distinguishable by natural markings.

[6] Often traveling in company with *S. fuscicollis*.

[7] A "supertroop" of 15-26 reported around concentrated food source.

[8] Reports of "up to 15" in the literature thought by authors to be attributable to temporary congregations around favorable food sources.

[9] Including as one unit the various sightings of same troop/group, (n = 24), the next single sightings.

group as large as 14 could consist of only one adult pair plus subadult offspring. (An observer could not necessarily distinguish such a group from one containing many adults due to the fact that individuals past nine or ten months of age can only be distinguished from adults based on size, and then only if seen adjacent to an adult.) This however makes the unlikely assumption of 100% survivorship to the age of 2 years. Survival of all three triplet members is unlikely in the wild, since they rarely survive in captivity without supplemental feeding (Hampton, Gross and Hampton, 1978; Deinhardt, et al., 1976; Gengozian, et al., 1978; Hearn, 1977). Since the maximum effective litter size is therefore two, the maximum number of young a pair could produce in two years is eight, giving a group size of ten if all survive. Thus groups as large as ten could theoretically be family groups in the same sense the term is applied to other monogamous primates. That would include all groups observed in this study except that numbering thirteen. However in this study area in most groups in most years only one litter of young was produced, so the maximum number added to a group in two years was not eight but probably between four and six, and not all survived. The same was true in Dawson's (1976) population of Saguinus geoffroyi. The unavoidable conclusion is that the occurrence of extra adults in groups was rather common in these two populations. If other callitrichid populations are similar in this respect, then the frequent occurrence of relatively large groups reported by field workers suggests (assuming the reproductive patterns to be similar) that the family may exhibit a basic social organization quite distinctive from other monogamous primates. This is suggested also by Izawa's (1976, 1978) observations of merging nuclear family groups in S. nigricollis and the occurrence of groups of 40 or more S. fuscicollis in the Colombian Amazon.

Extra adults were actually shown to be present in every one of the six groups that were captured for this study (Figure 16, p. 60). All contained either one or two extra adult males and three had more than one adult female (Bo, Ba, La). In the Bo group the eldest of the two females by tooth age was shown to be the reproductive. Tooth wear indicated a gradation in age in a group's adults of the same sex. This suggests the extras could not be littermate brothers or sisters of the like-sexed member of the reproductive pair. Unfortunately the evidence at hand did not permit me to distinguish whether these extra adults were non-littermate siblings of the reproductive pair, unrelated immigrants, or grown-up offspring which had simply not dispersed.

Four individuals were born into groups and became adults during the study; and all were still with their natal groups at three years of age (Table 15). Thus this study corroborates laboratory observations suggesting that offspring may be retained in callitrichid groups well into adulthood (e.g. Epple, 1975, 1978; Rothe, 1975). Behavioral mechanisms for peripheralizing them are evidently not developed to the same extent as in other monogamous primates. An important factor could be the role played by juveniles as "helpers" in caring for infants. Captive juveniles commonly contribute substantially in carrying, food-sharing with, and protecting their younger siblings. Since both members of a pair participate in carrying[1], the inclusion of older offspring in a group could be advantageous to both sexes, providing they were not a

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[1] Shown in laboratory studies and in various groups observed during the present study.

source of mate competition and offered no or low disadvantage in terms of resource competition. The presence of alternate carriers would allow both pair members to participate in inter-group encounters without endangering infants. A larger group could also be advantageous in territory defense or predator detection and defense. If opportunities for establishing a territory were rare enough the best strategy for a young adult in terms of overall fitness could be to help raise siblings. In extreme cases, some individuals might never produce their own offsprings, as occurs, for example, in wild dogs (Frame and Frame, 1976). There is substantial evidence also from laboratory observations showing that successful parental care in callitrichids requires learning and exposure to infants. Captive observations suggest the necessary experience may be normally acquired by the juvenile as it is exposed to and practices the handling of younger siblings (e.g. Epple, 1975b).

Unrelated adults may also be common in callitrichid groups. This is shown by the frequent incidence of immigration into and emigration out of groups in the present study area, as well as in the *S. geoffroyi* population studied by Dawson (1976, 1977). Dawson termed this the "shifting subordinate" group component. He concluded that immigrators and emigrators were more likely to be immatures than expected based on overall population age-class ratios. My data do not permit a similar statistical test, since there is no way to generate expected age-class ratios. They do not, however, suggest that transients were primarily individuals around maturation age. Eleven of twenty dispersers whose teeth I examined fell into the A3 and A4 tooth-age classes and were thus likely to have been over five years of age (see p. 35). Both studies, in any case, agree that unrelated adults may often be present in wild groups.

The ability of transients to join established groups already containing a reproducing pair was unexpected since captive groups show marked intolerance to introduced strangers. The stranger is attacked, often by all group members, but particularly by the pair member who is the same sex as the intruder. Adult females are especially hard to keep together and are prone to attack intruding females. Aggression toward strangers may be exaggerated in captivity by restricted space, constant contact, and food competition (Rowell, 1972). Interactions under natural conditions may be affected by factors not present in captivity, such as previous relations to intruding individuals or season (Epple, 1975). (The old male which joined the Ka group, for example, could easily have been related to the alpha male.)

Some large groups could have resulted from unusually high rates of immigration during some previous period. Home range quality might affect average group size by influencing either reproductive success or the tendency of immigrants to remain, or both. Dispersal factors could have been responsible for the unusually large size of the four largest groups observed, an hypothesis strengthened by the fact that three of them occurred in parts of the narrow forest strips adjacent to the main forest block of the study area (Figure 4), and the fourth in an intermediate area. The spatial configuration of these forest strips, which allowed exit only from a very small proportion of the home range perimeter, could have affected dispersal. Differences in vegetation could have affected habitat quality (see p. 63). The relative proportion of "edge", thought by some to be optimal foraging vegetation for callitrichids (Moynihan, 1970; Dawson, 1976) could be much higher in forest of a strip configuration than in a forest block. The effect was probably minimal in this study area, however, since a considerable amount of "edge" had been created within the forest block in the process of selective tree cutting. The locations of clearings and roads were still quite evident although hidden somewhat by several years' growth of vegetation. Also there was no evidence from group movements in the main forest block that the edge of the block was preferred (Figure 15).

It is lastly possible that transients originated in areas of human disturbances or destruction of forest outside the study area. The forest block which included the study area did not suffer such disturbance, but it was connected via tree-lined fences and arroyos to other areas where forest destruction had occurred in the recent past. This, however, does not account for the known movements between study area groups or for similar movements in Dawson's (1976, 1977) Panamanian *S. geoffroyi* population.

Transients are probably equivalent to dispersers in rodent populations or floaters in bird populations. Since data is lacking on the movements of transients, we cannot as yet say whether they wander freely or frequent a limited area "waiting" for a free territory, as Smith (1978) found in a population of *Zonotrichia capensis*.

The antagonism of the female of a reproductive pair toward introduced females in captive groups suggests that in the wild they should be active in intra-group encounters. They might well engage other females preferentially as do Kloss gibbon females (Tenaza, 1975). Further work may thus not verify the greater participation by males in inter-group encounters suggested by my preliminary data. Tenaza (1975) hypothesized that intra-sexual antagonism is inseparable from and necessary to the monogamous mating system, an hypothesis strikingly similar to Epple's contention, based on laboratory observations, that intra-sexual aggression is a mechanism assuring maintenance of the pair bond in callitrichids.

The inclusion of parous females among transients is puzzling. Two definite cases were observed of females leaving a territory in which they had produced young, and a third was suspected. A fourth parous female was included in the group of individuals present in the study area for only a short period. Everything we know about reproduction in callitrichids suggests that, in order to have reproduced, a female must at one time have been the dominant female in some group.[1] Where possession of a territory is crucial to breeding success (as was the case here since no transients were carrying young), and all territories are occupied, the best strategy for a female in terms of maximizing reproduction would seem to be to stay in her territory and continue reproducing. She could also look for a more productive territory, as Smith (1978) suggested for *Zonotrichia capensis*, a monogamous Costa Rican sparrow. Females rather than males adopted this strategy, she suggested, because females were dominant to males and could thus choose any territory and be certain of acceptance. Males may have been more site-attached in the present *S. oedipus* population. In two (Ka, Ca) of the three cited

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[1] In several callitrichid species captive studies have shown that only one female will reproduce in a group even if two or more potentially reproductively mature females are present (see reviews by Epple, 1975, 1978). Hearn's (1977) investigations with *Callithrix jacchus* linked this pattern to cessation in the non-reproducers of hormonal fluctuations indicative of normal ovarian function.

cases of emigrations by parous and presumably alpha females, the male component of the group remained the same. The third group (Ba) underwent drastic change between August 1976 and August 1977. Only the subadult male born in 1976 (and possibly his twin) were still present in 1977, along with four unmarked individuals presumed to be immigrants. The M:F sex ratio of transients (1:1.4) is not significantly different from 1:1. Sample size is however so small that a very great difference would be necessary to achieve significance. More field data are necessary to determine whether the trend is real and whether it is due to difference in site attachment between the two sexes, or other factors such as differential survivorship. It may be significant however that the M:F sex ratio for the population as a whole is skewed in the opposite direction.

Reproduction

The reproductive pattern of Saguinus oedipus, like that of other callitrichids, features a relatively high degree of paternal investment plus great flexibility in the parameters determining reproductive output and timing.

Direct paternal investment is indisputably much higher in callitrichids than in the vast majority of mammals, including most primates (see also Kleiman, 1977c). The participation by captive S. oedipus males in carrying young, defending them, and sharing food with them is substantial - even in many cases exceeding the female's contribution. In several wild groups males were observed to carry infants frequently and to retrieve them when threatened or unable to navigate the route taken by the rest of the group. A male's taking over a substantial part of carrying should enable the female to devote a relatively greater portion of her energy than otherwise possible to lactation and to the gestation of the next set of young. It could also affect the balance of selective pressures bearing on the female's participation in intergroup encounters. In some other monogamous primates, females participate little if at all in such encounters (Table 18) while the males devote a great deal of energy to display, chasing, etc., and risk damage more often. Group encounter participation could be considered a form of parental investment if the resulting exclusive access to resources provided key energy for gestation, lactation, transportation of young, and/or for the survival of newly weaned juveniles.

Does this unusual callitrichid parental care pattern increase offspring survivorship? The question cannot be answered with the data available. It may be significant however that the present *S. oedipus* population suffered a very low 25% loss rate of young born into groups during the study (six month and one year). Much higher "50% or more" pre-6-month mortality occurred in Dawson's (1976) Panamanian *S. geoffroyi* population. There most groups succeeded in raising only a single offspring, which was not the case in the present study. In both studies one group was unsuccessful at raising any young. (UB group in this study, upland group in Dawson, 1976.) The mortality rate in Dawson's study is comparable in absolute terms to the 45% (males) - 60% (females) one year mortality recorded for a *Macaca sinica* population (Dittus, 1975). In terms of the cohort fraction lost per given lifespan portion, however, the tamarins had - despite their smaller body and group size - a considerably lower death rate since one year represents a much larger fraction of the total tamarin lifespan.

The fact that only one set of young per year was produced by most females most years in this study area, despite the much higher physiological potential of the species as demonstrated in the laboratory, may indicate that resources were frequently limiting in this population. The inter-birth interval was much longer than the minimal five months. Only one case was noted in which a wild female produced two litters in a single year (Bo). The average inter-birth interval was on the order of 12 months (3 females, 5 intervals). Another difference from the laboratory reproductive pattern was that the minimum age of onset of reproduction was higher. All reproductive females examined were over 5 years old, judging from tooth wear (see p. 104). Females born into study area groups evidently matured physiologically at about the same age as in the laboratory. Wo and Vo (twins) when captured at about 100 weeks old had fully developed circumgenital glands, as did Kl when captured at about 130 weeks old. A reasonable conclusion is that social factors are probably responsible for delaying the onset of reproduction in wild females for several years past the age of physiological maturity.

The lower reproductive potential in the wild population studied compared to that possible in laboratory settings reflects a callitrichid flexibility in timing of births which Dawson (1975, 1976) has already pointed out, based on other evidence. He observed two birth peaks six months apart, the second much lower than the first. The frequency of embryos encountered in shot females during the months preceding the second peak, however, seemed to be much higher than expected based on the number of carried young later observed. Suggested causes for the discrepancy were early abortion, resorption of embryos, or early postnatal mortality.

Any hypothesis concerning the evolution of the callitrichid reproductive strategy must take into account not only their high potential reproductive output but also their capacity vary output. A high potential output might be expected based on their small size if one assumes predation pressure is apt to be heavier on smaller than on larger primates. This would explain the high potential output but does not account for the lowering of output in certain populations. Evidently then it is not high output alone that has been selected for. Rather it may be the ability to adjust the timing of births so as to conserve energy when the offspring are not likely to survive, as well as to raise output under favorable conditions (e.g. unusually productive years or the opening up or discovery of newly occurring habitat patches (Dawson, 1976)). An ability to conceive young at any time of the year, accompanied by selective resorption of embryos, would serve both ends.

Since variability in the timing of births seems to be a key facet of the callitrichid reproductive pattern it is pertinent to discuss further the mechanisms which may be involved.

The occurrence of births in 1974 in the semicaptive groups was strikingly similar to the wild groups living many miles away under a totally different resource situation but exposed to a similar climate regime (Figure 20, p. 100). This could be accounted for if some climatic factor acted as a proximate stimulus to cause onset of reproductive readiness. Variable survivorship in a habitat which is highly seasonal in nature could constitute the selective factor leading to such a pattern.[1] However the wide birth peak evident in the wild S. oedipus population, also evident in Dawson's (1976) Panamanian S. geoffroyi population as well as in laboratory populations, shows that the timing of births can't be strictly governed by climatic factors despite the seasonal nature of the habitat.

A second possibility is an internal rhythm paced by level of resources. The fact that one semicaptive group produced young in 1973 and 1975 when the wild groups did not corroborates the notion that adequate resources could act as a facilitator in the production of young. This group had access to fruit from trees in the owner's several acre lot as well as to supplements from the kitchen which were likely of good quality. The definite birth peak seen in captive Saguinus colonies (Hampton, et al., 1966; Gengozian, et al., 1977) also suggests either a seasonal effect or some internal rhythm which tends to disappear in successive captive generations (Gengozian, et al., 1977).

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[1] Applies not only to habitats occupied by the northernmost representatives of the family, but also probably to many populations inhabiting the Amazonian basin (Pers. obs; Terborgh and Jonson, in prep.).

Bibliography[1]

Aldrich-Blake, F.P.G. 1970. Problems of social structure in forest monkeys. In: Social Behavior in Birds and Mammals, ed. J.H. Crook: 79-101, Academic Press, N.Y.

Altmann, M. 1952. Social behavior of elk, Cervus canadensis nelsoni, in the Jackson Hole Area of Wyoming. Behavior, 4:116-143.

__________. 1956. Patterns of herd behavior in free-ranging elk of Wyoming, Cervus canadensis nelsoni. Zoologica, N.Y., 41:65-71.

Altmann, S.A. 1974. Baboons, space, time and energy. Amer. Zool., 14:221-248.

Baldwin, J.D. and J.I. Baldwin. 1972. The ecology and behavior of squirrel monkeys (Saimiri oerstedi) in a natural forest in western Panama. Folia Primatol., 18:161-184.

Baldwin, L.A., T.L. Patterson and G. Teleki. 1977. Field research on Callitrichid and Cebid monkeys: an historical, geographic, and bibliographic listing. Primates, 18:485-507.

Bates, B.C. 1970. Territorial behavior in primates: a review of recent field studies. Primates, 11:271-284.

Bernstein, I.S. 1967. Intertaxa interaction in a Malayian primate community. Folia Primatol., 7:198-207.

deBoer, L.E.M. 1974. Cytotaxonomy of the platyrrhini (Primates). Genen. Phaenen. 17:1-115.

Box, H.O. 1975. Quantitative studies of behaviour within captive groups of marmoset monkeys (Callithrix jacchus). Primates, 16:155-174.

Bradbury, J.W. and S.L. Vehrencamp. 1976. Social organization and foraging in emballonurid bats. I. Field Studies. Behav. Ecol. Sociobiol., 1:337-381.

Brown, J.L. 1963. Aggressiveness, dominance and social organization in the Steller jay. Condor, 65:466-484.

__________. 1964. The evolution of diversity in avian territorial systems. Wilson Bull., 76:160-169.

Burt, W.H. 1943. Territorality and home range concepts as applied to mammals. J. Mammal., 24:346-352.

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

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[1] See also: Additions to Bibliography (p. 151).

_______________. 1935. Behavior of red spider monkeys in Panama. *J. Mammal.*, 16:171-180.

_______________. 1940. A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comp. Psychol. Monogr.* 16:1-212.

_______________. 1964. *Naturalistic Behavior of Nonhuman Primates.* Pa. State Univ. Press, University Park, Pa. 464 p.

Castro, R. and P. Soini. 1977. Field studies on *Saguinus mystax* and other Callitrichids in Amazonian Peru. In: *The Biology and Conservation of the Callitrichidae*, ed. D. Kleiman: 73-78. Smithsonian Institution Press, Washington, D.C.

Chase, J.E. 1967. Seasonal cycle in teste size as related to conception in several primate species. Exptl. Breeding of Subhuman Primates, Zool. Soc. San Diego, 5th Annual Report 1966-67.

__________ and R.W. Cooper. 1969. *Saguinus nigricollis* - physical growth and dental eruption in a small population of captive-born individuals. *Am. J. Phys. Anthro.*, 30:111-116.

Chivers, D.J. 1973. An introduction to the socio-ecology of Malayan forest primates. In: *Comparative Ecology and Behaviour of Primates*, ed. R.P. Michael and J.H. Crook: 101-146, Academic Press, London.

____________, J.J. Raemaakers and F.P.G. Aldrich-Blake. 1975. Long-term observation of Siaming behaviour. *Folia Primatol.*, 23:1-49.

Clutton-Brock, T.H. 1974. Primate social organization and ecology. *Nature*, (Lond). 250:539-542.

__________________. 1975. Feeding behaviour of red colobus and black and white colobus in East Africa, *Folia Primatol.*, 23:165-207.

__________________. 1977. Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: T.H. Clutton-Brock (ed.) *Primate Ecology*: studies of feeding and ranging behaviour in lemurs, monkeys and apes: 538-556, Academic Press.

__________________ and P.H. Harvey. 1977a. Primate ecology and social organization. *J. Zool.*, Lond., 183:1-39.

__________________ and ___________. 1977b. Species differences in feeding and ranging behaviour in primates. In: *Primate Ecology*: studies of feeding and ranging behaviour in lemurs, monkeys and apes, (ed. T.H. Clutton-Brock), Academic Press, London.

Coimbra-Filho, A.F. 1977. Natural shelters of *Leontopithecus rosalia* (Linnaeus, 1766) and some ecological implications (Callitrichidae, Primates). In: *The Biology and Conservation of the Callitrichidae* ed. D. Kleiman: 79-89. Smithsonian Institution Press, Washington, D.C.

__________________ and R.A. Mittermeier. 1973. Distribution and ecology of the genus Leontopithecus Lesson, 1840 in Brazil. Primates, 14:47-66.

__________________ and ________________. 1977. Tree-gouging, exudate-eating and the "short-tusked" condition in Callithrix and Cebuella. In: The Biology and Conservation of the Callithrichidae, ed. D.G. Kleiman: 105-115. Smithsonian Institution Press, Washington, D.C.

Cronin, S.E. and V.M. Sarich. 1975. Molecular systematics of the New World monkeys. J. Human Evol., 4:357-375.

Crook, J.H. 1970. The socio-ecology of primates. In: Social Behaviour in Birds and Mammals, ed. J.H. Crook. Academic Press, N.Y.

__________. 1972. Sexual selection, dimorphism, and social organization in the primates. In: B.G. Campbell (ed.), Sexual Selection and the Descent of Man, 1871-1971:231-281.

__________ and J.S. Gartlan. 1966. Evolution of primate societies. Nature, 210:1200-1203.

Darling, F.F. 1937. A Herd of Red Deer, Oxford, London.

Dawson, G.A. 1976. Behavioral ecology of the Panamanian tamarin, Saguinus oedipus (Callitrichidae, Primates). Ph.D. Diss., Michigan State Univ.

___________. 1977. Composition and stability of social groups of the tamarin, Saguinus oedipus geoffroyi, in Panama: ecological and behavioral implications. In: The Biology and Conservation of the Callitrichidae, ed. D.G. Kleiman: 23-27. Smithsonian Institution Press, Washington, D.C.

DeVos, A. 1960. Behavior of Barren Ground caribou in their calving grounds. J. Wildl. Mgmt., 24:250-258.

Dice, L.R. 1952. Natural Communities. Univ. of Mich. Press, Ann Arbor, Mich., 547 p.

Durham, N.M. 1971. Effects of altitude differences on group organization of wild black spider monkeys (Ateles paniscus). Int. Congr. Primatol., 3:32-40.

___________ and L.H. Durham. In Press. Observations on the social groupings of the red-handed tamarin, Saguinus midas, of the Guianas.

Eisenberg, J.F. 1977. Comparative ecology and reproduction of New World monkeys. In: The Biology and Conservation of the Callitrichidae, ed. D.G. Kleinman: 13-22. Smithsonian Institution Press, Washington, D.C.

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

_______________ and Thorington, R.W., Jr. 1973. A preliminary analysis of a neotropical mammal fauna. Biotropica, 5:150-161.

Ellefson, J.O. 1967. A natural history of gibbons in the Malay Pensinula. Ph.D. Dissertation, U. California, Berkeley.

_____________. 1968. Territorial behavior in the common white-handed gibbon. In: Primates, ed. P. Jay: 180-199. Holt, Rinehart & Winston, N.Y.

Emlen, J.T. 1957. Defended area? A critique of the territory concept and of conventional thinking. Ibis: 99:352.

Enders, R.K. 1930. Notes on some mammals from Barro Colorado Island, Canal Zone. J. Mammal., 11:280-292.

Epple, G. 1967. Vergleichende Untersuchungen über Sexual und Sozialverhalten der Krallenaffen (Hapalidae). Folia Primat., 7:37-65.

________. 1968. Comparative studies on vocalization in marmoset monkeys (Hapalidae). Folia Primat., 8:1-40.

________. 1970. Maintenance, breeding, and development of marmoset monkeys (Callitrichidae) in captivity. Folia Primat., 12:56-76.

________. 1971. Discrimination of the odor of males and females by the marmoset Saguinus fuscicollis ssp. Proc. 3rd Int. Congr. Primat. (Zurich), 3:166-171.

________. 1972a. Social communication by olfactory signals in marmosets. Internat. Zoo Yearb., 12:36-42.

________. 1972b. Social behavior of laboratory groups of Saguinus fuscicollis. In: Saving the Lion Marmoset, edited by D.D. Bridgwater, pp. 50-58. Wheeling, West Virginia: Wild Animal Propagation Trust.

________. 1975. The behavior of marmoset monkeys (Callithricidae). In: Primate Behavior, edited by L.A. Rosenblum, pp. 195-239. New York: Academic Press.

________. 1977. Notes on the establishment and maintenance of the pair bond in Saguinus fuscicollis. In: The Biology and Conservation of the Callitrichidae, ed. D.G. Kleiman, 231-237, Smithsonian Institution Press, Washington, D.C.

________. 1978. Reproductive and social behavior of marmosets with special reference to captive breeding. Prim. Med., Vol. 10:50-62.

Espinal, T. and E. Montenegro-M. 1963. Formaciones Vegetales de Colombia. Republica de Colombia, Instituto Geográfico "Augustin Codazzi," Departamento Agrológico.

Fess, K.J. 1964. Observations on a breeding pair of cotton-top pinches (Oedipomidas oedipus) and nine twin births and three triplet births. J. Marmoset Breeding Farm, 1975. 9 p.

Fooden, J. 1964. Stomach contents and gastrointestinal proportions in wild-shot Guianan monkeys. Am. J. Phys. Anthro., 22:227-231.

Frankie, G.W., H.G. Baker and P.A. Oppler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol., 62:881-919.

Gartlan, J.S. 1968. Structure and function in primate society. Folia Primatol., 8:89-120.

Gaston, A.J. 1977. Social behavior within groups of jungle babblers (Turdoides striatus). Anim. Behav., 25:828-848.

Gates, F.C. 1949. Field Manual of Plant Ecology. McGraw-Hill, N.Y. 137 p.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. Amer. Zool., 14:205-220.

Gengozian, J., J.S. Batson, and T.A. Smith. 1977. Breeding of tamarins (Saguinus spp.) in the laboratory. In: The Biology and Conservation of the Callitrichidae, ed. D.G. Kleiman: 207-213, Smithsonian Institution Press, Washington, D.C.

____________, ___________, and __________. 1978. Breeding of marmosets in a colony environment. Prim. Med., 10:71-78.

___________ and F. Deinhardt (eds.). 1978. Primates in Medicine, Vol. 10: Marmosets in Experimental Medicine. Karger, Basel.

Hall, K.R.L. 1968. Aggression in monkey and ape societies. In: Primates, ed. P. Jay: 149-171. Holt, Rinehart, and Winston, N.Y.

Hamilton, W.J., III, R.E. Buskirk and W.H. Buskirk. 1976. Defense of space and resources by Chacma (Papio ursinus) baboon troops in an African desert and swamp. Ecology, 57:1264-1272.

Hampton, J.K., Jr., S.H. Hampton and B.T. Landwehr. 1966. Observations on a successful breeding colony of the marmoset, Oedipomidas oedipus. Folia Primat., 4:265-287.

________________ and __________ and B.M. Levy. 1971. Reproductive physiology and pregnancy in marmosets. In: Medical Primatology, 1970, ed. E.I. Goldsmith and J. Moor-Jankowski, pp. 527-535, Basel: Karger.

Hampton, S.H. and J.K. Hampton, Jr. 1967. Rearing marmosets from birth by artificual laboratory techniques. Lab. Anim. Care, 17:1-10.

____________ and ______________, and B.M. Levy. 1972. Husbandry of rare marmoset species. In: *Saving the Lion Marmoset*, ed. D.D. Bridgwater, pp. 70-85, Wheeling, West Virginia: Wild Animal Propagation Trust.

____________ and ______________. 1977. Detection of reproductive cycles and pregnancy in tamarins (*Saguinus* spp.) In: *The Biology and Conservation of the Callitrichidae*, ed. D.G. Kleiman:173-179, Smithsonian Institution Press, Washington, D.C.

____________, M.J. Gross and J.K. Hampton, Jr. 1978. A comparison of captive breeding performance and offspring survival in the family Callitrichidae. *Prim. Med.*, 10:88-95.

Harper, F. 1955. The Barren-Ground caribou of Keewatin. Univ. Kansas Misc. Publ. No. 6.

Hearn, J.P. 1977. The endocrinology of reproduction in the common marmoset, *Callithrix jacchus*. In: *The Biology and Conservation of the Callitrichidae*, ed. D.G. Kleiman: 163-171, Smithsonian Institution Press, Washington, D.C.

_________, D.H. Abbott, P.C. Chambers, J.K. Hodges and S.F. Lunn. 1978. Use of the common marmoset, *Callithrix jacchus*, in reproductive research. *Prim. Med.*, 10:40-49.

Hernandez-Camacho, J. and R.W. Cooper. 1976. The nonhuman primates of Colombia. In: *Neotropical Primates, Field Studies and Conservation*, ed. R.W. Thorington and P.G. Heltne: 35-69. National Academy of Sciences, Washington, D.C.

Hershkovitz, P. 1949. Mammals of Northern Colombia, preliminary report no. 4: Monkeys (Primates), with taxonomic revisions of some forms. *Proc. U.S. National Museum*, 98:323-427.

_____________. 1966. Taxonomic notes on tamarins, genus *Saguinus* (Callitrichidae, Primates), with descriptions of four new forms. *Folia Primat.*, 4:381-395.

_____________. 1968. Metachromism or the principle of evolutionary change in mammalian tegumentary colors. *Evolution*, 22:556-575.

_____________. 1970a. Dental and peridontal diseases and abnormalities in wild-caught marmosets (Primates, Callitrichidae). *Amer. J. Phys. Anthro.*, 32:377-394.

_____________. 1970b. Notes on Tertiary platyrrhine monkeys and description of a new genus from the late Miocene of Colombia. *Folia Primat.*, 12:1-37.

_____________. 1972a. The recent mammals of the neotropical region: a zoo-geographic and ecological review. In: *Evolution, Mammals, and Southern Continents*, ed. A Keast, F.C. Erk and B. Glass: 311-431. State University of New York Press, Albany.

______________. 1972b. Notes on New World monkeys. Int. Zoo. Yb., 12:3-12.

______________. 1974. A new genus of late Oligocene monkey (Cebidae, Platyrrhini) with notes on postorbital closure and platyrrhine evolution. Folia Primat., 21:1-35.

______________. 1975. Comments on the taxonomy of Brazilian marmosets (Callithrix, Callitrichidae). Folia Primatol., 24:137-172.

______________. 1977. Living New World Monkeys (Platyrrhini), Vol. 1. University of Chicago Press, 1117 p.

Hinde, R.A. 1956. The biological significance of the territories of birds. Ibis, 98:340-369.

Hladik, C.M. 1967. Surface relative du tractus digestif de quelques primates, morphologie et villosites intestinales et correlaciones avec le regime alimentaire. Mammalia, 31:120-147.

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

__________ and ______. 1972. Disponibilites alimentaires et domains vitaux des primates a Ceylon. Terre Vie, 2:149-215.

Hoage, R.J. 1977. Parental care in Leontopithecus rosalia rosalia: Sex and age differences in carrying behavior and the role of prior experience. In: The Biology and Conservation of the Callitrichidae, ed. D.G. Kleiman: 293-305, Smithsonian Institution Press, Washington, D.C.

__________. 1978. Biosocial development in the Golden Lion Tamarin (Leontopithecus rosalia rosalia [Primates: Callitrichidae]). Ph.D. Dissertation, University of Pittsburgh.

Husson, A.M. 1957. Notes on the primates of Suriname. Studies on the Fauna of Suriname and Other Guyanas, 2:13-40.

Ingram, J.C. 1977. Interactions between parents and infants, and the development of independence in the common marmoset (Callithrix jacchus). Anim. Behav., 25:811-827.

Instituto Geográfico "Augustin Codazzi." 1969. "Monografía del Departamento de Sucre." Oficina de Estudios Geográficos. Bedont, Bogotá.

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

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

________. 1978. A field study of the ecology and behavior of the black-mantle tamarin (Saguinus nigricollis). Primates, 19:241-274.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Behaviour*, 48:215-267.

Jay, P. 1965. Field studies. In: *Behavior of Nonhuman Primates*, ed. A.M. Schrier, H.F. Harlow and F. Stollnitz: 525-591. Academic Press, N.Y.

______. 1968. Comments on studies of variability in species behavior. In: *Primates*, ed. P. Jay: 173-179. Holt, Rinehart and Winston, N.Y.

Jewell, P.A. 1966. The concept of home range in mammals. *Symp. Zool. Soc. Lond.*, 18:85-109.

Johnson, G.W., S. Dreizen and B.M. Levy. 1970. Dental development in the cotton-ear marmoset, *Callithrix jacchus*. *Amer. J. Phys. Anthrop.*, 33:41-48.

Jolly, A. 1972. *The Evolution of Primate Behavior*. Macmillan Co., N.Y. 397 p.

Jones, C. 1972. Natural diets of wild primates. In: R.N.T.-W. Fiennes ed., *Pathology of Simian Primates*, Part 1. Karger, Basel.

Kaufman, J.H. 1962. Ecology and social behavior of the coati, *Nasua narica*. on Barro Colorado Island, Panama. Univ. Calif. Publ. Zool, 60:95-222.

___________. 1971. Is territory definable? In: A.H. Esser (ed.), *Behavior and Environment*: 36-40. Plenum Press, N.Y.

___________. 1974. The ecology and evolution of social organization in the kangaroo family (Macropodidae). *Amer. Zool.*, 14:51-62.

Kinzey, W.G., A.L. Rosenberger, P.S. Heisler, D.L. Prowse and J.S. Trilling. 1977. A preliminary field investigation of the yellow-handed titi monkey, *Callicebus torquatus torquatus*, in Northern Peru. *Primates*, 18:159-181.

Kleiman, D.G. 1977a. (ed.) *The Biology and Conservation of the Callitrichidae*. Smithsonian Institution Press, Washington, D.C.

___________. 1977b. Characteristics of reproduction and sociosexual interactions in pairs of lion tamarins (*Leontopithecus rosalia*)during the reproductive cycle. In: *The Biology and Conservation of the Callitrichidae*: 181-190. Smithsonian Institution Press, Washington, D.C.

___________. 1977c. Monogamy in mammals. *Q. Rev. Biol.*, 52:39-69.

Klein, L.L. and D.J. Klein. 1973. Observations on two types of neotropical inter-taxa association. *Amer. J. Phys. Anthro.*, 38:649-654.

__________ and __________. 1977. Feeding behaviour of the Colombian spider monkey. In: *Primate Ecology*: Studies of feeding and ranging behaviour in lemurs, monkeys and apes, ed. T.H. Clutton-Brock, Academic Press, London.

Knight, D.H. 1975. An analysis of late secondary succession in species-rich tropical forest. In: Tropical Ecological Systems, Ecological Studies, 11:53-59. Springer-Verleg, N.Y.

Kruuk, H. 1975. Functional aspects of social hunting by carnivores. In: Function and Evolution of Behaviour, ed., C. Beer and A. Manning: 119-141. Clarendon Press, Oxford.

Leyhausen, P. 1971. Dominance and territorality as complemented in mammalian social structure. In: A.H. Esser (ed.), Behavior and Environment: 22-33. Plenum Press, N.Y.

Linsdale, J.M. and P.Q. Tomich. 1953. A Herd of Mule Deer. Univ. of Calif. Press, Berkeley.

Lucas, N.S., E.M. Hume and H.H. Smith. 1937. On the breeding of the common marmoset (Hapale jacchus Linn.)in captivity when irradiated with ultra-violet rays - II. A ten years' family history. Proc. Zool. Soc. Lond. Ser. A., 107:205-211.

Marler, P. 1968. Aggregation and dispersal: two functions in primate communication. In: Primates, ed. P. Jay: 420-438. Holt, Rinehart and Winston, N.Y.

________. 1969. Colobus guerza: territoriality and group composition. Science, 163:93-95.

Mason, W.A. 1966. Social organization of the South American monkey. Callicebus moloch: a preliminary report. Tulane Studies in Zool., 13:23-28.

________. 1968. The use of space by Callicebus groups. In: Primates, ed. P. Jay: 200-216. Holt, Rinehart and Winston, N.Y.

Morris, P. 1972. A review of mammalian age determination methods. Mammal. Rev., 2:69-104.

Moss, M.E. and P.S. Chase. 1966. Morphology of Liberian Negro deciduous teeth. II. Arch dimensions and occlusion. Am. J. Phys. Anthrop., 25:261-276.

Moynihan, M. 1964. Some behavior patterns of platyrrhine monkeys. I. The Night Monkey (Aotus trivirgatus). Smithsonian Misc. Collection, 146:1-84.

________. 1970. Some behavior patterns of platyrrhine monkeys. II. Saguinus geoffroyi and some other tamarins. Smithsonian Contributions to Zoology, No. 28. Washington, D.C.

________. 1976a. The New World Primates. Princeton University Press.

____________. 1976b. Notes on the ecology and behavior of the pygmy marmoset, *Cebuella pygmaea*, in Amazonian Colombia. In: *Neotropical Primates: Field Studies and Conservation*, ed. R.W. Thorington Jr. and P.G. Heltne: 79-84. U.S. National Academy of Sciences, Washington, D.C.

Muckenhirn, N.A. 1967. The behavior and vocal repertoire of *Saguinus oedipus* (Callithricidae, Primates). M.A. Thesis, University of Maryland.

Napier, J.R. and P.H. Napier. 1967. *A Handbook of Living Primates*. Academic Press, N.Y.

Neyman, P.F. 1977. Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: *The Biology and Conservation of the Callitrichidae*, ed. D.G. Kleiman: 39-71, Smithsonian Institution Press, Washington, D.C.

Nice, M.M. 1941. The role of territory in bird life. *Am. Midl. Nat.*, 26:441-487.

Noble, G.K. 1939. The role of dominance in the social life of birds. *Auk*. 56:263-273.

Oppenheimer, J.R. 1968. Behavior and ecology of the white-faced monkey, *Cebus capucinus*, on Barro Colorado Island, Canal Zone. Ph.D. Dissertation, U. Illinois.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.*, 103:589-603.

Owen-Smith, N. 1977. On territoriality in ungulates and an evolutionary model. *Q. Rev. Biol.*, 52:1-38.

Perkins, E.M. 1975. The phylogenetic significance of the skin of New World monkeys (Order Primates, Infraorder Platyrrhini). *Am. J. Phys. Anthrop.*, 42:395-424.

Pitelka, F.A. 1959. Numbers, breeding schedule,and territoriality in pectoral sandpipers of Northern Alaska. *Condor*, 61:233-264.

Poirier, F.E. 1968a. Analysis of a Nilgiri langur (*Presbytis johnii*) home range change . *Primates*, 9:29-43.

____________. 1968b. Nilgiri langur (*Presbytis johnii*) territorial behavior. *Primates*, 9:351-364.

Ralls, K. 1971. Mammalian scent marking. *Science*, 171:444-449.

Ramirez-F, M., C.H. Freese and J. Revilla-C. 1977. Feeding ecology of the pygmy marmoset, *Cebuella pygmaea*, in Northeastern Peru. In: *The Biology and Conservation of the Callitrichidae*, ed. D.G. Kleiman:91-104. Smithsonian Institution Press, Washington, D.C.

Richard, A. 1974. Intra-specific variation in social organization and ecology of Propithecus verreauxi. Folia Primatol., 22:178-207.

Ripley, S. 1967. Intertroop encounters among Ceylon gray langurs (Presbytis entellus). In: Social Communication Among Primates, ed. S.A. Altmann: 237-253. University of Chicago Press, Chicago, 392 p.

Rothe, H. 1975. Some aspects of sexuality and reproduction in groups of captive marmosets (Callithrix jacchus). Z. Tierpsychol., 37:255-273.

________. 1977. Parturition and related behavior in Callithrix jacchus (Ceboidea, Callithrichidae). In: The Biology and Conservation of the Callitrichidae, ed. D.G. Kleiman: 193-206. Smithsonian Institution Press, Washington, D.C.

Rowell, T.E. 1972 . The Social Behavior of Monkeys. Penguin, London.

Schaller, G.B. 1972. The Serengeti Lion. University of Chicago Press.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.

Scott, N.J. Jr., T.T. Struhsaker, K. Glander and H. Chirivi. 1976. Primates and their habitats in Northern Colombia with recommendations for future management and research. In: First Inter-American Conference on Conservation and Utilization of American Nonhuman Primates in Biomedical Research: 30-50. PAHO, Scientific Publication No. 317.

Siddall, R.A. 1978. The use of marmosets (Callithrix jacchus) in teratological and toxicological research. Prim. Med., 10:215-224.

Smith, C.C. 1968. The adaptive nature of social organization in the genus of tree squirrels Tamiasciurus. Ecol. Monogr., 38:31-63.

Smith, S.M. 1978. The "underworld" in a territorial sparrow: adaptive strategy for floaters. Am. Nat. 112:571-582.

Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Am. Nat., 104:25-35.

Southwick, C.H., M.A. Beg and M.R. Siddiqi. 1965. Rhesus monkeys in North India. In: Primate Behavior: Field Studies of Monkeys and Apes, ed. I. DeVore: 111-159. Holt, Rinehart and Winston, N.Y.

Stevenson, M.F. 1976. Birth and perinatal behaviour in family groups of the common marmoset (Callithrix jacchus jacchus), compared to other primates. J. of Human Evolution, 5:365-381.

Struhsaker, T.T. 1967. Ecology of vervet monkeys (Cercopithecus aethiops) in the Masai-Amboseli game reserve, Kenya. Ecology, 48:891-904.

________________. 1969. Correlates of ecology and social organization among African cercopithecines. Folia Primatol., 11:80-118.

________________. 1974. Correlates of ranging behavior in a group of red colobus monkeys (Colobus badius tephrosceles). Am. Zool., 14:177-184.

Sussman, R.W. and I. Tattersall. 1976. Cycles of activity, group composition and diet of Lemur mongoz mongoz Linnaeus 1766 in Madagascar. Folia Primatol., 26:270-283.

Tanaka, J. 1965. Social structure of nilgiri langurs. Primates, 6:107-122.

Tenaza, R.R. 1975. Territory and monogamy among Kloss' gibbons (Hylobates klossi) in Siberut Island, Indonesia. Folia Primatol., 24:60-80.

Thorington, R.W. Jr. 1968a. Observations of squirrel monkeys in a Colombian forest. In: The Squirrel Monkey, ed. L.A. Rosenblum and R.W. Cooper. Academic Press, N.Y.

________________. 1968b. Observations on the tamarin, Saguinus midas. Folia Primatol., 9:95-98.

Tilson, R.L. 1977. Social organization of Simakobu monkeys (Nasalis concolor) in Siberut Island, Indonesia. J. Mammal., 58:202-212.

___________ and R.R. Tenaza. 1976. Monogamy and duetting in an old world monkey. Nature, 263:320-321.

Walther, F.R. 1972. Territorial behavior in certain horned ungulates, with special reference to the examples of Thomson's and Grant's gazelles. Zool. Afr., 7:303-308.

Waser, P.M. 1978. Patterns of inter-group spacing among primates. In: Recent Adv. in Primatol., ed. D.J. Chivers and J. Herbert, Volume 1: 845-847.

Wiley, R.H. 1973. Territoriality and non-random mating in Sage grouse, Centrocercus urophasianus. Anim. Behav. Monog. 16:87-169.

Willis, E.O. 1967. The behavior of bicolored antbirds. Univ. of Calif. Publ. in Zool., 79:1-127.

Wilson, E.O. 1975. Sociobiology, The New Synthesis. Harvard U. Press, Cambridge, Mass.

Wolfe, L.G., J.D. Ogden, J.B. Deinhardt, L. Fisher and F. Deinhardt. 1972. Breeding and hand-rearing marmosets for viral oncogenesis studies. In: Breeding Primates, ed. W.I.B. Beveridge: 145-157. Karger, Basel.

Wright, P.C. 1978. Home range, activity pattern, and agonistic encounters of a group of night monkeys (Aotus trivirgatus) in Peru. Folia Primatol., 29:43-55.

Ziemer, L.K. and A.J. Palfrey. 1979. Reliability of casts in reproducing geometrical surfaces. Amer. J. Phys. Anthro., 50:496 (Abstract).

Additions to Bibliography

Bernstein, I.S. 1968. The Lutong of Kuala Selangor. Behaviour, 32:1-16.

Brown, J.L. and G.H. Orians. 1970. Spacing patterns in mobile animals. A. Rev. Ecol. Syst., 1:239-262.

Budnitz, N. and K. Dainis. 1975. Lemur catta: ecology and behavior. In: Lemur Biology, ed. I. Tattersall and R.W. Sussman: 219-235. Plenum Press, N.Y.

Carpenter, C.R. 1958. Territoriality: a review of concepts and problems. In: Behavior and Evolution, ed. A. Roe and G.G. Sompson: 224-250. Yale Univ. Press, New Haven.

Chivers, D.J. 1974. The Siamang in Malaya. Contr. to Primatology, Vol. 4: 1-335. Karger, Basel.

Davies, N.B. 1968. Ecological questions about territorial behaviour. In: Behavioural Ecology, ed. J.R. Krebs and N.B. Davies: 317-350. Blackwell, Oxford.

Deinhardt, F., L. Wolfe and J. Ogden. 1976. The importance of rearing marmoset monkeys in captivity for conservation of the species and for biomedical research. In: First Inter-American Conference on Conservation and Utilization of American Non-human Primates in Biomedical Research: 65-71. PAHO Scientific Publ. #317, Washington, D.C.

DeVore, I. and S.L. Washburn. 1963. Baboon ecology and human evolution. In: African Ecology and Human Evolution, ed. C. Howell and F. Bourliere: 335-367. Aldine, Chicago.

DeVos, A. and A. Omar. 1971. Territories and movements of Sykes monkeys (Cercopithecus mitis kilbi Neyman) in Kenya. Folia Primat., 16:196-205.

Dittus, Wolfgang P.J. 1975. Population dynamics of the Toque monkey, Macaca sinica. In: Socioecology and Psychology of Primates, ed. R.H. Tuttle: 125-151. Mouton, The Hague.

Eisenberg, J.F. 1977. Comparative ecology and reproduction of New World monkeys. In: The Biology and Conservation of the Callitrichidae, ed. D.G. Kleiman: 13-22. Smithsonian Institution Press.

Ellefson, J.O. 1974. A natural history of white-handed gibbons in the Malayan peninsula. In: Gibbon and Siamang, ed. D.M. Rumbaugh, Vol. 3: 1-136. Karger, Basel.

Epple, G. 1975b. Parental behavior in *Saguinus fuscicollis* ssp. (Callitrichidae). *Folia Primatol.*, 24:221-238.

Freese, C.H. and P.G. Heltne. 1978. Some ecological correlates of body size in New World monkeys. Amer. Soc. Primatol. meetings, 1978.

Garber, P. 1979. Locomotor behavior and ecology of *Saguinus oedipus geoffroyi* (Callitrichidae, Primates). *Am. J. Phys. Anthrop.*, 50:440 (abstract).

Gartlan, J.S. and C.K. Brain. 1968. Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. In: *Primates: Studies in Adaptation and Variability*, ed. P. Jay. Holt, Rinehart, and Winston, N.Y.

Klopfer, P.H. 1969. *Habitats and Territories*. Basic Books, Inc., N.Y. 117 p.

Kummer, H. 1968. *Social Organization of Hamadryas Baboons*. Univ. Chicago Press. 189 p.

Leutenegger, W. 1973. Maternal-fetal weight relationships in primates. *Folia Primatol.*: 20:280-293.

Luckett, W.P. 1979. Use of developmental and reproductive features in assessing platyrrhine phylogeny. *Am. J. Phys. Anthrop.*, 50:460 (abstract).

Mitani, J.C. and P.S. Rodman. 1979. Territoriality and range defense among primates. *Am. J. Phys. Anthrop.*, 50:465 (abstract).

Petter, J.J. 1965. The lemurs of Madagascar. In: *Primate Behavior*, ed. I. DeVore: 292-323. Holt, Rinehart, and Winston, N.Y.

Pollock, J.I. 1975. Field observations on *Indri indri*; a preliminary report. In: *Lemur Biology*, ed. I. Tattersall and R.W. Sussman: 287-311. Plenum Press, N.Y.

Reynolds, V. and F. Reynolds. 1965. Chimpanzees of the Budongo forest. In: *Primate Behavior*, ed. I. DeVore: 368-424.

Richard, A. 1974. Intra-specific variation in social organization and ecology of *Propithecus verreauxi*. *Folia Primatol.*, 22:178-207.

Rosenberger, A.L. 1979. Phyletic perspectives and platyrrhine classification. *Am. J. Phys. Anthrop.*, 50:476 (abstract).

Schaller, G.B. 1965. The behavior of the mountain gorilla. In: *Primate Behavior*, ed. I. DeVore: 324-367.

Sugiyama, Y., K. Yoshiba, and M.D. Pathasarathy. 1965. Home range, mating season, male group and inter-troop relations in Hanuman langurs (*Presbytis entellus*). *Primates*, 6:73-106.

Sussman, R.W. 1975. A preliminary study of the behavior and ecology of *lemur fulvus rufus* (Audebert 1780). In: *Lemur Biology*, ed. I. Tattersall and R.W. Sussman: 237-258. Plenum Press, N.Y.

Trivers, R.L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man*, 1871-1971, ed. B. Campbell: 136-179. Aldine, Chicago.

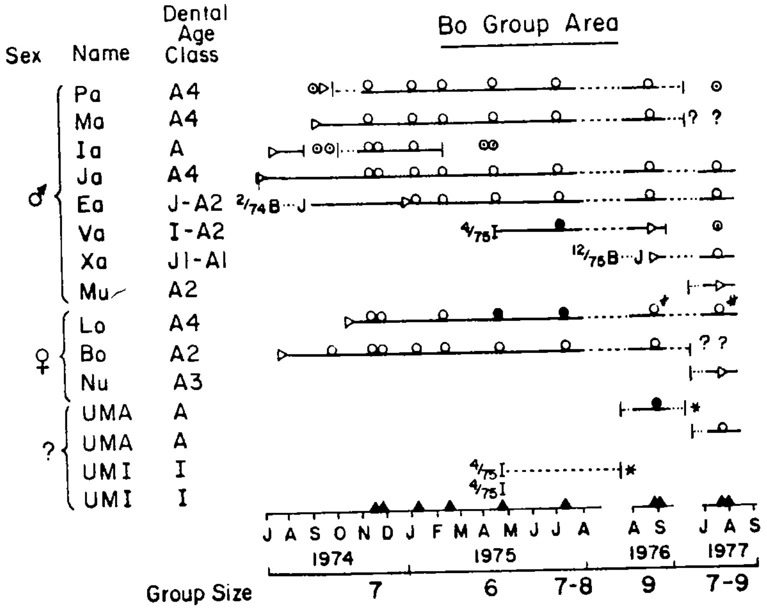
Waser, P.M. 1978. Patterns of inter-group spacing among primates. In: *Recent Advances in Primatology*, Vol. 1, ed. D.J. Chivers and J. Herbert: 845-847. Academic Press, N.Y.

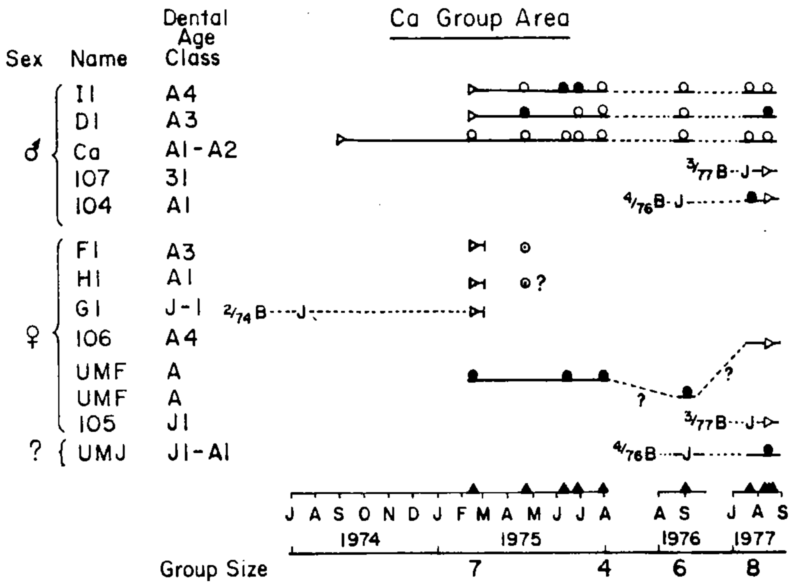
Yoshiba, K. 1968. Local and intertroop variability in ecology and social behavior of common Indian langurs. In: *Primates: Studies in Adaptation and Variability*, ed. P. Jay. Holt, Rinehart and Winston, N.Y.

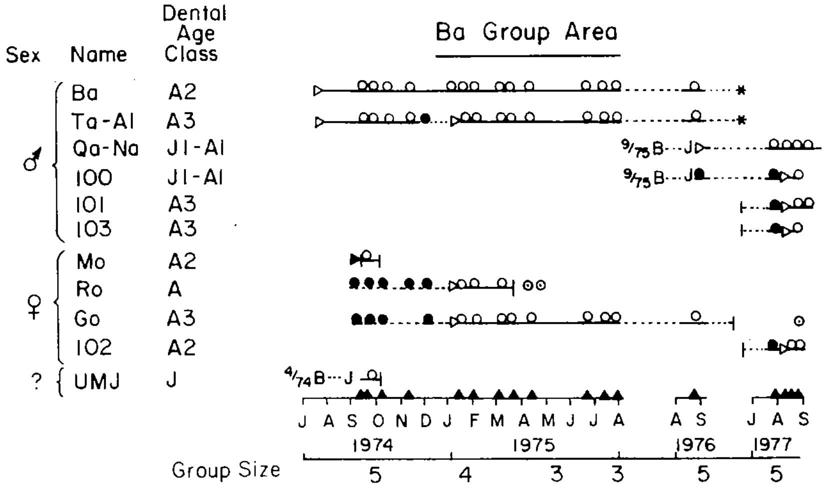
APPENDIX 1

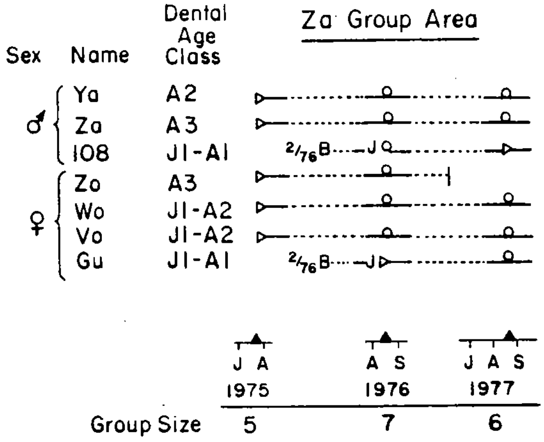
Histories of Saguinus oedipus groups

In the following figures, each line represents an individual's history in the home range indicated. Dental age classifications are according to the definitions in Table 2 . For consistency it has been assumed that all subadults observed in these groups had been born into them. Thus some individuals first captured as young adults in 1977 were assumed to correspond to juveniles seen with the groups (but not marked) the preceding year. Other unmarked individuals were figured as though they were new immigrants, although they may in fact have corresponded in some cases to unmarked individuals present the preceding year.




Ca Group Area


Ba Group Area


Za Group Area

Conventions used are as follows:

—— Present in group

---- Probably present in group

○ Seen with group (definitely identified)

● Tamarin thought to be this individual seen with group

⊙ Seen outside the area

▷ Date marked or first identifiable

| Disappearance or appearance

I,J First sightings of (carried) infant or (independent) juvenile

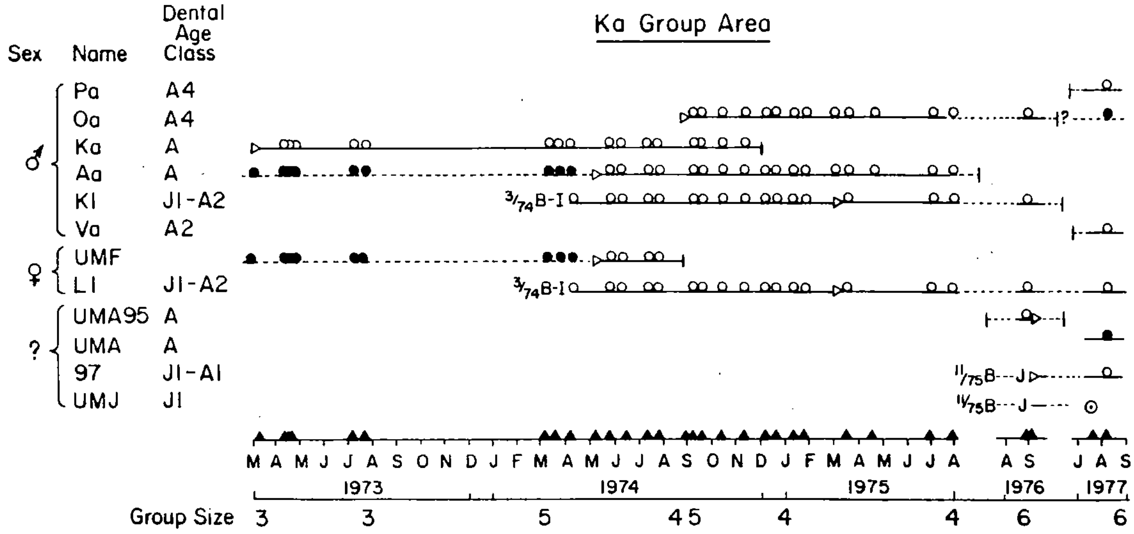
B Estimated birth date

? May have been present - possible insufficient observation

--?-- Possibly same individual

▲ Inventory dates

UMA, UMF, UMJ, UMSA - unmarked adult, adult female, juvenile, subadult



APPENDIX 2

Characteristics of A Secondary Forest of the Caribbean Coast of Colombia

The following conventions are used (refer to columns below):

1-Str.-Stratification: stratum the species usually is found in. u, upper (height exceeding 15 m); um, upper middle; m, middle (5-15 m); l, lower (under 5 m).

2-Arm.-Armation: sp, spinous; n, no spines.

2-Sh.-Leaf shape: si, simple; co, compound.

4-Si.-Leaf size: (Raunkiaer classes): l, leptophil (under 25 mm^2), n, nanophil (between 25 and 9x25 mm^2); mi, microphil (between the preceding maximum and 9^2x25 mm^2); Me, mesophil (between preceding maximum and 9^3x25 mm^2); Ma, macrophil (between preceding maximum and 9^4x25 mm^2); MM, megaphil (exceeding the preceding maximum). If the leaf is compound, refers to the entire leaf, not individual leaflets.

5-Abun.-Relative abundance: in this forest, a, among the most abundant species; f, frequent; i, infrequent; r, rare; e, principally along edges; j, immature individuals only present in woods; V, in vicinity of study area but not in woods - cf. in pasture or early regrowth.

6-S.o.-Species used by Saguinus oedipus as food resources: F, consume fruit or aril; F? visiting fruits but not obviously eating them (see text); fl, eating flowers or parts thereof; fl?, visiting flowers but not damaging them; L, eating leaves.

7-Others-Use by other species, as follows: A, howler (Alouatta seniculus); C, capuchins (Cebus capucinus); S, squirrels (Sciurus granatensis); P, parrots (Amazona sp.) or guacamayos (Ara sp.); R, guazalé (Ramphastos sulfuratus); D, diostedé (Pteroglossus torquatus); B, small birds. Conventions for item used (in parentheses) are as in Column 6.

	1 Str	2 Arm	3 Sh	4 Si	5 Abun	6 S.o.	7 Others
			Trees				
Cavanillesia platanifolium	h,u	n	si	Ma	f	F?	A(F)
Ceiba pentandra	h,u	n	co	mi	i		
Bombacopsis quinatum	h,u	Sp	si	Me	i		
Enterolobium cyclocarpum	h,u	n	co	mi	i		C(F)
Fagara	h,u	Sp	co	Me	i		
Sterculia apetala	h,u	n	si	Ma	i	F?	P(F)
Senegalia	h,u	n	co	l	f		
Sabal mauritiaeformis	h	n	si	MM	a		
Astrocarym standleyanum	h	Sp	co	MM	a		CS(F)
Anacardium excelsum	h	n	si	Ma	rVf	F	C(F)
Pseudobombax septenatum	h	n	co	Ma	f		A(L)
Pithecellobium saman	h	n	co	Me	f	F?	
I	h	n	si	Me	f?		
I	h	n	co	mi	f?		
I	h	n	co	l	i	F	PDB(F)
Lecythis magdalenica	h	n	si	Ma	a		C(F),AS(fl)
Cedrela (cf. angustifolia)	h	n	co	mi	i		
Prioria copaifera	h	n	si	Me	i		
Ficus	h	n	si	Me	a	F	ACS(F)
Luehea	h	n	si	Me	a		A(fl)
Ormosia	h	n	co	Me	f		
Quararibea sp.	h	n	si	Me	f	F	A(F)
I	h	n			r?		
Cecropia peltata	m	n	si	MM	f	Ffl	
Cecropia sp.	m	n	si	MM			
Spondias mombin	m	n	co	mi	a	F	AC(F)
Calycophyllum candidissimum	m	n	si	Me	a		
Ficus duquei	m	n	si	Ma	i		
Ficus palmicida	m	n	si	mi	V	F	ACPDB(F)
Brosimum	m	n	si	Me	f	Ffl	AC(FfL)
I	m	n	si	Ma	i	F	
I	m	n	si	Me	i		

	1 Str	2 Arm	3 Sh	4 Si	5 Abun	6 S.o.	7 Others
Rheedia	m	n	si	Me	r		
Cassearia (1)	m	n	co	Me	a	F	
I	m	n	co	Me	f	F	C(F)
Chrysophyllum	(m)	n	si	Me	j,v	F	
I	m	n			f		
Alseis blackiana Hemsl.	m	n	si	Ma	f		
Genipa americana L.	m	n	si	Ma	V	F	
Brownea ariza	m	n	co	Me	r		
Cocoloba (1)	m	n	si	Me	f		
Cordia alliodora	m	n	si	Me	r		
Sapium	m	n	si	mi	f		C(F)
Ocotea	m	n	si	Me	f		
Batris (3)	m	Sp			f		
Trichilia	m	n	co	Me	a	F	
I	m	n	co	Me	i		
Inga punctata	m	n	co	Me	f	F	C(F)
Inga sp.	m	n	co	Me	i		
Inga sp.	m	n	co	Me	r		
Garcia nutans	m	n	si	Me	a		
Guazuma ulmifolia	m	n	si	Me	a	F	C(F)
Cochlospermum vitifolium	m	n	si	Me	i		
Swartzia sp.	m	n	co	mi	a		
Gustavia	m	n	si	MM	a		
Muntingia calabura	m	n	si	Me	fo	F	
Hirtella	m	n	co	Me	i	F	
Hasseltia floribunda	m	n	si	mi	i	F	
Picramnia latifolia	m	n	co	Me	f		
I	m	Sp	si	Ma	f	F	
Cupania	m	n	si	Me	f		
I	m	(Sp)	si	mi	i		
Pittoniotus trichantha Griseb.	m	n	si	Me	i	F	C(F)
Psychotria grandis Sw.	m	n	si	Ma	f	F	
I	m	n	si	Me	i		
Ardisia	m	n	si	Ma	i	F	
I	m	n	si	Me	a		
Tabebuia	m	n	co	Ma	rjV		
Triplaris	l	n	si	Ma	a		
Talisia oliviformis	l	n	co		f	F	
Hamelia	l	n	si	mi	i		
Hybanthus prunifolius	l	n	si	Me	f		
Tabernaemontana	l	n	si	Me	a		
Rauvolfia litoralis	l	n	si	Me	i		

	1 Str	2 Arm	3 Sh	4 Si	5 Abun	6 S.o.	7 Others
I	1	n	si	mi	i		
Randia sp.	1	Sp	si	Me	i		
Swarzia simplex	1	n	si	Me	r		
Bactris (1)	1	Sp			a		
Bactris (2)	1	Sp			f		
Elaeis oleifera	1	n			a		S(F)
Astrocaryum malybo	1	Sp			a		S(F)
Casseari a (2)	1	n	si	mi	i	F	
Mayna	1	n	si	Me	a	F	S(F)
Psidium guajava	1	n	co	Me	rVo	F	
Psidium friedrichstalianum	1	n	co	Me	rV		
I	1	n	se	Ma	f	F	
Pereskia bleo	1	Sp	si	mi	r		
Quassia	1	n	si	Me	f		
Sapindus saponaje (1)	1	n	co	Ma	i		
Urera	1	Sp	si	Ma	a		D(F)
Bunchosia	1	n	co	Me	I	(F)	
Crescentia sp	1	n	si	mi	i		
Coccoloba (2)	1	n	si	mi	a		
Capparis	1	n	si	Me	f	F	
Stylogyne turbacensis	1	n	si	Me	i	F	
Herrania	1	n	co	MM	r	F	
Carica microcarpa	1	n	si	Ma	a		
I	1	n	si	Me	a		
I	1	n	si	Me	f		
Clavija sp.	1	n	si	Ma	f		
Piper (1)	1	n	si	Me	f		
Piper (2)	1	n	si	Me	f	F	
I	1	n	si		i		S(F)
Ground Vegetation							
Cryosophila		Sp		MM	a		
Carludovica palmata		n			a		
Capsicum		n	si	mi	ae		
Calathea lutea		n			io		
Heliconia mariae		n	si	Ma	i		
Heliconia sp		n	si	Ma	ae		
Aechmea (?)		Sp	si	Ma	ie		
Diffenbachia sp.		n	si	Ma	a		
Vines							
Paullina (1)		n	co	mi	f	F	
Bignonia spp.		n			a		
Zizyphus		Sp	si	mi	f	F	
Trichostigma octandrum		n			f	F	A(F)

APPENDIX 3

Phenological Observations in a Dry Tropical Forest Near the Caribbean Coast of Colombia

Methods

The forest in which this data was collected has been described in detail in other sections of this work. The phenological data presented was gathered by three means: (1) Periodic survey of marked individuals, (2) Periodic "state of the species" notations for a number of species listed in a notebook kept for that purpose, and (3) Casual observations also noted in the above-mentioned notebook under the appropriate date.

The periodic survey included about 250 marked individual trees. About 85 species were represented by 2-4 individuals, the rest by one. The original sample was not intended to be random, nor to represent all species present in the forest. Rather, a survey route was laid out according to its usefulness for another purpose, namely the completion of standard surveys for monkeys. Along this route I selected trees that I could at that time recognize. To these approximately 60 species I kept adding each time I traversed the survey route. The trees were marked with numbered pieces of impression-lettering tape ("Dymo" tape), attached with a nail.

The survey was traversed monthly or bimonthly from February through August 1974, and again in December, March and July of 1975. My sampling frequency dropped off after I realized the incorrectness of my assumption that several individuals of a species would give a representative idea of the behavior of the species as a whole. Problems with the transect method led to my initiating the "state of the species" list. It included many species which were not present on the transect route. These observations were at first made as a supplement to the transects, but gradually replaced them. The process of doing a transect, although tedious and requiring an entire day, was valuable in tending to increase my awareness of the vegetation in general. The list of species I kept data on included most species which I had observed the tamarins eating, plus others which interested me for other reasons. In some cases these turned out later to also be food species.

The analysis of the resulting data required the dropping of various species which were chiefly observed when in flower or fruit. Their presence in the sample would have given misleadingly inflated percentages for flowering and fruiting frequencies during those months. In the analysis therefore I included only those species which I sampled regularly once I began observing them. A bias toward first inclusion of new species while in flower or fruit still exists; I am not certain what effect this could have on the data presented.

Sample size varied from 60 to 80 species (18-32 per stratum). I have therefore expressed frequencies in terms of percentages. An index of sampling frequency has also been provided (Figure 1).

The following types of entries were used to categorize the state of a species or condition of an individual. Leaves, flowers and fruit were noted as being absent, scarce, moderately abundant, or abundant. Fruit or unusual numbers of leaves on the ground were noted as well as the presence of immature fruit, newly sprouted or yellow leaves, and flower buds.

Species identifications were made using samples collected from representative individuals. I wish to acknowledge with great gratitude the assistance of Dr. Jesus Idrobo B. at the Herbario, Instituto de las

Ciencias Naturales, Universidad Nacional, Bogota in identification of the large majority of these species. Dr. Jorge Hernandez C. also helped me a great deal with identifications. A few specimens were identified by Dr. Joe Kirkbride and Dr. Jose Cuatrocasas (Smithsonian Institute Herbarium). The palms were identified by Dr. H.E. Moore, Cornell University. I would also like to acknowledge valuable discussions with Dr. Jorge Hernandez C. regarding the vegetation of Northwestern Colombia, in which he freely shared his considerable knowledge and his ideas with me.

Results

Leaf Loss

In all trees which were completely or partly deciduous, loss occurred mainly during the driest months, January through April, with a few species extending loss into December and May. This is very similar to the pattern found by Frankie et. al. (1974) in a dry tropical forest on the Caribbean coast of Costa Rica, although the percent of deciduousness is apparently less (74% in Costa Rica versus about 42% in Colombia, including 15% partly deciduous). The total annual rainfall is much greater at the Costa Rican site (a mean of 1533 mm versus around 1000 mm).* The mean rainfall in the rainiest month is about 165 mm at the Colombia site; it is almost double that in Costa Rica. By contrast the Colombia site has somewhat more rainfall on average, thus the contrast between peak rainfall and low months is much greater at the Costa Rican site, which may account for its greater deciduousness. The length of the dry season appears to be about the same in both areas. The driest month at both study sites was February in the years under consideration.

The period of leaflessness of a given species tended to be longer in the drier of the two dry seasons for which data were taken (i.e., 1975).** Leaf loss was also more extensive that year in species which were only

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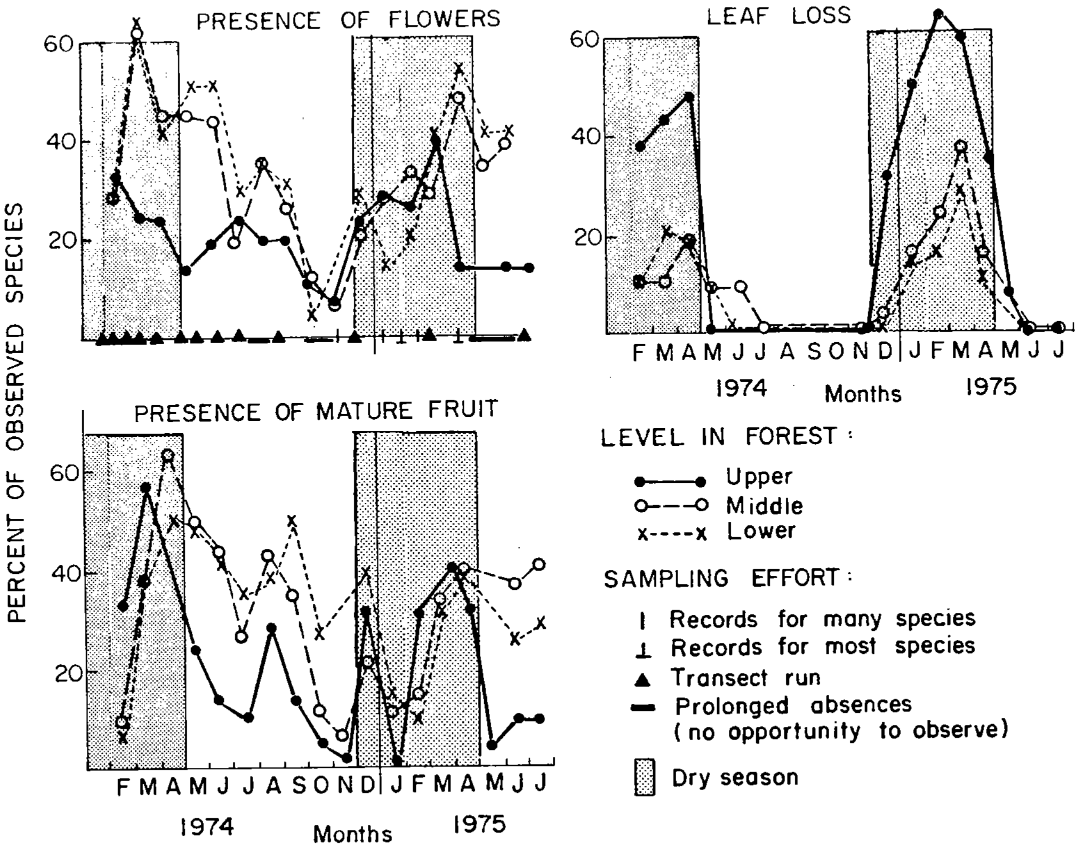
*Total rainfall in Tolu, a coastal town about 15 Km WSW of the study site, in 1972: about 1200 mm (Data from Servicio Colombiano de Meteorologia e Hidrologia). In Toluviejo, farther inland than the study site and to the SE of it, it averaged 896 mm between 1950-1957 (Instituto Augustin Codazzi, 1969).

**Rainfall at the study site was recorded in terms of number of days with rain and the heaviness of rainfall on a 1 to 5 scale (Recording instruments were unfortunately not available). These records show that the dry season was drier (fewer rainy days with less intensity) and longer in 1975 than in 1974.



Appendix 3, Figure 1

partly deciduous in 1974. For those species which could be compared, onset of leaf loss tended to be earlier in the drier year. Also the peak frequency of leaflessness occurred earlier in the drier year (Feb.-Mar. in 1975 vs Mar.-Apr. in 1974) (Figure 1).

Of 99 species whose leaf cycles were observed, 24 were completely without leaves for at least a month and three other showed brief loss of less than a month, giving 27/99 (or 27%) completely or partially deciduous species. This figure may be an underestimate, as many species were not recognizable to me when without leaves and therefore may have been overlooked even though they were included on my list. Also, briefly deciduous trees are easily overlooked. The three observed were of the middle (2) and lower (1) layers.

Somewhat over half of the completely deciduous group (14/24 or 58%) consisted of trees whose height most commonly exceeded 45 feet (henceforth to be termed the "upper level," as in Figure 1). The remaining 10 were evenly divided between the "middle" (15-45 ft.) and "lower" (less than 15 ft.) tree levels.

Fifteen additional species were partially deciduous, in that they showed noticeable leaf reduction during a defined period.

There was a striking difference in percent of completely or partly deciduous species at the various levels. Eighty four percent of upper level trees were seasonally deciduous as opposed to 31% and 28% in the middle and lower levels. Of the five upper layer species not showing noticeable leaf reduction, two were palms and two were species distinguished for their thick waxy leaves (Anacardium excelsum and Ficus sp.). The three certainly identifiable individuals of the remaining species (Quararibea sp.) were all very near to water sources which failed only during the height of the dry season.

The peak frequency of leafless species in the middle and lower levels is delayed about a month compared to the upper levels and is much briefer. (Figure 1). The delay in leaf loss in these lower levels might be attributable to their initial protection by the overstorey from increased transpiration. Nevertheless it is notable that the majority of species growing side by side with the deciduous ones did not show this adaptation.

Flowering Patterns

All three levels showed a low in number of species flowering during the wettest season (Oct.-Nov., Figure 1). All three showed a minor peak followed by a major peak during the driest season (Dec.-Apr.). The minor peaks are offset between levels: the lower level in December, followed by the upper level in January and the middle level in February. Each is followed by a drop, short and slight in the middle and upper layers, more pronounced and longer in the lower level. The major peaks occur first in the upper level (March), followed by the middle and upper levels one month later. The same pattern appears in both years. The possibility that the late 1974-1975 pattern might be an artifact due to irregular observation or differential noticing of flowering in lower storey species, which tend to be more inconspicuous (cf. Frankie et.al., 1974; pers. obs.) seems to be ruled out by the similarity of the 1974 data based on systematic regular observations.

The major flowering peaks of all levels were earlier in the wetter year (1974), in contrast to the reverse relation for leaf loss peaks. The percent of middle and lower level species in flower was less in the drier year (1975) by about 10%.

Outside of the major dry season there occurred other (lower) flowering peaks.

The similarity between the flowering patterns observed in this forest and those observed by Frankie et.al. (1974) are striking, particularly considering the relative crudity of the methods of data collection used and the fact that I did not become aware of their work until my data had already been collected and plotted. The similarities include the lows seen during high rainfall months, the placement and relative height of the various peaks at different times of the year, and the temporary lull in flowering in the middle of the long dry season. Also in both forests the flowering peaks of the lower levels are offset from those of the upper levels. A marked May increase in flowering in the lower levels corresponds in both sites exactly to a depression in numbers of species flowering in the upper storey.

Fruiting Patterns

Peak numbers of trees in fruit occurred in March and April of 1974, at the end of the dry season (Figure 1). In both years the upper level peak preceded by a month that of the lower and middle levels. The latter two were coordinated. The peaks were lower for all three layers (decreased numbers of species fruiting) in the drier year (1975).

There also occurred at the beginning of the dry season a minor peak, separated from the yearly major peak by a temporary lull similar to that which occurred in flowering during the dry season. All three levels showed this pattern.

The March-April yearly high was followed by a decline of fruit availability continuing until July. Beginning in July all three layers showed an upswing culminating in the secondary annual peak of August-September. Then there was further decline in availability, especially in the upper and middle levels, continuing until an all-year low in October and November. The latter coincides with the end of the wet season.