

**Aspects of the Ecology and
Social Organization of
Free-ranging Cotton-Top
Tamarins (*Saguinus oedipus*) and
the Conservation Status
of the Species**

ABSTRACT

Fifty-three *Saguinus oedipus* were live-trapped, marked, and released in one section of a relatively mature secondary forest located in the Western Caribbean coastal lowlands of Colombia. In a total of over 2,500 active field hours, approximately 750 hours of contact were made with marked and unmarked groups of tamarins.

Captures were made with decoy-type live traps and several types of collars were used for marking. Trapping and marking methods are discussed in detail since they may be applicable to future callitrichid field studies.

Certain groups containing between three and thirteen members restricted their movements to a well-defined home range. Although some groups changed considerably in size and composition during the study, they continued to occupy the same areas. Contact with neighboring groups or intruding individuals could usually be characterized as agonistic, including frequent "Rasp" vocalizations, vocalizations associated with separation of members from the group ("Dips" and "Long Calls"), frequent short chases, and occasional body contact. Encounters occurred most often in the overlap areas entered frequently by both groups, and terminated with the two groups gradually drifting apart.

¹Author's name previously Warner.

Groups of from one to five were present occasionally within the home ranges of "established" groups. Some "transient" groups contained individuals which previously had been observed with "established" groups. Usually "transients" were chased vigorously by the resident group on contact, but two strange individuals joined resident groups with no sign of antagonism. Individuals examined from "transient" groups were adults whose age (based on weight and tooth wear) ranged from young to rather old. Both sexes were included.

Home-range sizes for three groups were 7.8, 7.8, and 10.0 hectares, with the corresponding group size (maximum and minimum numbers) ranging from 13 to 5; 5 to 3; and 6 to 3 individuals. Adjoining group home-range overlap was 20 to 30 percent. Density based on these three groups ranged from 0.3 to 1.8 tamarins per hectare.

Movement patterns, daily routine, group cohesion, and relations with other species are briefly described. Most of the 25 observed sleeping sites were broad tree forks, but a few were dense branch masses. Sites were frequently reused. In all but two cases, all individuals of a group slept together.

Food items included fruits of trees, vines and epiphytes, insects, newly sprouting leaves

or buds, leaves, leaf stems, and in one case a frog. Unidentified material was gathered from flowers, surfaces of certain fruits and tree branches or trunks, and the decayed parts of certain trees.

Variation in tooth wear indicated a probable spectrum of ages among the adults of the larger groups examined (eight members). Only one or a pair of infants or juveniles were observed in any group. Present data are not sufficient to support or reject the "extended family" social organization advanced by various workers (Epple, 1972b; Eisenberg, Muckenhirn, and Rudran, 1972); However, the changes in group size and composition observed in this and other studies on *Saguinus* (Dawson, 1976, 1977; Thorington, 1968; Durham and Durham, in press; Castro and Soini, 1977; Izawa, 1976) argue against the suggestion.

It is suggested that the availability of *Saguinus oedipus* to exporters is a misleading index of their abundance. The habitat destruction now occurring is the major threat to this species' future in the wild. The immediate establishment of adequately protected reserves can assure its long-term survival. The need for broad long-term policies on fauna preservation and financing of basic research, especially on callitrichids, is emphasized.

SUMARIO

Cincuenta y tres *Saguinus oedipus* fueron atrapados vivos, marcados y posteriormente liberados en un área de un bosque secundario relativamente maduro, ubicado en la costa Oeste del Caribe, en Colombia. De un total de 2,500 horas de trabajo activo en el terreno, 750 hrs fueron de contacto con grupos marcados y no marcados de dicha especie.

Las capturas fueron hechas con trampas de señuelo vivo fabricadas con alambre por la gente del lugar. Collares de cuero, envueltos en cinta plástica en colores, medallas numeradas hechas de "Formica", y pequeñas campanitas fueron utilizadas en el marcaje. El método de captura, marcaje y determinación de la edad relativa de los individuos se discute en detalle puesto que pueden ser utilizados en futuros trabajos similares con otros Callitrichidae.

Algunos grupos restringieron sus movimientos a 'home ranges' (área de actividad) bien definidos, conteniendo entre 3 a 13 miembros. A pesar de que algunos de estos grupos cambiaron considerablemente en tamaño y composición durante el estudio, permanecieron sin cambios en los límites de los 'home ranges'. Los contactos con grupos vecinos o individuos que pretendieron entrar al área pudieron ser, en general, caracterizados como agonísticos, que incluyeron pequeños en-

frentamientos, aumento considerable en la cantidad de vocalizaciones emitidas, persecuciones, y ocasionales contactos cuerpo a cuerpo. Los encuentros ocurrieron en las zonas de sobreposición de las áreas de actividad de los grupos, terminando con una gradual separación de estas.

Grupos de uno a cinco individuos estuvieron temporariamente presentes en varias oportunidades dentro las áreas de los grupos 'establecidos' descritos más arriba. En varios casos, contenían individuos marcados previamente observados con algún grupo establecido. En general, los visitantes fueron perseguidos vigorosamente por el grupo residente; sin embargo en dos ocasiones un individuo ajeno al grupo pasó a formar parte del grupo residente sin ningún signo de rechazo. Los individuos en estos grupos transeúntes cuya edad se pudo estimar basada en peso y desgaste de dientes, fueron en su mayoría adultos maduros, y de ambos sexos.

El tamaño del 'home range' en tres grupos fue de 7.8, 7.8 y 10.0 hectáreas, respectivamente, con un amplitud de variabilidad correspondiente en el tamaño del grupo. Los mínimos y máximos dados a continuación fueron determinados durante el estudio: 13 a 5; 5 a 3; y 6 a 3 individuos. La sobreposición entre grupos contiguos fue de 20 a 30 por

ciento. La densidad basada en estos tres grupos tuvo una variabilidad de 0.3 a 1.8 tamarinos por hectárea.

Los patrones de movimiento, actividad diaria, cohesión de grupo y sus relaciones con otras especies se describen brevemente. Las características de 25 sitios para dormir se resumen. Estos sitios fueron a menudo reutilizados. La mayoría de ellos eran esencialmente árboles con gruesas ramas laterales, unos pocos fueron densas masas de ramas. La cantidad de cobertura presente fue altamente variable. Con la excepción de dos casos, todos los miembros de un grupo dormían juntos.

La alimentación consistió básicamente en frutos e insectos. Los frutos provenían de árboles, enredaderas y algunas epífitas. Con menor frecuencia fueron ingeridas hojas nuevas o yemas, hojas, tallos, y en un caso, una rana. Material no identificado fue recogido de algunas flores, valvas de ciertas frutas, ramas o troncos y de algunas porciones aéreas de ramas en descomposición.

La variación en el desgaste de las dientes, probablemente indica un espectro de edades entre los adultos de los grupos más grandes examinados (8 miembros). Sólo uno o un par de infantes o juveniles fue observado en algún grupo. De tal modo, los datos aquí presenta-

dos no son suficientes para decidir si los grupos pertenecen al tipo de familia extendida, hipotetizada por varios autores basados en trabajo de laboratorio (Epple, 1972b; Eisenberg, Muckenhirn and Rudran, 1972). No obstante, la hipótesis no predeciría los substanciales cambios en el tamaño y la composición del grupo observados en este estudio y algunos recientes tratando de otras especies de *Saguinus* (Dawson, 1976, 1977; Thorington, 1968; Durham and Durham, en imprenta; Castro and Soini, 1977; Izawa, 1976). Estudios a largo plazo en poblaciones marcadas son necesarias para completar el esquema parcial que tenemos ahora de la estructura social de estas especies.

El presente estado del hábitat de *Saguinus oedipus* es discutido en extensión con énfasis en el hecho de que las cifras otorgadas por los exportadores llevan fácilmente a errores con respecto a la abundancia de esta especie. El substancial agotamiento del hábitat que está ocurriendo actualmente es la mayor amenaza para la especie. Sólo a través del establecimiento inmediato de reservas protegidas puede asegurarse su supervivencia. A pesar de los problemas la singular riqueza de la fauna colombiana hace que esta medida sea valiosa de tomar.

Introduction

*Saguinus oedipus*², the cotton-top tamarin, was one of the first callitrichids to become well known in the United States. The proximity of its range to Barranquilla, Colombia's second major animal export center, ensured that this species early became one of the cheapest and most easily available New World primates for the North American pet and biomedical market. However, despite the large numbers that have been held in captivity, there have been relatively few studies of its basic biology. Some information is available on the following: reproductive behavior and physiology (J. K. Hampton et al., 1966, 1971; Epplé, 1967, 1970); general behavior (J. K. Hampton et al., 1966; Wendt, 1964); vocal repertoire (Epplé, 1968; Muckenhirn, 1967); scent marking behavior (Epplé, 1972a); skin and scent gland morphology (Wislocki, 1930; Perkins, 1969) and cytotaxonomy (DeBoer, 1974). Some of these topics have been treated for three other species of *Saguinus* in captivity: *S. geoffroyi* (Moynihan, 1970; Muckenhirn, 1967); *S. fuscicollis* (Epplé, 1970, 1971, 1972a, 1972b, 1977); and *S. midas* (Mallinson, 1971). Substantial information has accumulated on the maintenance and propagation of these species in captivity (Epplé, 1970; Lorenz, 1972; J. K. Hampton et al., 1966; S. H. Hampton and J. K. Hampton, 1967; S. H. Hampton et al., 1972).

Field observations of callitrichid species have been short-term or lacking, except for a one-year study of *Saguinus geoffroyi* (Dawson, 1976, 1977). Reports based on one to several weeks of field observation are available for the following species: *S. geoffroyi* (Moynihan, 1970; Muckenhirn, 1967); *S. midas* (Thorington, 1968; Durham and Durham, in press); *S. nigricollis* (Mazur and Baldwin, 1968—semi-natural conditions); *S. fuscicollis* (Izawa, 1975, 1976; Castro and Soini, 1977); *S. mystax* (Castro and Soini, 1977); *Cebuella pygmaea* (Ramírez et al., 1977; Izawa, 1975, 1976) and *Leontopithecus rosalia* (Coimbra-Filho, 1977; Coimbra-Filho and Mittermeier, 1973). Studies of free-ranging populations are completely lacking for the remaining 23 callitrichid species (cf., Napier and Napier, 1967), and for *Saguinus oedipus*.

This paper restricts itself to group characteristics, general aspects of the use of space and resources,

and relations with other species by cotton-top tamarins in a single study area, plus a review of problems concerning conservation of the species. Methods have been described in some detail because of their possible applicability to future field studies of callitrichids. Other results and conclusions from the study will be presented in subsequent publications.

Study Area

The study area was located about 15 km to the east-northeast of Tolú, Sucre, on the Caribbean coast of Colombia, at about 9°34'N, 75°27'W (Figure 1). It forms part of an alluvial plain at about 100 m elevation at that point, formed from the San Jacinto hills lying just to the east (560 m maximum altitude). The area appears level, but after a heavy rain the standing water can be seen flowing along the surface of the ground and the area drains rapidly into a network of gullies (*arroyos*), 3 m to 7 m deep and 5 m to 15 m wide which carry the water seaward.

Using the Holdridge classification, Espinal and Montenegro (1963) described the region as one capable of supporting "very dry tropical forests," with relatively low rainfall (500 mm to 1000 mm annually) distributed in a highly seasonal pattern. Between December and April when there is practically no precipitation, an estimated 60 percent of trees lose their leaves. During the heavy rainfall months of August through November, large areas of the forest become flooded. About 30 percent of the study area was flooded to three feet or less at the worst of a 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—has a marked effect in drying out the forest floor. During the dry season, the water found in *arroyos* is the sole water supply for the entire area.

The study area is in one of the larger remnant forests still existing in that part of Colombia (Figure 1), totaling about 600 hectares, and surrounded by pasture. It contains an essentially isolated population of *S. oedipus*, although some dispersal is possible via fence lines which connect to *arroyos* since both often are lined with trees. The study groups frequented the southeastern corner of the forest block (about 45 hectares) plus an adjoining strip of forest along a fence line and *arroyo* (about 7 hectares) (Figure 2).

Human exploitation of the forest probably dates

²Although Hershkovitz, 1966, suggested that the rufous-naped tamarin (*S. geoffroyi*) and cotton-top tamarin (*S. oedipus*) be considered subspecies of *Saguinus oedipus*, they will be considered as separate species in this paper in accordance with Hernandez and Cooper (1976).

HABITAT FOREST PRESENT IN *Saguinus o. oedipus* RANGE

LEGEND

- Primary forest limits in 1966¹
- ◼ Secondary forest (1966)¹
- ◼ Verified remaining forest (1974)²
- ⊙ Department capitals
- Other important cities
- + Present supply center *Saguinus o. oedipus*
- - - Limits of former *S. o. oedipus* range³
- ? Uninvestigated area

0 10 50 100
METERS

1- After "Mapa General de Bosques", Instituto Geografico
Agustin Codazzi, Dept. Agrológico, Vol. III No.2, 1967
Republic of Colombia. (1966)

2- Struhsaker et al., 1975

3- Southern limit of Andes foothills probably
less than 1000 m.

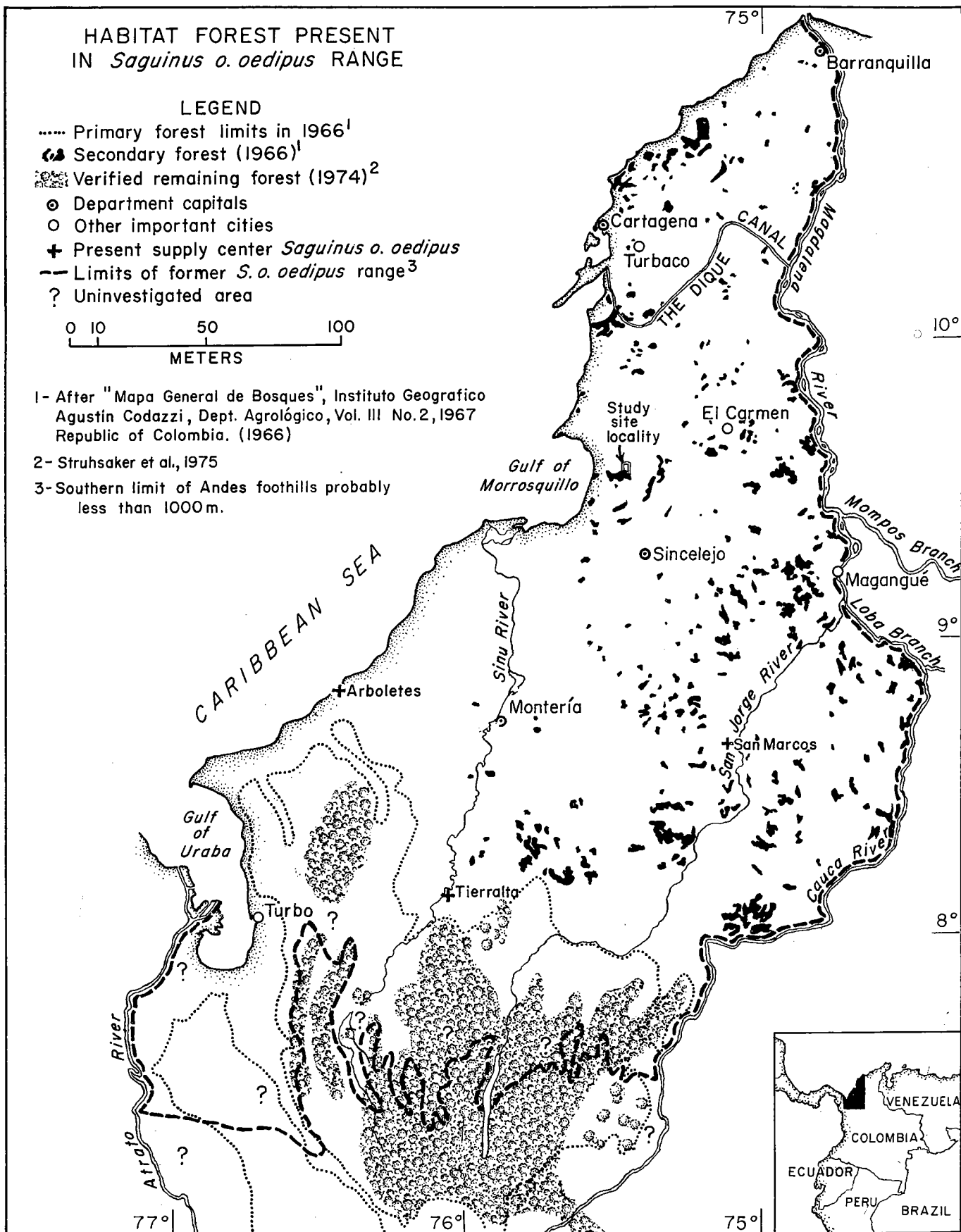


Figure 1. Location of study site and distribution of forest remaining in the original range of *Saguinus oedipus* (as given by Hernandez and Cooper, 1976). This is a composite showing 1966 forest limits together with 1974 aerial reconnaissance estimates of remaining forest in the southernmost section (Struhsaker et al., 1975). Part of the latter may be primary forest, but extensive clearcutting was already occurring there in 1966. Forest designated in 1966 as secondary is shown as black patches. Many of these may no longer exist.

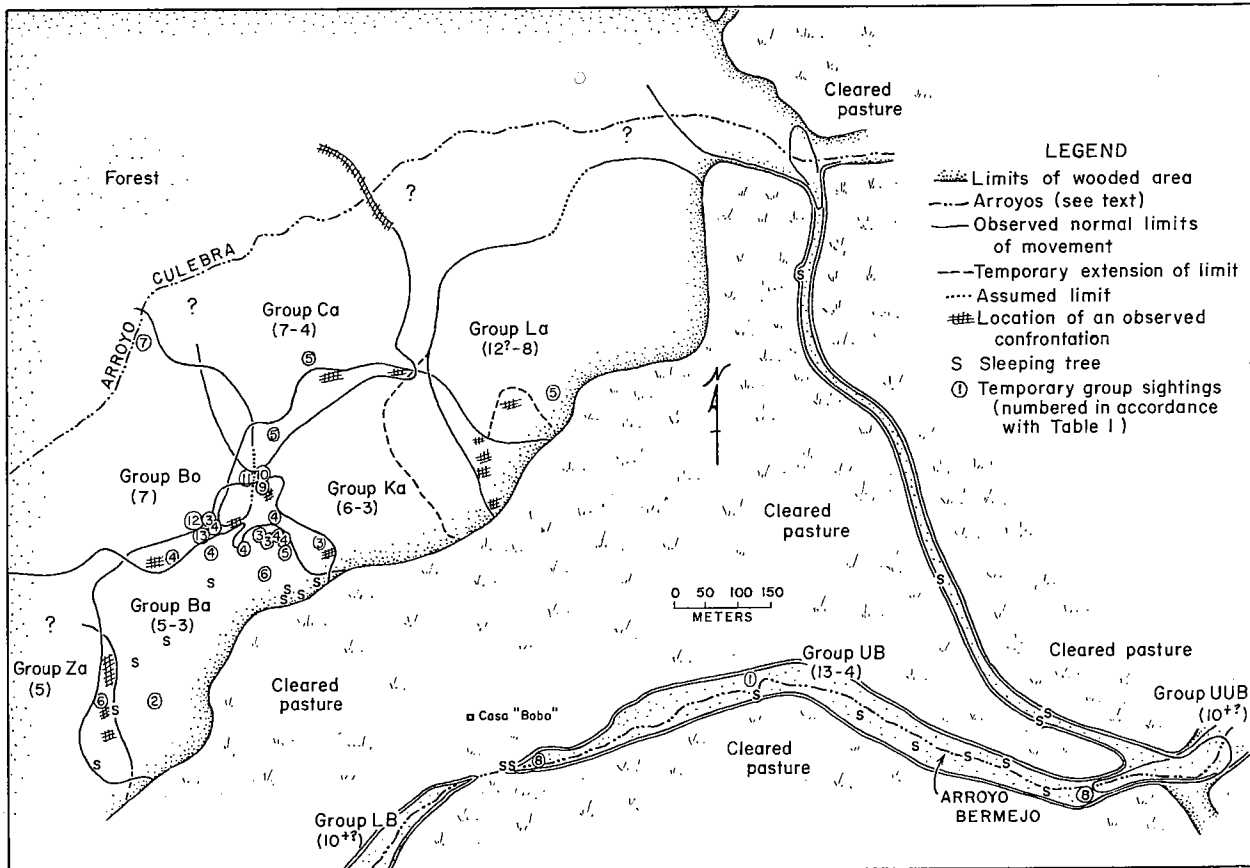


Figure 2. Map of main study area (see text). Surrounding areas are pasture, as indicated. Partial or complete limits of eight "established" groups in and adjacent to the study area are shown, together with observation locations of "transient" or temporary groups. The latter are numbered in accordance with Table 3. Sleeping trees for the Ba and UB groups are indicated. Maximum and minimum size of groups shown in parentheses. Hatched areas show points of inter-group encounters.

back to at least precolonial times, as Indian remains are common in nearby areas. The pastures are fairly recent in origin; those immediately adjoining the study area were cleared less than fifteen years ago. Exploitation of the forest is continuing. Middle-stratum trees are utilized for fence posts, corals, houses, and bridges. Also some selective cutting is occurring, chiefly for *Cedrela*, *Ceiba*, *Bombacopsis*, and *Lecythis*. Few usable large specimens of the first three species remain. Hunters also frequent the study area. As far as is known, the resident primates (*Alouatta seniculus*, *Cebus capucinus*, and *Aotus trivirgatus* in addition to *S. oedipus*) are not presently subject to hunting pressure; however, they are commonly chased when encountered in vulnerable places, such as on fence lines, on the ground, or in low vegetation. The notable shyness of *A. seniculus* suggests that they may have been molested in the past. They react to an observer by hiding, often sitting without moving for long periods, and attempting to sneak away. This contrasts with the typical alarm patterns which this species shows in other forests in northern Colombia (branch shaking, grunting, urination, and defecation).

Common easily recognizable tree species are those typical of secondary forests in northern Colombia: *Luehea* sp., *Bursera simaruba*, *Anacardium excelsum*, *Cavanillesia platanifolia*, *Pseudobombax septenatum*, *Cecropia* sp., *Inga* sp., *Spondias mombin*, *Pithecellobium saman*, *Lecythis magdalenica*, *Gustavia* sp., *Triplaris* sp., *Calycophyllum* sp., *Guazuma ulmifolia*, *Brosimum* sp., *Muntingia calabura*, *Swartzia* spp., *Garcia nutans*, *Sapium* sp., *Ormosia* sp., *Cas-searia* spp., *Mayna* sp., *Nectandra* sp., *Trichilia* sp., *Urera* sp., *Hybanthus prunifolius*, *Clavijsa* sp., *Picramnia* sp., *Randia* sp., *Panopsis* sp., *Quararibea* sp., and others including various species of palms (e.g., *Bactris* spp., *Astrocaryum* spp., and *Sabal* sp.) Much less common, but also present are: *Ceiba* spp., *Bombacopsis septenatum*, *Cedrela* sp., *Enterolobium cyclocarpum*, *Prioria copaifera*, *Fagara* sp., *Sterculia apetala*, *Cochlospermum* sp., and *Cordia alliodora*. In many places the forest floor is dominated by a very spiny palm which branches from ground level (tentatively identified as *Astrocaryum* sp.). In other areas, a mixture of saplings and low palms (cf., *Cryosophila* and *Heliconia* spp.) predominates. In places more recently cleared and therefore receiving more sun, the *Heliconia* may form dense stands to over 3 m in height. All areas can be penetrated with the aid of a machete, though not always at the speed necessary to maintain contact with a *Saguinus* group.

The relative scarcity of densely vined areas and the openness of the floor in most places suggest forest of some maturity. Nevertheless, the brokenness of the canopy is marked—only infrequently is travel possible for more than 50 m in any one direction at a height of over 15 m. Breaks in the canopy are due to both selective logging and tree falls occurring during seasonal high winds (September–November). In 1973 a high wind blew over so many trees in one section of the study area that a continuous canopy did not remain at any level. Also, the fall of one large tree always causes extensive damage to adjacent trees.

Methods

Between August 1973 and August 1975 about 750 contact hours were spent with free-ranging cotton-top tamarin groups. Total active field time was conservatively estimated at 2,500 hours.

Basic procedure consisted of searching for groups and following them until contact was lost. Success in following was greatest with one group (UB) which frequented the narrow forest strip of 7 hectares (Figure 2) and with those groups in which one member was marked with a bell (see below). Over half of the total contact time was spent with the UB group. The three most-studied groups (UB, Ka, Ba) became somewhat conditioned, but always showed nervousness if observed intently, especially if binoculars were used. Their disquiet could often be allayed by rapidly glancing away whenever they began to stare at me, but frequently attempts to observe them even from a distance of 20 m resulted in their moving to more hidden branches or leaving the area completely. Conditioning such small animals is complicated by the fact that the observer is constantly disappearing and reappearing in their visual field as they forage.

Minimal data were obtained on unmarked groups, as it was not possible to distinguish individuals (except in one case), 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 identify troops, was not helpful here. Tamarins cannot be sexed at a distance, and the rapid growth of juveniles renders them indistinguishable from adults after the age of about ten months if seen from a distance (unless adjacent). Group size was not a useful criterion either, as difficulties in detecting all members of moving groups often rendered group counts questionable. Marked ani-

mals were indispensable therefore for group and individual identification as well as for making complete group counts. Some individuals were always bolder than others and were seen repeatedly while others, particularly juveniles and adults carrying young, tended to hide.

The route followed by a group was crudely marked with a machete in order to follow or map its route later. An attempt was made to keep the noise 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 again.

The Trapping Program

The trapping program was initiated in January 1974 and the first animals marked in May 1974. National Live Traps similar to those successfully used by Dawson (1977) in the capture of *S. geoffroyi* and using the same bait (*Musa* sp.) proved ineffective. This was probably due to the greater variety of strata available for movement and the lack of predictable crossing routes reachable by climbing in this study area. 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 and measured 1 m × 1 m × 0.8 m



Plate 1a. Trap unit containing captured cotton-top tamarin (nearest) and decoy. Door is still set open in compartment opposite the captured individual. Protective wire mesh covering the decoy's half can be clearly seen.



Plate 1b. Cotton-top tamarin wearing collar and bell. This "jingle" type bell was not very satisfactory for localization purposes, despite its size (see text).



Plate 1c. Sleeping tree, *Lecythis magdalenica*, used by *S. oedipus* group. Sleeping site and animals are circled.



Plate 1d. Sleeping tree, *Pseudobombax septenatum*, with the site and animals circled. The cotton-tops are clearly visible.

(Plate 1a). The trap units were placed on poles tied between trees at a height of about 1 to 1.2 m, in an area with visibility from above (yet shaded from the midday sun) and where vines or trees provided easy access for approaching tamarins. A live decoy tamarin was maintained continually in the trap as an attractant, and nearby tamarins would respond to its calls and approach. There was usually only a few days' delay before catching the first animals if the trap was placed in an area where the resident group had recently been seen.

With these traps, 118 captures were made in a total of 1,016 trap-days (12 percent "success"). Fifty-three individuals were caught, 21 of which were recaptured one or more times (one enthusiastic tamarin was retrapped eight times and various others were recaptured four or five times).

Trap Design Problems

Visiting tamarins were often aggressive towards the decoy. In order to prevent injury, double walls or an extra layer of wire mesh were added to the decoy's section. 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 mesh floor was used at first, as it conveniently allowed excrement 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 with waste to a tolerable level and still protected it from outside attacks. Openings in the sides of the cage large enough for the visitors to reach in had to be eliminated; otherwise they could grab the decoy and draw it to within biting reach. Food and water were placed so that visitors could not reach or disturb it and fecal matter would not fall into it. One corner was provided with a shelf for sleeping and covered with plastic to provide protection from rain.

It was most convenient to manufacture the trap section of the unit separately from the decoy section to facilitate transportation to or through the forest

(by mule or foot). The trap section was subdivided (as in the complete unit) into two compartments (Plate 1a). On arrival at the trapping site a trap and decoy section were wired together. By adding a second and third trap section on top of the two original sections, the trap's capacity could be increased to a maximum of six compartments. Additional trap sections without an adjacent decoy were sometimes placed a few feet away.

Tamarins were captured in the latter despite being farther from a decoy, indicating that the bait (*Musa* sp., "platano") had an attractive effect. On the other hand, many captures were made in unbaited compartments adjacent to a decoy, indicating that the trap was entered during the course of interactions with the decoy.

Decoy Maintenance

Maintaining live decoy tamarins was difficult in a remote area with an irregular and scarce supply of fruit and protein. Obtaining food for them required frequent time-consuming trips to the nearest reliable supply of fruit and eggs, in this case a city some three hours travel one way. The lack of refrigeration limited the quantity of supplies that could be bought in any one trip.

Marking Methods

By drawing them into reach from outside the trap using the tail, captured animals were administered the anaesthetic "Ketalar" in the tail or thigh. They were fitted either with a leather collar about 0.8 cm wide wrapped with colored fiber-backed plastic tape in different color combinations and designs (Plate 1b), or with a light neck chain bearing a numbered tag (18 mm diameter). The tag was attached to the chain by a wire ring, which assured that the tag faced forward. The tamarins were measured, weighed, and examined for dental wear, signs of reproductive state, and external parasites. In some cases, a drop of blood was taken by a puncture in the heel of the forefoot. (The toes yielded no blood.) Most animals were released as soon as they recovered from anaesthesia but some were kept overnight or several nights and used as decoys to attract the remainder of their group, a tactic that was often successful.

Animals recaptured many months after marking were found to be in good condition. They showed no hair loss below their collars and generally the collars were undamaged. One captive, however, developed hair loss and lesions under a too-snug collar, although it exhibited 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 are probably preferable to collars since they appear more comfortable to the animal. Light-weight ordinary ball-link chain is suitable, providing the linking piece is crimped with pliers (uncrimped chains were opened in at least two cases.) The tags, however, can only be read when the wearer is stationary and facing the observer. The identity of an animal overhead could often not be ascertained because the face of the tag was not visible. On the other hand collar colors were sometimes difficult to distinguish. Yellow and white, red and orange, and green, blue and black may 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.

A third promising marking method (R. Cooper, pers. comm.) utilizes colored plastic beads (about 3/8-inch diameter) on a chain. These should be more comfortable for the animals than the collars while retaining the desired readability, providing nonconfusable colors are used. Also they may prove more durable, since leather and plastic tape could succumb to tropical heat and high humidity over a long period. Movement of the beads around the chain is simply prevented by placing a chain-link connector on either side of the group of beads.

One or two animals in each group were marked with a bell as an aid in following the group. The bells of lowest tone were the most easily localizable and carried furthest—the sound of the “jingle bell” type shown in Plate 1b did not carry far. The bell with the lowest tone doubled the range of detection (normally a maximum of 15 to 25 meters), and facilitated tracking without visual contact, as when a group entered a dense vine area, or when I fell behind. Nearly all bells were lost almost immediately, probably through continual twisting of the wire with which they were attached. Bells and attachment should be cast in one piece—an inserted or soldered wire is easily worked loose.

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.

Age Estimation

Three measures were taken as possible indices of age: weight, head and body length, and dental

state. Written descriptions of the teeth of captured individuals were fitted into two juvenile and four adult “dental age” categories, defined as follows:

- J1 Upper permanent canines not yet erupted
- J2 Upper permanent canines partly erupted
- A1 Fully grown permanent canines, very new white teeth with no visible wear
- A2 Slightly worn canines and incisors, teeth quite white
- A3 Canines and incisors moderately worn, teeth somewhat to quite discolored, tooth decay sometimes evident
- A4 Very worn canines and incisors, teeth very discolored, one or more canines frequently broken

Ease of examination and measurement dictated the focus on incisors and canines. These are rooted teeth and undoubtedly of great importance in feeding; there is no reason to suspect they would not wear according to age.

Molar eruption was not examined since all but one of the juveniles exhibited partly erupted permanent canines. Permanent canines in marmosets are too strikingly different from deciduous ones to be confused, and are probably the last permanent teeth to erupt, as in *Callithrix jacchus* and *S. nigricollis* (Johnston et al., 1970; Chase and Cooper, 1969). Tooth eruption sequences have never been published for *Saguinus oedipus*.

The juveniles captured were about ten to fourteen months old (Figures 3 and 4). They were still distinguishable from the adults by various nondental characters. Overall size and weight was smaller (Figures 3 and 4). Also they still retained the typically juvenile extra facial hair and had a shorter topknot than the adults (see photographs in S. H. Hampton and J. K. Hampton, 1967). Lastly, in the male, testicles measured only about 3 to 6 mm (as compared to 13 to 15 mm in the adults), and the circumgenital gland in the females was not developed. All A1 adults, however were indistinguishable from the other adult dental-age classes in these characters.

In Table 1 the “dental age structure” of various groups is presented. The interpretation of these findings is hindered by the lack of a known-age series of teeth with which to estimate actual ages. Apparently A1 and A2 embrace a growth phase, since seven of eight recaptured individuals from these categories showed a weight gain seemingly unseasonally related (Figure 3), and the two classes also were nonoverlapping with respect to weight in the expected direction. The A3 and A4 catego-

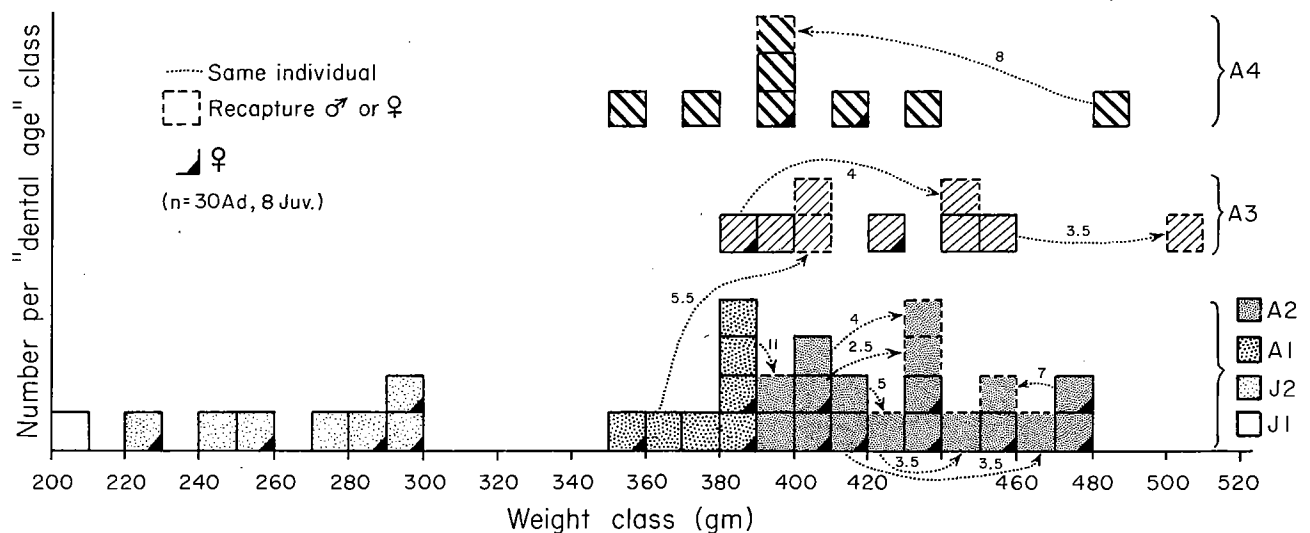


Figure 3. Weight distribution of individual *S. oedipus* in each "dental age" category (see text). Dotted lines connect different weights for a given individual; the

arrow shows direction of change. Figures beside arrows are approximate number of months between captures.

Table 1. Age-sex composition of six *S. oedipus* groups during the month indicated (1975).

"Dental Age" Class	Definition	La (Mar)		Ca (Mar)		Za (July)		Bo (Feb)		Ba (Jan)		Ka (Jan)	
		M	F	M	F	M	F	M	F	M	F	M	F
J1	Permanent canines not yet erupted	1											
J2	Permanent canines partially grown		1 ⁱ		1 ⁱ		2 ⁱ	1				1	1 ⁱ
A1	Teeth very white, sharp, no wear	2	1 ⁱ	1	1 ⁱ	1							
A2	Teeth white, barely noticeable wear		1 ^d				1 ^d			1	1 ⁱ		
A3	Definite wear, and discoloration			1	1 ^m	1		2	1 [*]	1			
A4	Very discolored— canines very worn/broken, incisors worn down	1	1 ^m	1								1	
A?	Teeth not examined							2	1		1 ⁱ	1	
	Juveniles	1	1		1		2	1				1	1
Subtotals:	Adults	3	3	3	2	2	1	4	2	2	2	2	
	Adults not captured				1								
Group totals		8		7		5		7		4		4	

Nipple-length designation

n—nipples undeveloped (nulliparous) (1/2–1 mm long)

i—intermediate development (1-1/2–2 mm)

d—well developed, possibly parous (3–4 mm)

m—maximal development, probably parous (5 mm)

(not all females were examined for this character)

Boldface individuals left group before August 1975.

*This female (Lo) had increased weight by 60 gm since 4 months previously, nipples had changed from i to m, and she "seemed fat." Possibly pregnant—twins seen in this group late in April.

ries overlapped both with each other and with the A1 and A2 categories. Longitudinal growth probably ceases or becomes too slight to detect at an earlier age than weight gain: there was no difference between the adult "dental-age" classes in head and body length distributions. A more repeatable length measure depending on fewer growing elements, such as knee-heel length, might be a more sensitive measure of growth.

Males and females were combined in Figure 3, as within dental-age class means showed no significant difference, due to the wide distribution and low number of values. The lack of sexual dimorphism in weight and body length (Figure 4) is evident at all ages. Nor was a sexual difference in canine length or breadth evident, as reported for *Callithrix jacchus* (Johnston et al., 1970).

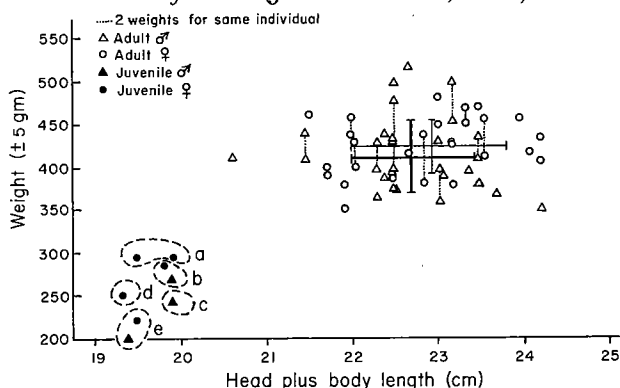


Figure 4. Relationship between weight and head and body length in *S. oedipus*. Cross arms are one standard deviation in length (heavy line = males, light line = females). Juveniles from differing groups are circled, "a-e." The birth date of pair "b" (Ka group) could be placed within an 11-day period: at the date of capture, they were nearly a year old (352-363 days). Pair "e" was known to be around 10 months old when captured (group La). The latter had considerable facial hair (see text), while the year-old ones had very little remaining. Pair "a" was about 13-14 months old (estimated by weight) and had extremely little, if any, extra facial hair, and their upper canines were almost the adult length (about 4½ mm—adults range 5 to 6 mm maximum).

Nipple length was taken on many females (Tables 1 and 3) as a possible means of distinguishing between parous and nulliparous adults. The nipples of parous females become more elongate (R. W. Cooper, pers. comm.). Whether some elongation may also occur at sexual maturity or in parous females who lose their young and do not suckle is not known.

In this sample, length ranged from 1/2 to 5 mm. The measurements fell into four classes (see legend for Table 1). The 5 mm class contained

only A3 and A4 females while the lowest (1/2 to 1 mm) group contained all the juveniles and A1 adults. Aside from this, there was no clear correlation with "dental age": A2 females occurred in all three lower classes and an A4 female occurred in the 3 to 4 mm class. One A3 female (Lo), moved from the 1-1/2 to 2 mm class to the 5 mm class in four months; on the latter occasion, she appeared pregnant (Table 1). Thus, some females can show seasonal (?) changes. There was a tendency for nipple color to darken with age (whitish or pinkish to dark); but a few had dark though small nipples (1/2 to 1 mm).

Results

Group Size and Composition

Groups frequenting established home ranges in or adjacent to the study area (hereinafter referred to as "established" groups) contained between three and thirteen individuals, including carried young (Table 2). Groups only temporarily present in the study area ("transient" groups) consisted of one to five individuals.

The age-sex composition of six groups is analyzed in Table 1. None of these (or any other group observed) contained more than two juveniles. Two to six adults were present, of both sexes, except in one group (and later also possibly a second) which lacked females. No more than three adults of a given "dental age" were present but not all ages were represented in every group. Five groups whose composition was known in early 1975 contained a total of 31 individuals: 6 juveniles about 6 to 10 months old (3 ♂♂, 3 ♀♀) and 25 adults (15 ♂♂, 9 ♀♀, 1 sex unknown). By the end of July the composition of a sixth group was known and the other groups had undergone changes. The six groups then contained 30 animals: 7 juveniles (3 ♂♂, 4 ♀♀) and 23 adults (15 ♂♂, 7 ♀♀, one sex unknown). The sex ratio among adults in these samples is insignificantly unbalanced in favor of males (1.8:1, omitting the one of unknown sex). The sex ratio among juveniles up to one year is about equal.

Various changes in composition were observed in "established" groups, despite the fact that they were followed in some cases for only a few months. These changes are summarized in Table 2 and Figure 5, but the Ka group's history may serve as an example. When first observed, this group consisted of three animals—two adult males and an adult female. It increased to five with the birth

Table 2. Size of "established" groups in the study area and adjacent areas, cause of changes therein, and known facts concerning individuals involved.

Group	Dates	Group size ¹		Cause for change in group size ⁵			Disappear	Death	Leave
		Begin	End	Born	Appearance	Reappear			
UB ⁶	8/72-8/75	13	5	4	?	?	11	1+?	?
Ka	3/73-8/75	3	4	2	1(MA4) ⁴		2(FA,MA)	?	
Ba	7/74-8/75	5	3		1(FA2)		1(J)	?	2(FA2,FA)
Bo	7/74-8/75	7	7? ⁷	2		2(2MA)			3(2MA)
Ca	2/75-8/75	7	4						3(FA3, FA1,FJ)
La	3/75-7/75	8	7? ⁸						

The following only observed one or a few times, as shown by dates:

La?² 3/74-4/74 Min.³ 12

Ua 5/73 Min. 8

7/74 Min. 9

7/75 4

Za 4/75 5

UUB 9/72 Min. 10

LB 10/72 10

4/75 6

F 8/72 Min. 8

¹Includes carried infants and juveniles;

²Unmarked group followed for over a month in the same area which the La group (marked later) occupied—could have been La group;

³Min. = minimum, the number actually verified; but due to visibility conditions, observer felt there was a relatively high probability that not all group members were seen. (Counts lacking "Min" felt to be complete);

⁴A = adult; J = juvenile, the numbers following A or J designation indicate "dental age" (as per Table 1) M = male; F = female;

⁵For category definitions, see text. Animal "disappearing" could have wandered into rest of woods (study area constituted only 52 hectares of a 600 hectare woods). This was suspected in cases of "disappearance" but was not differentiable from death. If the individual was observed at least once apart from its group, it was considered to have "left" its group;

⁶Uncertainties in UB group are due to its containing very few or no (most of study) marked members;

⁷Only one infant seen of two possible (3 mos. old), but both could well have been present;

⁸Bad visibility, 8th may well have been present.

of twins, and then to six by the addition of another adult male (Oa). When the twins were about six months old the female disappeared, followed soon afterward by one of the original males. Eight months later, at the end of the study (August 1975) the group still consisted of the same two adult males and two juveniles, then 17 months old. One other group (Ca) lost three of its seven members (all females) in the month after it was marked. Some groups maintained their numbers, however, during this same period. Four of the six established groups showed an overall decrease in size during the period observed (5 to 22 months depending on the group). The group whose size decreased most (UB) may have had some members captured by local people, since its home range was a narrow strip of woods flanking a well traveled footpath.

There was no reason, however, to suspect human interference of other groups.

Fluctuations in numbers prevented the calculation of an "average" group size, as any method of selecting data from the varying time periods that the different groups were under observations is arbitrary and does not give a sample from which a central tendency can be derived. Nor can data from study area groups be combined with that of unmarked infrequently observed peripheral groups (Table 2, lower half). Until more detailed data are available, it seems better to view cotton-top tamarin groups in terms of maximum and minimum size rather than average size.

Regular group splitting or coalescing such as reported for *Saguinus fuscicollis* (Castro and Soini, 1977), and *S. midas* (Thorington, 1968; Durham

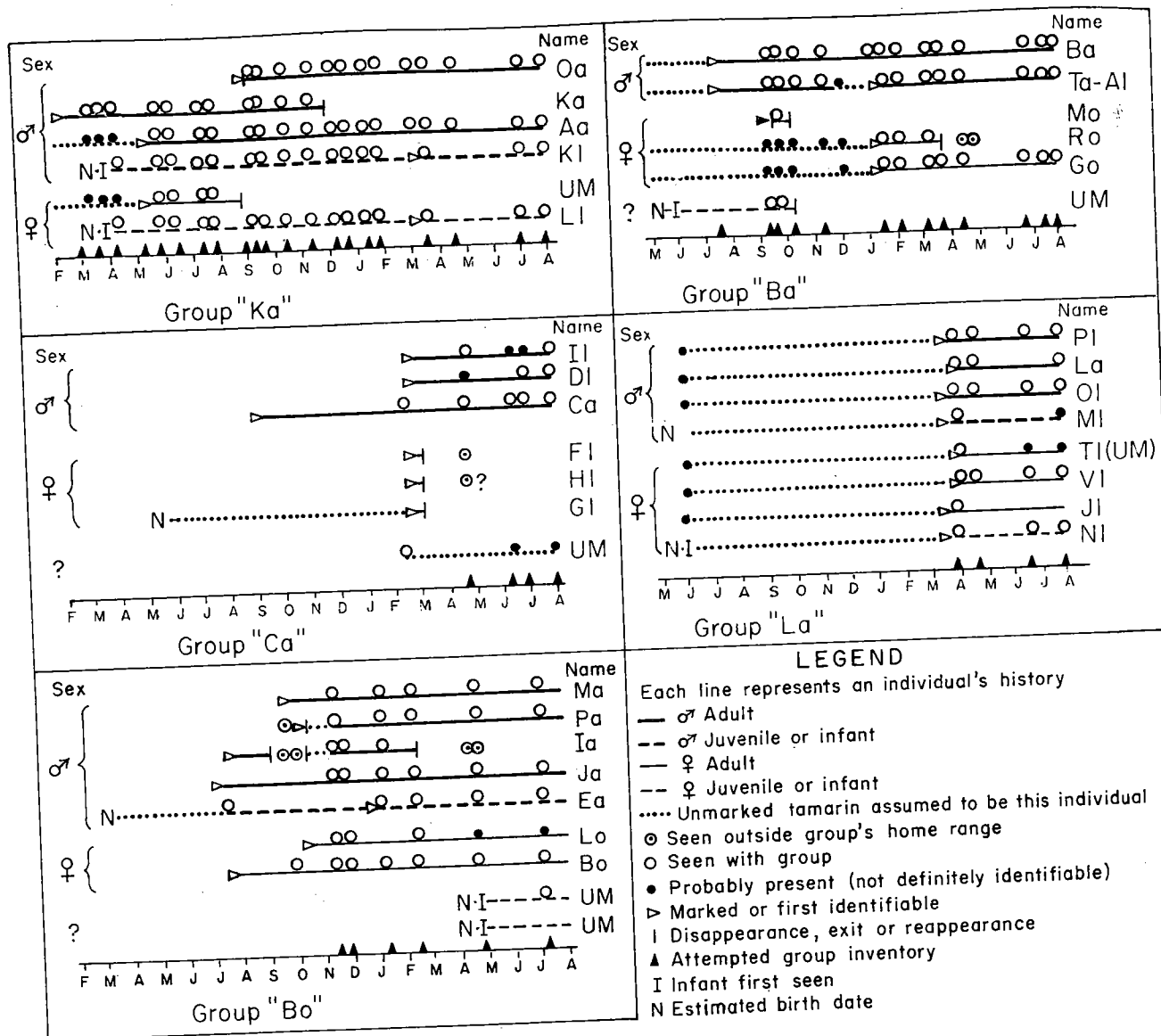


Figure 5. Changes in composition of five *Saguinus oedipus* groups over 5 to 18 months, ending in August 1975. Shaded triangles indicate those occasions on which a reasonably complete group count was obtained. Group size on those dates equals the total number of horizontal lines (solid, dotted, or dashed), each of which represents an individual's history in the group. Named individuals were all marked. UM = unmarked, (UM) = marking lost. In three groups (Ka, Ca, La) one adult remained unmarked. The Ka group UM individual must have been a female, since infants appeared and the other two group members were males. Infants and juveniles were assumed to remain with the same group, and so are figured as identifiable although unmarked.

and Durham, in press) did not occur in the established groups studied. In over 300 hours of contact with group UB, no instance of prolonged splitting or joining of subgroups was seen.³ Two cases of temporary splitting were observed. In both cases the separated subgroups exchanged contact vocali-

zations until one moved to join the other. Individuals separated from their group typically ran back and forth through the trees calling loudly ("Long Calls," Figure 6). When other group members vocalized in response such isolated animal(s) moved toward the source of the sound, and the exchange of calls ceased as soon as they rejoined the group. Thus, a certain group cohesion was evident, apparently reinforced by the tendency of separated individuals to find and rejoin their groups. Nevertheless, individuals did at times lag behind the rest of the group by several minutes. More important, some individuals were observed to leave their home groups. The most striking case was that in which an adult male previously seen with the Bo group

³The UB group numbered 13 when observations began in August 1972 and 7 in July 1973.

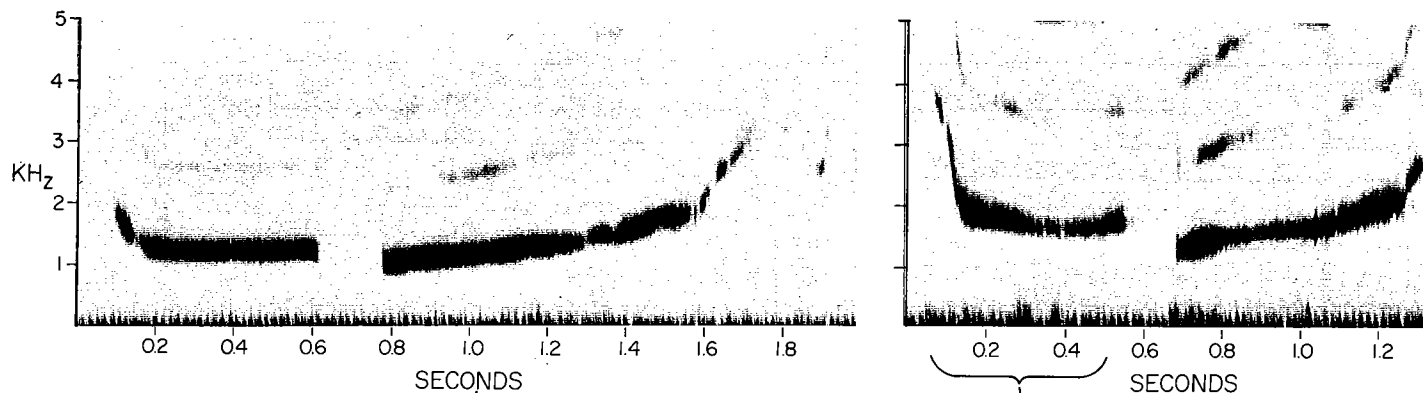
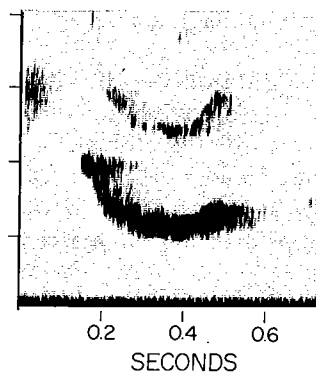
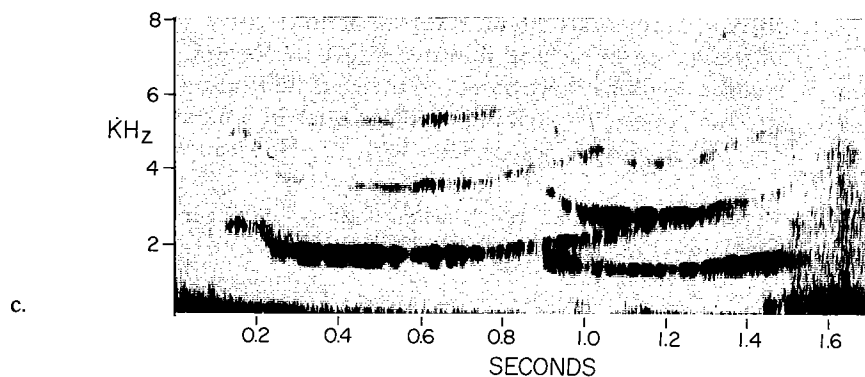
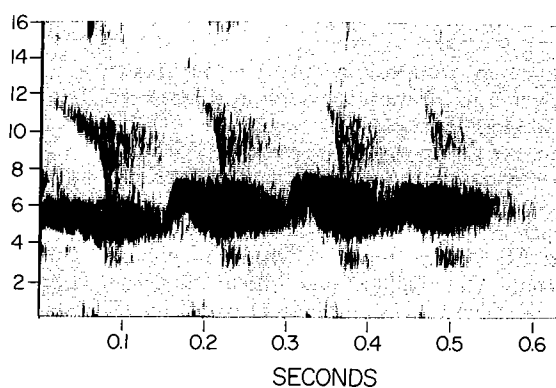
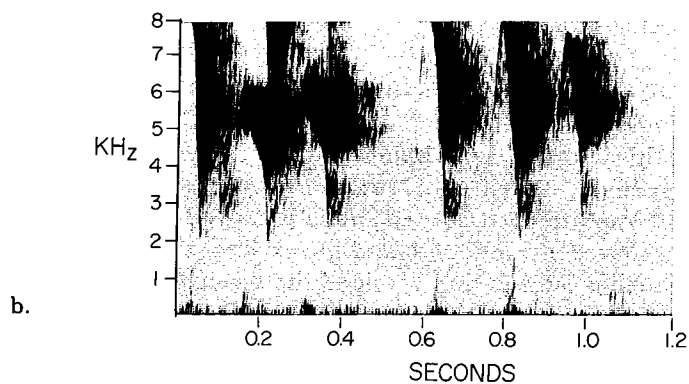
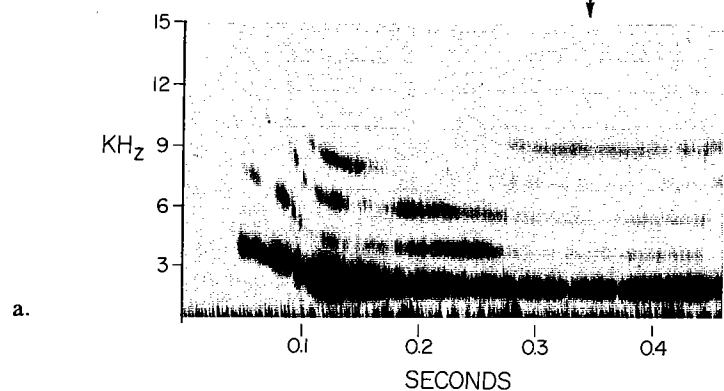


Figure 6. Sound spectrographs of three *S. oedipus* vocalizations. Recordings were from captive animals of unknown origin.

a. 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.

b. 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.

c. 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.



(Ia—Figure 5) along with a second male (Pa) formed a group with two females (Ho, Jo) which was seen at various times during a three-week period, usually near the edge of the neighboring (Ba) group's home range (Figure 2). The Ba group was twice observed chasing them vigorously during encounters. The two males joined the Bo group after three weeks, and the two females were later observed or trapped together several times elsewhere in the study area. The females were not seen during the last five months of the study. Some six months after the return of the two males to the Bo group one of them (Ia) was again observed outside of his group's area, this time with a female from the Ba group (Ro, Figure 2). These two were observed twice within a few days in the Ba group's

area, but not again during the remaining four months of the study. The second of the two males (Pa) was sighted during this period carrying a new infant in the Bo group.

The individuals involved in these cases were not "lost"; they were in or near the area frequented by their original group and probably could have rejoined it. This suggests that at least some "disappearances" (Table 2) of marked animals resulted from individuals choosing to leave the home group, possibly voluntarily.

For convenience, animals observed within "established" groups' home ranges but not part of the group have been designated as "transient" groups (Table 3, Figure 2). They were observed only once or a few times and contrasted with

Table 3: Summary of observed "transient" groups and characteristics of captured members.

Group Number ¹	Number of Individuals	Marked Ind. Present	Date	No. Times Seen	Sex	Weight (gm) ^{3,7}	Dental Age ²
1	1		7/73	1			A
2	4	Mo	9/18/74	1	F	470	A2, 3A
3	1	Mo	9/16,18/74	3	(above)		
4	4	Ia, Pa, Ho, Jo	9,10/74	many	M M F F	430 400 430 450 ⁿ	A A2 A A2
5	2	So ⁴ Jo	2,3/75	4	F (above)	400 ⁿ	A2
6	2	Ro, Ia	4/75	2	F M	420 ⁱ 430 ⁱ	A A
7	2(3?) ⁵	F1, H1, (G1)	4/75	1	F F F	420 ^m 380 ⁿ 250 ⁿ	A3 A1 J2
8	5	Au, Bu, Cu, Eu	7/75	various	F M M F	455 350 395 435 ⁱ	A2 A4 A3 A2
9	2		7/13/74	1	M ⁶		
10	2	Jo	7/24/74	1	(above)		
11	2	Yo To	7/18/74	1	F F	430 ^m 480 ⁿ	A A
12	2	Yo No	9/20/74- 9/24/74	3	(above) F	390 ⁿ	A
13	1	Wa	9/11/74	1	M	430	A4

¹Keyed to Figure 2.

²A, adult, J, juvenile, dental age categories as in Table 1.

³Weight to nearest 10 gm;

⁴Probably same individual as Ho;

⁵The third individual not seen, but disappeared at same time from Group Ca;

⁶Escaped before marked;

⁷Letters in this column indicate nipple length (Table 1).

"established" groups in lack of attachment to a specific area. One of the females (Jo) which formed the group with Ia and Pa, for example (above), was captured or observed in the territories of several groups (Table 3, Figure 2). The aggression toward transient groups typically shown by "established" groups has already been mentioned. One "transient" group of five (Table 3, number 8) first was seen near the end of the study at the tip of the UB group's home range. Three of four captured individuals from that group had fresh slash wounds which probably resulted from fighting. These were the only animals ever caught with wounds. The injuries could have resulted from the aggression of resident animals. The limited extent of the woods in that area and its conformation—a strip—(Figure 2) would 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 her 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 other case, that of Oa and the Ka group has already been discussed in the summary of the Ka group's history. I did not observe Oa joining the group, but he remained with it until the end of the study nearly a year later, while two of the original three adults present left.⁴ The ability of the above-de-

⁴Such turnover makes the use of the term "established" in reference to these groups dubious; it may well become more dubious as further investigation reveals more complications. For the present, however, the term serves to emphasize the cohesion of these groups and their attachment to a specific area despite the turnover observed.

scribed animals to join "established" groups without apparent aggression contrasts with the reception normally accorded to extra-group individuals both in this study and in captivity. That immigration and emigration may be normal in wild populations is supported by Dawson's observations of *S. geoffroyi* in Panama (Dawson, 1976, 1977). Only the long term study of marked animals can ascertain whether individuals which enter "established" groups without aggression are related to members of those groups.

The summary of "transient" groups (Table 3) includes all extra-group individuals observed subsequent to the initiation of marking, together with weight, "dental age," and nipple length where known. Of a total of 23 individuals observed, 22 were adults, 11 of which were examined. There was a strong skew in the sex ratio, 4 males: 7 females. The majority of females (4 of the 7) fell into the A2 category, with one additional individual in each of the other three adult categories. Judging by nipple condition, two parous females were included. The males were distributed only in the A2 (1), A3 (1), and A4 (2) categories. It appears from this small sample that older males are more prone to become transients, while females of any age may become transients, including parous and so presumably dominant females. These data include adults which "left" but not those which "disappeared" from their groups (Table 2) among which one other parous female is included.

Home Range and Density

Data concerning home-range size, overlap, density, and daily travel for the three best known groups are shown in Table 4. The observed movements of groups (Figure 7) leave no doubt as to the site attachments of "established" groups. Boundaries remained predictable despite changes in group composition, but extensions of both Ka group and possibly the La group were seen into neighboring areas.

Due to changes, group size and density are best expressed in terms of maxima and minima. For the three best known groups, sizes were: UB (13 to 4), Ka (6 to 3) and Ba (5 to 3), with corresponding home ranges of 7.8, 7.8, and 10.0 hectares. Including only half of the overlap area (20 to 30 percent of the home range), the density for these groups was between 0.3 and 1.8 individuals per hectare.

Relations Between "Established" Groups

Nothing resembling the morning calling between groups of *S. midas* (Thorington, 1968) was noted

Table 4. Group-size maxima and minima, estimated home range, shared area, density, and daily travel distance of three *Saguinus oedipus* groups.

Group	Group Size	Home Range ¹ (Hectares)	Shared Portion (Ha) %		Density ² Individ/Ha Max Min		Path length ³ Km/day M/hr	
UB	13-5	7.8	1.6	20	1.8	0.7	1.5-1.9	120-140
Ka	6-3	10.0	2.5	25	0.7	0.3		
Ba	5-3	7.8	2.1	27	0.7	0.4		

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

¹As shown in Figure 2.

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

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

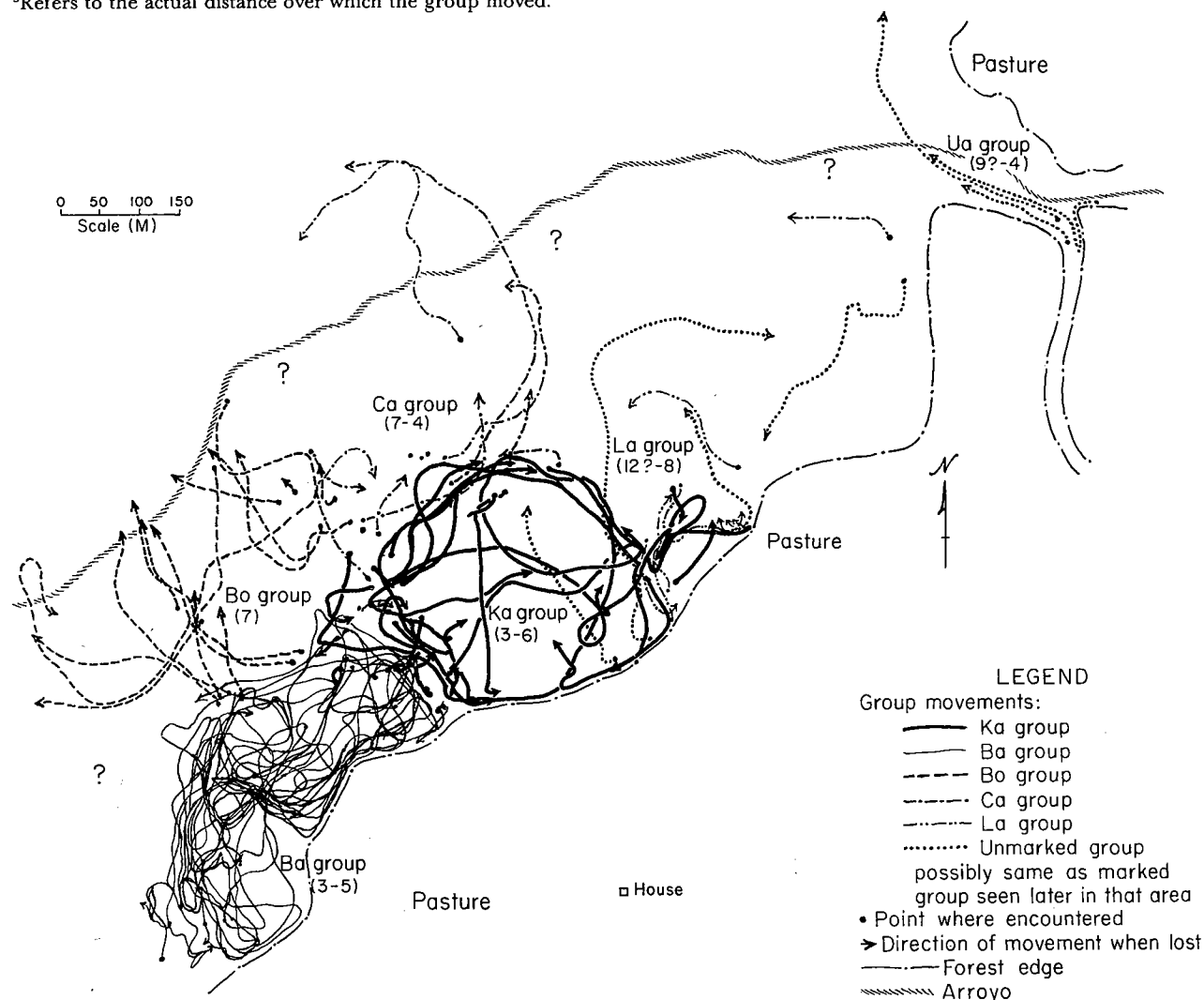


Figure 7. Map of major study area, showing routes taken by followed groups. Home-range outlines in Figure

2 were based mainly on these data, supplemented by point localizations of marked groups.

in this species. Contact between neighboring groups occurred at irregular intervals about once every few days. Chasing, occasional grappling, and approach and staring at the other group from a

distance were common during encounters, as was the "Rasp" (Table 5), a vocalization often associated with chasing or grappling. Encounters usually occurred near home-range boundaries in the over-

lap area and terminated gradually with the two groups drifting apart toward their own area. On one occasion, the two groups moved simultaneously along the presumed boundary for about 230 m before separating (Figure 2). Once when the Ka group had intruded over 45 m farther than the norm for the preceding months into the La group's area, they retreated precipitously on appearance of that group to within the more usual limits of their movements, suggesting the existence of a mutually recognized boundary. In addition, repeated observations of agonistic interactions between neighboring groups at boundary areas suggest that *Saguinus oedipus* is territorial in the sense

Table 5. 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

¹As per Moynihan, 1970 (*Saguinus (oedipus) Geoffroyi*).

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

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

of exclusion by aggression at definable boundaries. On several occasions, however, two groups were within auditory range near a boundary area, but did not exchange calls or move into visual contact. Occasionally, groups were observed to reverse or change direction of movement, apparently to purposely avoid an encounter.

Aside from agonistic behavior and "Rasps," the most striking feature of an encounter is the greatly increased incidence (Table 5) of clear whistle-like vocalizations of two basic types. The "Dip" is given singly, is about one second long, and first decreases in pitch then rises immediately and smoothly (Figure 6c). The second is a call of up to several seconds duration ("Long Call") (Figure 6a), consisting of one to six syllables separated by definite breaks. Two and three syllables are most common in the "Long Call." Often the first indication I had that a group encounter was beginning was the alternation of "Long Calls" from the two groups often in not quite synchronous "choruses" as though one member's beginning a "Long Call" stimulated the

others to vocalize. During encounters, some individuals are engaged in chases while others are immobile, emitting frequent "Dips" and "Long Calls." These same calls also are used to maintain or regain group contact in situations not involving intergroup encounters (see following section).

In the few encounters which involved marked animals, the most obvious participants were males. They were seen chasing, feinting, and grappling. Females, however, were difficult to localize. Either they did not attract attention because they remained relatively motionless or their movements more often carried them out of my sight.

There was always much movement during encounters. Often I could only follow events by the vocalizations. "Rasps" suggesting close contact were heard over a wide area up to about 40 m², implying considerable mixing of individuals in space and also possibly that eventual separation does not primarily depend on visual recognition, but may require close proximity and perhaps olfactory contact.

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. Adults were sometimes observed foraging during confrontations. Juveniles and infants definitely stayed or were kept out of the area of conflict. Once the Ka group left their twins of about two months (semi-independent) in a tree just out of sight of a trap which contained a decoy that 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. 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 action. When these infants were about a year old and fully independent, they remained relatively immobile during an intergroup encounter while the adults ranged well out of sight. Nonparticipants were not exclusively juveniles, however, since the adult female of the Ba group was once sighted some 25 m from an interaction, foraging quietly, while the males were involved in chases.

Movement Patterns and Daily Routine

Cotton-top tamarins move through the trees using mainly a quadrupedal gait, at times jumping from one vertical support to another. Bridging of gaps, typical of howlers and spider monkeys, was not observed. Instead, gaps are traversed by jumping. Landing surfaces may be branch-end masses of

foliage and all sizes of branches or vines. The tamarins often jumped onto single branches no more than 1 cm in diameter and crossed open spaces on vines of similar dimension. Travel routes occasionally incorporated palms (although not in proportion to their abundance in this forest), including the spineless top surface of the very spiny *Astrocaryum*, but only when other movement routes were restricted. They never foraged in palms.

Animals were observed to fall eight times. Twice intruders fell while being chased by residents, but the actions were so abrupt and in such unlikely places as to seem deliberately evasive rather than accidental. Both animals moved along the ground after dropping, and were not followed by their pursuers. In a third case, one of two grappling animals fell and caught itself on vegetation below. Twice adults fell to the ground while traveling 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 one and one-half and two 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 being carried by a group member the following day; however, there were two young in the group at the time, so identification could not be certain. The juvenile 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.

Like *S. geoffroyi* (Moynihan, 1970), the cotton-top tamarin begins moving and feeding relatively late in the morning compared to most primates—up to an hour and twenty minutes after dawn (0550 to 0650). Observations of animals lifting heads and stretching indicate that the tamarins are awake before movement begins, at which time they all immediately leave the tree in quick succession.

A foraging group may spread out over an area up to 35 m or more in diameter. Certainly, they frequently lose visual contact. "Dips" and "Long Calls" (or parts thereof) (Figure 6) were sometimes emitted during foraging, but their frequency and the incidence of "answering" varied. While individuals followed devious paths, the group as a whole traveled in a seemingly definite direction and tended to repeat previous routes.⁵ There was no obvious leader in either of the two best studied marked groups (Ka and Ba). Routes were apparently dictated by custom or location of cur-

rently available fruits. Trees in fruit were sometimes visited daily or more than once a day. Nevertheless, the home range was fairly well covered in the course of a few days (Figure 7 shows typical patterns of movement). The rate of movement (UB and Ba groups) varied between 0.12 and 0.24 km per hour, and total daily path length was between 1.5 and 1.9 km.

After about 0730 hours, the monkeys began taking short rests, often of only a few minutes, during which they lay along a wide branch with the legs hanging down or tucked under, or engaged in allogrooming. Occasionally, they rested in dense vine entanglements. Individuals lay alone or in pairs or trios within a few feet of each other or groomed in changing combinations. 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. Inactive periods of 30 to 60 minutes occurred as early as 0900 (in the sun) while the longest rests, occasionally up to two hours, occurred around midday (in the shade).

Around 1630 hours, the behavior of the tamarins acquired a characteristic pattern: the group became more cohesive and often traveled quickly and quietly, though foraging still sometimes occurred. Vocalizations were noticeably subdued. The group often appeared to be trying to get away from me. If they saw me near a sleeping tree as they approached it, they would not enter but continued traveling (see Figure 8). This behavior was effective in "losing" me and may function similarly with predators. When the animals were apparently unaware of me, they would gradually approach the sleeping site and forage sporadically near it for about an hour, often sitting quietly and looking around (a normal foraging component) for long periods between progressions. Then, one by one, they would enter the tree.

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. Foraging, however, was individualistic. There was no food announcement vocalization, or other means of advertizing a favorable food source, except in one possible case. On this occasion, a juvenile spotted a favored and scarce food (*Her-*

⁵Routes were to some extent influenced by the irregular nature of the middle and upper strata (see section on Study Area).

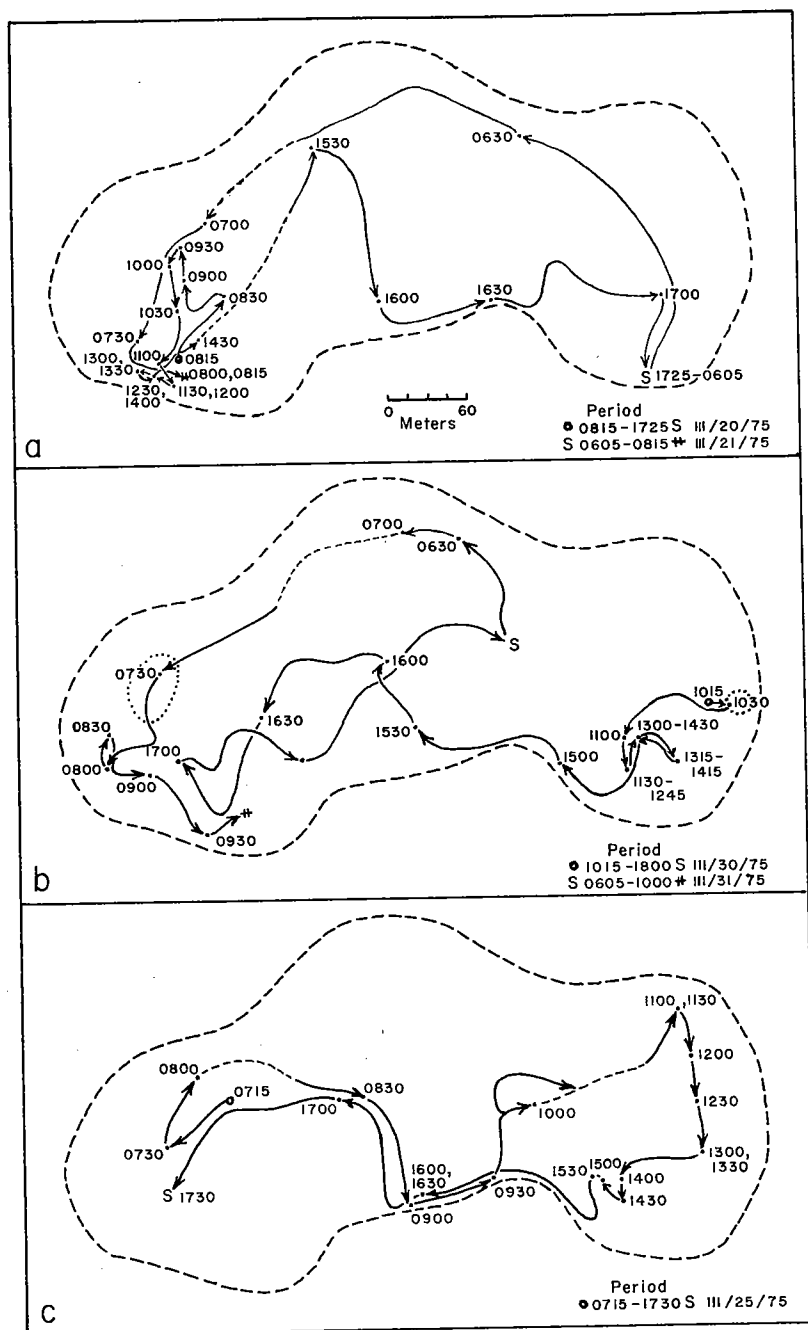


Figure 8. Typical movement patterns of the Ba group within its home range. In a and b the group was picked up during the morning (o), followed to its sleeping tree (S), and picked up the next morning as it left the tree. Dotted circles enclose the approximate area of an encounter with a neighboring group. At 1700 hours on b, the group was headed toward a sleeping tree, but they immediately changed direction when they saw me near it and passed two other previously used trees before settling at dusk in a thickly vine-covered tree.

rania sp.) but hesitated to approach due to my presence, particularly as the height of the tree was only about 1.5 m. Meanwhile, the other group

members had left the vicinity. The juvenile then uttered a long series of distinct loud chirps upon which the group immediately returned and approached the food. The frequency of "Rasp" vocalizations was noticeably greater around favored foods, especially in trees where fruits were few in number, large, and sparsely distributed.

Sleeping Habits

Between 1630 hours and 1830 hours a tamarin group entered one of various sleeping trees in its home range (Figure 2). Over a period of about 18 months, the UB group was traced 32 times to a sleeping tree, accounting for 14 different trees. The Ba group was traced to a sleeping site 13 times over a 5-month period, and a total of 9 trees were used. The 25 different sleeping spots used in these and other trees identified over the course of the study were of four types:

	Group		
	Ba	UB	Other
1. Broad tree branch near trunk or wide main fork (at 10-22 m) (Plate 1c, 1d)	3	13	2
2. Among bases of grown-out leafy branches of broken-off tree (at 13-20 m)	4	—	—
3. Low trees with dense crown (at 3-7 m)	1	2	—
4. End branch among dense vine mass (at 17 m)	—	1	—

Group location was verified by observations on the following morning, except for the latter two categories. The greater proportion of category 1 sleeping sites used by the UB troop is probably due to the greater relative frequency of tall broad-branched trees in their home range.

In some sleeping sites, very little cover was present and the animals were visible from the ground (Plate 1c, 1d), while in others they were largely or completely hidden by leafy branches or vines. In a few cases, I was not able to determine exactly where in the tree they were.

Certain species of trees were favored as sleeping sites: *Lecythis magdalenica* (9 sites), *Ceiba* sp. (1 often used site), and *Pseudobombax septenatum* (3 sites). Also used were *Prioria copaifera*, *Spondias mombin* and *Samanea samanea*.

In all but two cases, the entire group slept together. Splitting was seen twice in the UB group when it had 13 and 10 members and thus may have been related to limited space, rather than social factors. 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 (*Lecythis magdalenica*) while the tamarins settled in two crotches close to the trunk.

The use of a hole in a tree for sleeping was not observed, in contrast to the habits of *Leontopithecus rosalia* (Coimbra-Filho, 1977).

Food Habits

Cotton-top tamarins were observed eating fruits of trees, vines and epiphytes, insects, newly sprouting leaves or buds, leaves, leaf stems, and in one case a frog. They may also lick nectar or gather pollen or insects from certain flowers or fruits. They extracted unidentifiable material from the surfaces of the branches and trunk of some trees by pressing the mouth to the surface and possibly pulling. In some trees the same sites were visited by a succession of individuals. Such spots were frequently but not always decaying. It was not possible to ascertain whether insects or perhaps sap or resin was taken. *Cebuella pygmaea* and *S. fuscicollis* have been observed to utilize sap and resin (respectively) as a food resource (Ramirez et al., 1977; Izawa, 1975, 1976), so the latter possibility cannot be dismissed. In one case, caterpillars were found on the trunk surface at about 2 m suggesting that these, if present on higher parts of the tree also, could have been the prey.

Known genera and species of trees, vines, and epiphytes which were eaten are summarized in Table 6. It was not possible to determine what proportion of the diet each type of food represents, since both insects or small fruits may be taken during long periods when the monkeys are foraging in dense vegetation. Also, some flowers and fruits are not eaten, but may be visited for their pollen or nectar, or for the insects they attract (Table 6). This was suspected when the monkeys visited different fruits or flowers of a species, contacting them with their mouth but apparently removing no part of them (for example the fruits of *Pithecellobium saman* or *Sterculia apetala* which seem too woody to be edible). Vegetative parts usually constituted a minor proportion of the diet. They are most important during the December to April/May dry season when fruit is less available and trees are flowering and leafing out.

The tamarins were observed foraging and feeding on the ground (fallen guava of *Psidium guajava* fruits) and in all strata, although the majority of food trees species identified were middle-canopy (5 m to 15 m) species (see Table 7).

A group was observed licking water from leaf

surfaces after a rain. Tamarins were not seen to come to the ground for water or other resources, such as minerals, as Izawa observed (1975) in *Ateles belzebuth* and *Alouatta seniculus* in the Amazon.

Interspecific Relations

Cotton-top tamarins clearly compete in this forest with squirrels (*Sciurus granatensis*), other diurnal primate species (*Cebus capucinus* and *Alouatta seniculus*) and various birds, as evidenced by repeated observations of overlap in food habits. Many nocturnal species might also be competing including *Aotus trivirgatus*, *Didelphis marsupialis*, *Marmosa cinerea*, *Caluromys* sp. and other fruit- and insect-eating species, including bats.

Only three cases of aggressive interspecific interactions were noted:

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

Other interspecific contacts observed were neutral. In particular, both squirrels and howler monkeys fed in the same tree with *Saguinus* without interacting. No polyspecific feeding associations between the tamarins and either *Alouatta* or *Cebus* were observed as described for various other South American primate species (Klein and Klein, 1973; Castro and Soini, 1977). In fact, two primate species were rarely seen within 100 feet 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).

Important predators could be arboreal or aerial, and the tamarins used different alarm vocalizations for the two. *Eira barbara*, a mustelid with marked arboreal tendencies reported to prey on *Saguinus geoffroyi* (Dawson, 1976), was sighted seven times near tamarin groups, usually at a distance greater than 35 m, either on the ground or in the trees. In one instance, an *Eira* began feeding in the same

Table 6. Some plant food sources utilized by *Saguinus oedipus*.

Family	Species	Type		Local Name	List Number
Anacardiaceae	<i>Anacardium excelsum</i>	Th	F	Caracolí	27
	<i>Spondias mombin</i>	Tmh	F	Hobo	18
Anonaceae		Tm	F	Yaya	1
Apocynaceae		Tlm	F	Tomate del Monte	46
Araceae	<i>Monstera pertusa</i>	E	F		25
Bignoniaceae	<i>Bignonia</i> sp.	V	(F1)		21
Bombacaceae	<i>Cavanillesia platanifolia</i>	Th	(F1)	Volandero	21
	<i>Quararibea</i> sp.	Th	F	Palo de Leon	3
Boraginaceae	<i>Tournifortia</i> sp.	V	F		36
Capparidaceae	<i>Capparis</i> sp.	Tl	F		29
Elaeocarpaceae	<i>Muntingia calabura</i>	Tlm	F	Niguito	2
Flacourtiaceae	<i>Casearia</i> sp.	Tm	F		48
	<i>Casearia</i> sp.	Tm	F		56
	<i>Mayna</i> sp.	Tm	F		52
	<i>Hasseltia floribunda</i>	Tm	F		51
		Tm	F		59
Guttiferae		Tm	F		12
Leguminosae	<i>Inga punctata</i>	Tm	F	Guamo	16
	<i>Pithecellobium saman</i>	Th	(F)	Campano	37
Malpighiaceae		Tl	F		30
Marantaceae		V	F		43
Meliaceae	<i>Trichilia</i> sp.	Tm	F	Mangle	47
Moraceae	<i>Brosimum</i> sp.	Tm	F,Fl	Caucho	8
	<i>Cecropia</i> sp.	Tm	F	Guarumo	34
	<i>Ficus palmicida</i>	V	F	Abrazopalo	10
	<i>Ficus</i> sp.	Th	F		13
	<i>Ficus</i> sp.	Th	F		13c
	<i>Ficus</i> sp.	Th	F		13d
	<i>Ficus</i> sp.	Tm	F		31
	<i>Ficus</i> sp.	Tm	F		39
Myrsinaceae	<i>Ardisia</i> sp.	Tm	F	Corosita	45
	<i>Stylogyne turbacensis</i>	Tlm	F	Pie Paloma	35
Myrtaceae	<i>Psidium guajava</i>	Tm	F	Guayabo del Monte	17
Phytolacaceae	<i>Trichostigma octandrum</i>	V	F		44
Piperaceae	<i>Piper</i> sp.	Tl	F		23
Rosaceae	<i>Hirtella</i> sp.	Tm	F		4
Rubiaceae		Tm	F	Loma de Caiman	57
		Tm	F		*
	<i>Melicoccus bijugus</i>	Tm	F	Mamón	49
	<i>Talisia oliviformis</i>	Tm	F	Mamón del Monte	85
	<i>Paullina</i> sp.	V	F		50
Sapotaceae	<i>Serjania</i> sp.	V	F		R
Sterculiaceae	<i>Chrysophyllum</i> sp.	Tm	F	Caimito Morado	28
	<i>Guazuma ulmifolia</i>	Tm	F		42
Ulmaceae	<i>Herrania</i> sp.	Tl	F	Cacao	60
	<i>Sterculia apetala</i>	Th	(F)	Camajón	7
	<i>Zizyphus</i> sp.	V	F		32
Urticaceae		Tm	F		26
Verbenaceae	<i>Cytanexilum</i> sp.	Tm	F		9
Unidentified		Tm	F		14
		Tl	F		24
		Th	F	Manao	53
		Tm	F	Mangle	54
		Tm	F		58
		V	F		38

Key: T, tree; V, vine; E, epiphyte; l, low (0-5m); m, medium (5-15m); h, high (over 15m); F, fruit eaten; Fl, flowers eaten; (F1)(F), visited flowers or fruit but could not verify consumption; R, reported to me by a reliable source; *, at Los Borrachos site. Identifications supplied by Dr. Jesus Idrobo B., Herbario Nacional, Universidad Nacional, Bogotá, Colombia.

Table 7. Heights of food-resource tree species shown in Table 6.

Food Item Type and stratum(a)	Number of Species	Proportion (of tree species used)
Low (height 5 m and below) tree	5	.11
Low and medium tree	3	.07
Medium (5-15 m) tree	27	.60
Medium and high tree	1	.02
High (over 15 m) tree	9	.20
Epiphyte	1	
Vine	10	

large fig tree as the tamarins. The tamarins always reacted with extended series of piercing elongate calls falling in tone mnemonically described by the word "Thew" (Figure 6b) (possibly equivalent to the "Loud Sharp Notes" of *S. geoffroyi* described by Moynihan, 1970) mixed with loud chirps in varying combinations. The *Eira* appeared to ignore them completely. The same vocalization was elicited by two other potential terrestrial predators, humans and dogs. Vocalizing individuals would stop frequently and look around at or for other group members. As in *S. geoffroyi* (Moynihan, 1970), this type of alarm response tended to be contagious; however, only group members in the immediate vicinity responded while those out of sight usually continued foraging.⁶

Birds flying overhead elicit a series of 5 to 10 loud short chirps, "Chirp Burst," possibly similar to the components of the "Short Whine" of *S. geoffroyi* (Moynihan, 1970), but never repeated. The reaction is commonly although not invariably

⁶During 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 of 10 or 12 during such an alarm (or even after hours of following) except under unusual conditions where there was very open vegetation. With smaller groups invariably one or two individuals were missed. Since a group often renews the alarm response 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 too low, because group counts are often made under such conditions.

Table 8. 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

given to hawks (Table 8). Once a hawk has alighted, even if relatively close to the group (e.g., in one instance, 3 m away) no further alarm is given until it flies again, when the alarm is usually repeated, even if the hawk is only changing perches. An unsuccessful predation attempt on *Saguinus* by a hawk was seen.

Discussion

J. K. Hampton et al. (1966), Epplé (1972b, 1975), Eisenberg et al. (1972), and Moynihan (1976) have hypothesized that the basic social unit of callitrichids in the wild is probably the extended family group. The term "family group" here means a nuclear family, an adult pair with one or two sets of offspring, as exemplified by *Hylobates lar* and *Callicebus moloch* (Ellefson, 1968; Mason, 1968). In these species, the subadults leave or are forced to leave the family group in order to reproduce. Moynihan (1976) argues that, despite considerable variability in group size, the social organizations of New World monkeys clearly are of two types, families and troops: "... there seems to be a significant hiatus between families, no matter how extended, and troops, no matter how reduced. Even when groups are of the same size, the types may be distinguished by the nature of the internal sexual and parental relations within them." (p. 116). (Callitrichids, of course, are included in the first type). Unfortunately, there exist practically no data on the genetic relationships between group members in any New World primate species. The callitrichid "extended family" may actually include members not related by birth as suggested by data from this study and Dawson's (1976, 1977).

Six types of observations on callitrichids have been used to support the extended nuclear family group hypothesis: (1) the small size usually reported for wild groups (Table 9); (2) the formation

Table 9. Reported group size in various free-ranging callitrichid species.

<i>Species</i>	<i>Duration of study⁴</i>	<i>Size range</i>	<i>No. units observed</i>	<i>Splitting coalescing observed</i>	<i>Location</i>	<i>Reference</i>
<i>S. midas</i>	1 wk(i)	1-7	8	yes ¹	Brazil	Thorington, 1968
<i>S. midas</i>		5-20			Surinam	Geijesko, in Husson, 1957
<i>S. midas</i>	9 wks(W)	2-17	11	C, S ²	Surinam, French Guiana	Durham and Durham in press
<i>S. mystax</i>	months	2-6 ⁵	12		Peruvian Amazon	Castro and Soini, 1977
<i>S. fuscicollis</i>	months	2-10 ⁶	25	yes	Peruvian Amazon	Castro and Soini, 1977
<i>S. fuscicollis</i>	months(W)	20-40+	46		Colombian Amazon	Izawa, 1976
<i>S. fuscicollis</i>	months(D)	to 12			Colombian Amazon	Izawa, 1976
<i>S. geoffroyi</i>	Intermittent	1-9	28	C	Panama	Moynihan, 1970
<i>S. geoffroyi</i>	1 year(m)	1-19	71 ⁸	C ³	Panama	Dawson, 1977
<i>S. oedipus</i>	years(m)	1-13	25 ⁸	no	Colombia	Neyman, this study
<i>Cebuella pygmaea</i>		1-10	9		Peruvian Amazon	Izawa, 1976; Castro and Soini, 1977
<i>Leontopithecus r. rosalia</i>		2-8 ⁷		poss. ⁷	Brazil	Coimbra-Filho and Mittermeier, 1973

¹Coalescing for travel and defense.

²Coalescing during travel.

³Two largest groups (14 and 19) around concentrated food sources.

⁴W = "wet" season; D = "dry" season; m = marked animals; i = animals individually distinguishable by natural markings.

⁵Often traveling in company with *S. fuscicollis*.

⁶A "supertroop" of 15-26 reported around concentrated food source.

⁷Reports of "up to 15" in the literature thought by authors to be attributable to temporary congregations around favorable food sources.

⁸Including as one unit the various sightings of same troop/group.

of long lasting preferential bonds between pairs in mixed groups of adults in captivity; (3) the universal participation by the male in carrying and caring for offspring, often exceeding that of the female in captive groups; (4) the fact that strangers introduced to an established group are usually attacked, often by all adults; (5) the fact that only one female reproduces in captive groups; and (6) the markedly greater stability of family groups in captivity compared to groups of unrelated adults. Instability in the latter is due to fighting between members of the same sex, especially females. By contrast, aggression serious enough to require separation rarely occurs in even large family groups where the eldest offspring are several years old.

Also in contrast to observation 4, family members can often be reunited successfully after a long period of separation. In both cases, fighting is most likely to involve the like-sexed member of the dominant pair. The literature on these topics has been reviewed recently by Epplé (1975).

The nuclear family hypothesis implies a relatively stable pair bond, lasting over at least a number of years. It has been suggested that in the wild the pair bond functions to ensure the female of the help of the male which is necessary for successful reproduction (Epplé, 1975; Eisenberg, 1977). Since male or female *Callithrix j. jacchus*, *Saguinus oedipus*, *Saguinus midas* and *Saguinus fuscicollis* often attempt to mate with members of other groups

if given the opportunity (Epple, 1975; Rothe, 1975; J. K. Hampton et al., 1966), Epple has suggested that the aggression often evident between like-sexed individuals may function in the wild to maintain the exclusiveness of the pair bond (Epple, 1975). The limitation of reproduction to one female, in captive *Callithrix jacchus* at least, is effected by hormonal changes in the subordinates (Hearn, 1977). Field data also indicate the restriction of reproduction to one female. No *Saguinus oedipus* group observed contained more than two juveniles or infants. Dawson (1976, 1977) saw a maximum of three young (one case) in *Saguinus geoffroyi* groups and cites indirect observations to indicate the presence of only one reproductively active female per group.

Nevertheless, the data presented here indicate that *Saguinus oedipus* social organization does not fit the nuclear family model. The mobile sector of the population did not correspond in age structure to that expected in a social system based on stable nuclear pairs where offspring leave the group in order to breed. Although females were mainly in the younger tooth-wear and nipple-condition brackets (see Methods: Age Estimation and Table 2), at least two and possibly three parous individuals were included. The origin of one (Yo) is unknown. The second (F1) left the Ca group, probably together with the subadult and older juvenile females from the group. This left four in the group, of which three were known to be males. The sex of the fourth is unfortunately unknown. In the third case, the female's exit (as opposed to possible death) was not verified, but here the three remaining adults were definitely all males (Ka group).

Males also left their groups, and some transients appeared to be old animals (e.g., Oa). According to laboratory observations and the nuclear family theory, parous females would not be expected to be transients, nor to leave their groups. Thus the data are suggestive, although certainly not conclusive, that pair bonds may be of a different nature than has heretofore been surmised, perhaps centered only around the rearing of young, or varying between pairs due to other factors. *Saguinus geoffroyi* groups at Dawson's (1976, 1977) study site showed greater instability (and less area defense) in drier upland areas where food supplies were inadequate during the dry season. No such correlation was obvious in my study area, which is equally as seasonal, but this point needs further investigation. The markedly stable group size that was maintained despite composition changes in

Dawson's study contrasts to the fluctuations seen in the present one.

The size of some groups of *Saguinus oedipus* exceeded that which the nuclear family model would predict. Four groups of ten or more were observed; the UB group with 13 members was followed for several months and was stable and cohesive during that period,⁷ not merely a temporary feeding aggregate or uniting of two groups. What size would groups be expected to reach? Let us assume that reproductive maturity occurs at two years and that two sets of twins are produced annually, both reasonable given laboratory findings. Although triplets occur, they are relatively infrequent even under presumably optimal laboratory conditions (J. K. Hampton et al., 1966). An extended nuclear family could be expected to contain a maximum of eight individuals, if young were ejected from the group at reproductive maturity. If only one set of twins (or less) was born annually, as was the case in this study area, the maximum group size which did not include reproductively mature offspring would be six. A group of 13, if it was an extended nuclear family, might contain offspring up to five years old, assuming 100 percent survival. Alternatively, larger groups may indicate a higher rate of reproduction than is so far apparent (perhaps during a series of unusually favorable years), or the frequent inclusion of unrelated adults.

The prevalent concept of very small group size in wild tamarins, a keystone to the nuclear family hypothesis, may be misleading. Moynihan (1976) suggests that the small mean group size in Panamanian tamarins may be a result of human interference. Perhaps the same may be true in other studies done in disturbed areas with high human density. Complications in making accurate group counts might in many cases have also resulted in misleadingly low figures. It should be noted, however, that the majority of groups in the present study area did have less than eight members most of the time. The forest they inhabited could be said to be semidisturbed and certainly the population was almost completely isolated.

By contrast, in the Peruvian and Colombian Amazon, recent observers have reported *Saguinus fuscicollis* groups numbering over 20 individuals (Castro and Soini, 1977; Izawa, 1976). In the latter

⁷The group did however gradually become reduced in size until by August 1975 it numbered four members. See footnote 3 and discussion on group size in text.

case, apparently seasonally correlated differences in group size were evident. In one area, five groups whose size was estimated at 40 or more were present, although groups of about 10 were also frequently seen. The "large" groups were observable from November 1971 to February 1972 when no dry season was discernable, and again during similar weather in September to October 1973. But in the same and another location during the following dry period (November 1973 to February 1974), only groups of 12 or less could be found (Izawa, 1976). Group splitting and coalescing is implied, and has been reported by others for *S. geoffroyi*, *S. midas*, and *S. fuscicollis* (Dawson, 1977; Thorington, 1968; Durham and Durham, in press; Castro and Soini, 1977). Dawson (1977) observed his largest groups (14 and 19) of *S. geoffroyi* in the vicinity of concentrated food sources.

Lastly, the exclusiveness of group membership and expulsion of extra-group individuals predicted from laboratory observations, although usually evident in wild groups, was not observed consistently. As Epplé has already suggested (1975), under natural conditions, interactions may be affected by factors not present in captivity; for example, season or previous relations to the intruding individuals. Aggression toward strangers may also be exaggerated in captivity by restricted space, constant contact (visual or olfactory) and food competition (Rowell, 1972).

Further study should aim at following the life history of marked individuals, their relationships, and the longitudinal changes that occur in groups. Reliable aging criteria for individuals at close range and at a distance need to be developed. These will necessitate samples of individuals of known ages, obtainable only in conjunction with long-term studies. Growth and tooth-wear studies on captives could provide potentially useful supplemental data, although it appears that infant and juvenile growth rates in captivity are considerably higher than in the wild (compare Figure 4 with Chase and Cooper, 1969). Finally, insight into the immediate and ultimate causes for changes in group size will require analysis of relevant environmental factors, particularly seasonal and regional differences in the resource base on which different tamarin species rely.

Conservation Status

The cotton-top tamarin, endemic to northwestern Colombia (Hershkovitz, 1949; Hernandez and Cooper, 1976), occupies an area that supported

an extensive indigenous pre-Colombian population, and is today a densely inhabited region. By 1966 at least 70 percent of the original forest cover in the original range of the cotton-top tamarin⁸ had been replaced with pasture and farmland (Figure 1). The more densely settled northern three quarters of the area accounted for only about 5 percent of remaining forest, which was scattered in over 270 isolated tiny secondary patches. Some of these are known to lack tamarins even though they appear to be suitable habitat (Struhsaker et al., 1975; pers. obs.). The future of these forest patches is at best uncertain, not only because wood and wildlife are constantly being extracted, but because in Colombia forested land not yielding cuttable timber is considered to be "unexploited." By law and custom such land may be colonized, a not uncommon event, which discourages private owners from maintaining naturally forested areas.

As of 1966 (the date of the most recently available vegetation map), the less accessible southern portions of the cotton-top tamarin's range (Andean foothills, Figure 1) contained fairly extensive tracts of primary forest. Satellite photographs in 1973 (NASA) and 1974 low-altitude flights (Struhsaker, 1974; Struhsaker et al., 1975, Figure 1) over the area indicated extensive deforestation in the intervening years, including disappearance of much of the primary forest. Since cotton-top tamarins survive well in secondary forests, a scattered discontinuous population probably remains there. Indeed, where secondary forest has recently replaced primary, some increase in numbers might even be temporarily expected. Moynihan (1970) cites evidence that the closely related rufous-naped tamarin of Panama (*S. geoffroyi*) does better in secondary than in primary growth. Nevertheless, the prognosis for the long-term future of even those populations is bleak. Habitat destruction will continue at an even more rapid pace than in the past, as the density of colonizers increases in this

⁸While Hershkovitz (1949) and Hernandez and Cooper (1976) postulate the Magdalena River as the eastern boundary of the original range in the north, Struhsaker et al. (1975) obtained reports of its previous possible occurrence in areas to the east of the Magdalena. They suggest that "the apparent control of distributions (of *S. o. oedipus* and *S. leucopus*) by major rivers may be only an artifact of agricultural patterns that obscure the true former distributions. *Saguinus oedipus* may be characteristic of the drier forests of all of northernmost Colombia while *S. leucopus* appears in the wetter southern forests" (p. 61).

newly opened-up area. At best, any remaining forest will be reduced to tiny patches such as remain in the northern and central parts of the cotton-top tamarin's range.

The present population situation is, however, even more serious than this brief review of habitat changes would indicate. Animal dealers in Colombia maintain that the cotton-top tamarin is still easy to obtain and therefore not endangered. This index of abundance is, however, misleading. The number of tamarins that exporters can obtain is probably less a reflection of actual population levels, than of the level of habitat disturbance in the southern part of its range, containing the majority of the surviving populations. These same areas until recently⁹ represented the primary supply source for commercial exploitation (S. Daza, pers. comm.).

It is important to realize that the animal trade in Colombia is organized only loosely through established buying and selling contacts, originating in the most rural areas where local traders buy animals brought to them by local inhabitants. They are then passed from buyer to seller until they reach the major exporters (pers. obs.; Green, 1976). In some cases, exporters contract with buyers for certain species to be shipped at regular intervals. Although some trapping of tamarins was occurring, my observations (1972-1974) indicated that an exporter's stock was drawn from a wide area and that most tamarins were captured by local inhabitants who encountered them by chance in low vegetation or in some other similarly vulnerable location created by clearing and settling activities. At such times, country dwellers will frequently chase the tamarins, hoping to run them down or cause them to fall. They then capture an animal by hand (or by throwing something at it). Thus, the rate of capture is not primarily related to tamarin density, but to two other factors: the frequency with which tamarins enter vulnerable places, and the frequency with which they are encountered by people, in situations allowing capture by hand. These factors indisputably increase as the human population density increases. They also increase according to the degree of habitat disturbance, as clearing activities may force tamarin groups to cross exposed areas in order to traverse

their accustomed home range. They may cross on fences (jumping from one fence post to another) or on the ground (C. A. Leon, pers. comm.). The relatively high price that a tamarin brings on the local market (equivalent in 1974 to two or three days' wages) also is some incentive to their capture, although they are also valued as pets and may be sold only after being held for some time, when economic necessity prevails.

Since the situation just described is prevalent in the very areas containing the majority of presently surviving tamarin populations, the number available for export will tend not to respond to decreased tamarin numbers until they have already become dangerously low. Continued availability does not reflect sustained cropping from the total species' range, but the progressive depletion of populations as new portions of its habitat are colonized. Therefore, I believe that the cotton-top tamarin should be considered at least a threatened if not actually endangered species (in terms of remaining numbers).

It is not possible to provide an estimate of numbers of remaining cotton-top tamarins since we have limited knowledge of the state and extent of the remaining forest, much less the numbers contained in the various isolated forest remnants. It is unlikely that there are many forests currently large enough to maintain sufficient tamarins for a viable long-term breeding population.

At present, Colombia does not have even one park or reserve with an established population of cotton-top tamarins.¹⁰ Ideally, a series of areas should be set aside which includes representative habitat and fauna within the cotton-top tamarin range from the very dry deciduous forests in the north to the humid tropical forests in the Andean foothills. Within Inderena (Instituto de Desarrollo de los Recursos Naturales Renovables), there is considerable interest in the establishment of these reserves. International support for these measures would go a long way toward circumventing the financial and political problems involved. Also, as in so many countries, conservation interests often lose when balanced against immediate needs of an expanding population.

An even more basic need then, as in all countries, is to convince the public that their natural resources are uniquely important and worthy of preservation in all their diversity. Conservation of diverse natu-

⁹Inderena resolution No. 392 (1973) stopped all legal export of primates from Colombia; exceptions were temporarily made for scientific use until 1974 when all legal export was halted.

¹⁰While this paper was in press, two reserves were established in areas where *S. oedipus* could occur.

ral systems is in fact not a luxury, but a basic need (Watt, 1972). Each species constitutes a reservoir of genetic information which is unique and not replaceable once destroyed; each region possesses complex relationships which are still inadequately understood and which could serve as models for solutions to man-made problems arising from manipulations of the environments. Yet these resources are being destroyed daily because no "economic value" can be demonstrated for them. This is true for Colombia as for many countries, including the United States. Colombia is, however, a country of an unusual faunal diversity. It has more primate species (22) and genera (13) than any other country in South America, except Brazil, and more bird species than any other country. Thus, efforts at establishing reserves in Colombia are extremely important despite the problems involved.

Although habitat destruction is clearly the major threat to the cotton-top tamarin's future, exportation has taken its toll; and demand for tamarins abroad provides impetus for their capture. Between 1968 and 1970, about 2,700 to 3,800 imports into the United States were registered yearly (USDI, cited in Green 1976). In 1972, the United States Department of Interior reports of imports totaled about 2,400, while increases in demand for 1974 were indicated in an Institute for Laboratory Animal Resources (ILAR) survey (Muckenhirn, 1975, p. 30). The actual number extracted from the wild is of course greater than these figures, as considerable attrition (3 to 33 percent in marmosets; Thorington, 1972) must occur between capture and export, particularly as tamarins are delicate and difficult to maintain in captivity. The numbers are still relatively small compared to many other primates, but they are large for a primate of such restricted range, and their impact on the total remaining population could be considerable.

Halting export alone will not assure the survival of the cotton-top tamarin, but, since it is not a species relied on for food, the removal of the monetary incentive would reduce the number removed from the wild. In recognition of this, and the inadequate knowledge of the state of natural populations, Colombia in 1973 prohibited the export of cotton-top tamarins. The United States Endangered Species Act of 1970 provides for United States collaboration in preventing the import of any species whose export has been declared illegal by the government of the country involved, including the cotton-top tamarin. Nevertheless, there have been recent (1975) cases of

cotton-top tamarins being offered for sale in the United States. They are imported "legally" by securing the required papers in an intermediate country with no regulations regarding wildlife exportation, such as Bolivia or Panama. Clearly, the law requires changes. Imports should require permits from the country of origin of the species, not the country of shipment. This could do much to protect a species with localized distribution whose point of origin is unquestionable. Of course, import officials must have reference sources enabling them to distinguish different species to avoid name falsification.

Since the biomedical community is the major user of imported cotton-top tamarins, it has a particular responsibility to adjust its research strategy with regard to conservation needs. Future usage should take into account the range, size, and abundance of natural populations, and where the need is greater than the sustained yield of natural populations, researchers should establish breeding colonies. Breeding programs, investigations of basic husbandry problems, and basic biological studies are long overdue. Interest in these subjects has recently increased in the biomedical community since various countries have restricted primate exports. Nevertheless, such projects are still not being funded in proportion to their urgency and relative importance. Furthermore, field research on basic biology is being ignored almost entirely. Only a few species of New World monkeys are presently serving as models for biomedical investigations. Although this approach is understandable, given the need for research continuity, the biomedical community must take a long-range view. Callitrichids have barely been tapped as a resource. Only a minority of species have either been utilized in the laboratory or are known from field studies, and others could perhaps serve as better models for certain studies than species being presently utilized. The cost of the necessary basic field research is cheap compared to the cost of laboratory studies, and given the rate at which habitats are disappearing, such studies cannot be postponed indefinitely.

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For more information on captures and timing phase- see my thesis = one of the appendices includes complete timelines of various individuals and their captures, by group.

Also there is more phenological information in the forest in another appendix.