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The Use of Time and Space by the Panamanian Tamarin, *Saguinus oedipus*

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Abstract. Tamarin activity patterns and habitat utilization strategies in the Tropical Dry Forest of the Panama Canal Zone were monitored quantitatively using radio-location telemetry. The daily tamarin activity pattern differed from that of other Neotropical primates in that early morning and late afternoon activity normally did not occur. Total daily activity time averaged 676 ± 62 min. Sleeping trees, and behaviors associated with their use, were documented. Daily path length averaged $2,061 \pm 402$ m. Mean travel distance was 468 ± 66 m. Approximately one-third of the home range was utilized on a given day. Wet season home ranges for two social groups were 26 and 32 ha in area. Areas of low brush, forest edge, and vine-entangled second growth were heavily used by foraging tamarins. Large shade trees, particularly evergreens, were important as refuges from solar radiation. Open-canopy forest types and areas of grass were avoided. Social groups on resource-stable lowland sites defended territories; those on unstable upland sites used a system of time-space segregation. Upland groups became seminomadic during the dry season. Suitability of home range site may affect social group stability, natality, and infant survivorship.

Introduction

The Panamanian tamarin, *Saguinus oedipus geoffroyi* (classification according to Hershkovitz [1966]), is the only callitrichid endemic to Central America. Its ancestors apparently immigrated from South America, the locale of the family's evolutionary radiation, in the late Pliocene [Hershkovitz, 1969]. The modern range of this species extends from the Colombian province of Chocó

north to central Panama. Moynihan [1970] indicates that population densities of this tamarin are greatest in areas of moderate humidity, and that it is almost absent from the humid Atlantic coast. However, numerous specimens have been collected along the Atlantic coast and in the humid evergreen forests of Panama's Darién province [Hershkovitz, 1977]. Moreover, observations by Telford et al. [1972] indicate that it is abundant in a strip of disturbed vegetation about 5 km wide on the Atlantic coast in the Province of San Blas. Lack of Habitat in the appropriate early seral stages, rather than a climatologically determined habitat type, appears to restrict the species' range in Panama's humid lowlands.

The Study Site

Information on tamarin ecology was gathered during a 19-month field study (December 1972 to August 1974) on the Pacific slope of the Panama Canal Zone. The former Rodman Naval Ammunition Depot (hereafter referred to as Rodman), a fenced, 1,015 ha biomedical research area administered by Gorgas Memorial Laboratory, served as the principal study site.

Topographically, Rodman consists of a series of hills and valleys rising from near sea level to 168 m. Two seasonally intermittent streams, the Río Velasquez and a branch of the Río Cocolí pass through Rodman and empty into the Panama Canal to the northeast. Forest cover consists mainly of second growth which has been little disturbed since World War II. Rodman lies within the confines of the Dry Tropical Forest Life Zone [Holdridge and Budowski, 1956; Holdridge, 1967]. A more detailed description of the study site may be found in Fleming [1971] and Dawson [1976].

While mean monthly temperatures average approximately 80 °F (26.7 °C), rainfall is markedly seasonal, with a distinct, 8-month wet season from mid-April to mid-December and a 4-month dry season from mid-December to mid-April. Annual rainfall averages approximately 68 in (1,727 mm), with all but about 5 in (127 mm) falling during the wet season (Panama Canal Company, 72 years of continuous records). The environmental impact of the dry season is exacerbated by desiccating winds, which average 10 mph (16.1 km/h) and gust to over 25 mph (40.2 km/h).

During the course of a normal dry season, upland areas may lose 20–40% of their vegetative cover due to leaf drop by deciduous trees and physiological wilt and consequent leaf drop by nondeciduous trees. Exposed hillsides are drier and experience a greater degree of deciduousness than lowland sites. Insect abundance and diversity in the tropical dry forest also decrease over the dry season, and, again, exposed upland areas suffer greater losses in both parameters than do lowland areas [Janzen and Schoener, 1968]. Additionally, fruit abundance is at a yearly low [Smythe, 1970a, b]. This period of scarcity results in a general shift of vertebrate activity from dry uplands to lowlands, which are less affected by drought. Here, in a reduced area and in competition with other species for limited food resources, the local fauna passes through an ecological bottleneck. Fat reserves are depleted; mammals examined are in poorer condition. Adult tamarins, for example, weigh signifi-

cantly less than in the wet season. By the time the April rains commence, there is no trace of the subdermal or omental fat seen during the wet season. Many mammalian species experience high rates of mortality as a result of dry season hardships [Kaufmann, 1962; Smythe, 1970a, b; Fleming, 1971; Mittermeier, 1973].

The primary fruit peak begins with the coming of the rains in mid-April and early May and continues into the month of August [Smythe, 1970a; Fleming, 1971; Dawson, 1976]. Insect populations also recover rapidly [Janzen and Schoener, 1968]. Upland areas, which weeks before were practically devoid of insect life, now harbor insect (and probably fruit) biomasses which exceed those of lowland areas. The reproduction of most mammalian species, including tamarins, is in synchrony with this phenomenon of abundance, with the young of most mammals being produced at this time [Fleming, 1973].

The secondary peak of larger fruits noted by Smythe [1970a, b] on Barro Colorado Island did not occur in the study area. While the availability of smaller fruits most heavily utilized by tamarins was more seasonally equable than that of larger fruits, a noticeable decline in their availability was evident in the late wet season [Dawson, 1976]. The abundance and diversity of insects also decline in the late wet season [Janzen and Schoener, 1968; Galindo, personal commun.]. Thus, both fruit and insect biomasses are in decline prior to falling to yearly lows in the dry season.

The vertebrate fauna of this community is rich and varied, with possible combinations of interspecific interactions almost limitless. The reader is referred to Fleming [1971] and Dawson [1976] for a more detailed discussion than that which follows. Only those species obviously important as potential competitors or predators will be considered here.

Four species of primates are extant in Rodman: the Panamanian tamarin (*Saguinus oedipus*); the night monkey (*Aotus trivirgatus*); the capuchin monkey (*Cebus capucinus*), and man (*Homo sapiens*). *Aotus*, which is not uncommon, and may be a nocturnal ecological equivalent of *Saguinus* [Moynihan, 1964], is an important, but temporally segregated competitor. *Cebus* is locally rare – only three (one group) were seen during the entire study. Even if it were more numerous, *Cebus* would not be an important competitor, since its diet does not broadly overlap that of *Saguinus* [Oppenheimer, 1969; Hladik et al., 1971]. Man is both a potential predator and competitor. Tamarins are sometimes hunted for their flesh, but the small return is currently not worth the expenditure of ammunition. A more important source of 'mortality' is the capture of young for the local pet and biomedical trade, which may exert heavy pressure in some localities. A third, and the most pervasive, influence of man is the destruction of tamarin habitat through land clearing practices. None of these negative interactions was important in the study area; however, the third factor has been, and continues to be, of paramount importance in the demise of tamarin populations in the Republic of Panama.

A number of didelphids, procyonids, sciurids, and microchiropterans have diets which broadly overlap that of *S. oedipus*, as do numerous birds, particularly those which hold 'gleaning' and frugivorous niches. Two sciurids, *Sciurus variegatoides* and *S. granatensis*, were frequently involved in interspecific disputes with tamarins. *Oropendolas* (*Zarhynchus wagleri*) and chachalacas (*Ortalis cinereiceps*), which compete with *Saguinus* for small fruits, were chased from fruit trees by the primate.

Large hawks and hawk-eagles are probably the most important predators of tamarins. Local raptors of proven or potential importance include the white hawk (*Leucopternis*

albicollis), the black hawk-eagle (*Buteogallus urubitinga*), the tyrant hawk-eagle (*Spizaetus tyrannus*) and the ornate hawk-eagle (*S. ornatus*). Turkey vultures (*Cathartes aura*) are a potential predator of tamarin infants [Smythe, personal commun.]. In regard to mammalian predators, the tayra (*Eira barbara*) is known to take tamarins. Yaguarundi (*Felis yaguarundi*) may catch tamarins on the ground and in low brush. The ocelot (*Felis pardalis*) an arboreal cat, is capable of preying upon tamarins. Large arboreal snakes may also be important predators [Hershkovitz, 1977].

Materials and Methods

Data obtained in this study are from a number of sources: (1) a detailed radio-location telemetry study of two social groups; (2) observations of 68 individually marked animals from at least six social groups; (3) observations made while conducting 168 strip censuses over a 4.3-km route in Rodman; (4) less structured observations made throughout the study area, but particularly of nonmarked groups in Rodman, and (5) examination of 131 specimens collected for biomedical purposes at the rate of 5 animals biweekly for 1 year. All collecting sites were located more than 1 km from observation areas; most were at least 3 km from Rodman. I will discuss the first two data sources in detail, since they contribute most of the data cited herein. For a detailed description of the last three data sources, the reader is referred to Dawson [1976].

All live tamarins utilized in this study were captured in No. 201 Tomahawk Live Traps (Tomahawk Live Trap Co., Tomahawk, Wis.) baited with either mango or banana. Traps were wired to branches and vines 3–10 m above the ground in areas frequented by the tamarins. Traps were set in clusters of 3–5 to promote multiple captures. Ketamine anesthesia (Ketalar; Parke-Davis & Co.) was administered intramuscularly to animals prior to handling.

The radio-location telemetry system used has been described by Montgomery et al. [1973]. I will, however, describe the component parts and their functions.

All telemetric materials used were manufactured by the AVM Instrument Company (Champaign, Ill.). Model St-1 transmitters mounted on bioperm plastic collars equipped with whip antennas constituted the transmitter package. Originally, both continuous signal and pulsating transmitters were used, but the former were abandoned in favor of the lighter (20–25 g), longer-lived pulsating model. The weight of the pulsating transmitter package was 4–5% of animal body weight, a permissible load for the study of free-ranging animals [Brander and Cochran, 1969]. The output frequency of all transmitters was controlled by a crystal which oscillated in the 50 MHz range. A custom-made LA-11 receiver mounted with a two element yagi antenna received signals at the third harmonic (150 MHz); a five element yagi antenna was used to receive signals at the ninth harmonic (450 MHz). While the effective range of the 150 MHz signal may be 1,200 m or more under some tropical forest conditions [Montgomery et al., 1973], signal-impeding vegetation and topographic discontinuities limited 150 MHz signal reception to approximately 300 m. The 450 MHz option was used at ranges of less than 100 m for precise determination of location. Through the use of the 450 MHz option, it was possible to 'pinpoint' the position of hidden tamarins and tamarin 'nest' sites in the overhead foliage.

Two tamarin social groups were chosen as subjects for detailed studies regarding the utilization of time and space within their respective home ranges. The first group, the 'lowland group' by designation, occupied a home range which was bisected by one of the seasonally intermittent tributaries of the Río Velasquez. A gallery forest of the non-deciduous *Anacardium excelsum* lined the stream; vegetation typical of increasingly droughty sites appeared as one moved out of the river valley to upland portions of the home range. Site altitude ranged from 12 to 55 m, with approximately 70% of the area lying below 30 m. In contrast, the 'upland group' occupied a hilly home range where up to 40% of the leaf cover fell during the height of the dry season. The altitude of the upland site varied from 43 to 127 m, with over 85% of the home range lying above 60 m.

I compared the use of time and space between these two groups inhabiting disparate sites as a preliminary test of an hypothesis suggested by Janzen and Schoener [1968], which holds that insectivorous vertebrates (tamarins require large quantities of animal protein) inhabiting seasonally-xeric upland areas must radically alter their patterns of spatial and temporal usage in order to exploit seasonal insect resources, while insectivores occupying lowland areas in which insect populations are more stable maintain their pattern of usage throughout the year.

Telemetered animals from each group were followed for several days to determine the approximate boundaries of the home ranges. A system of trails, arranged in a grid system 100 yd (91.5 m) on a side, was constructed in the home ranges to supplement an existing road system. The superposition of this grid system on a preexisting contour map - 20 ft (6.1 m) intervals - with numerous points of known location for reference allowed precise location of telemetered tamarins. Over 12,500 ft (3,813 m) of foot trails were cut and marked by machete in the lowland area; over 16,000 ft (4,880 m) of trail were cut in the upland area. All movements of the lowland group took place within the borders of the trail system; the system constructed in the upland group's home range was large enough to monitor the group's wet season activities, but was insufficient during the dry season, when the group ranged widely and eventually abandoned the drier parts of its home range. With the use of the 450 MHz option, group location on the grid could usually be determined to within 10 m of actual location. When the group was hidden in dense foliage, triangulation from the grid lines determined location to within 20 m.

Eight physiognomically distinct habitat types were identified and mapped on the home range of the lowland group prior to gathering data on habitat usage. The null hypothesis predicted usage proportional to habitat area. Time spent and distance travelled within habitats were designated as usage criteria; usage-availability analysis followed Neu et al. [1974]. Telemetric and timing problems precluded this analysis in the upland area.

Distance travelled per 2-hour time unit was used as a gauge of the tamarin's daily activity pattern. I adopted the null hypothesis that distance travelled during the 2-hour time unit would be proportional to total time logged in that time block. Again, analysis follows the usage-availability method of Neu et al. [1974].

More than 500 radio-contact hours were logged with the lowland group. This included 26 complete days of radio tracking during the wet season and 3 complete days during the dry season. Data for the upland group represent information from more than 100 h of radiocontact on 14 wet season days and 17 dry season days. Regrettably, equipment failure and lack of time made full-day analysis of the upland group impossible.

In preparation for complete day tracking periods, the group was located about 2 h prior to sunset on the preceding evening and then followed until it reached the sleeping tree for that night. Behavior at the sleeping tree was observed for at least 30 min prior to terminating contact. I then returned to the sleeping tree before sunrise to begin the day's tracking routine. Behavior in the sleeping tree was noted, and the time the first tamarin left the tree was recorded. Locality and behavioral data were noted at 15-min intervals throughout the day. Contact with the group was maintained throughout the day and continued for at least 30 min after the group entered its night sleeping tree.

Data on home range utilization were also gathered by observing patterns of spatial usage by eight groups of tamarins. In five of these groups, all members were marked with color-coded collars and small mammal ear tags. Of the remaining three groups, two contained several marked animals, and a third was identifiable due to the presence of a bob-tailed alpha female. The five individually marked groups include the upland and lowland groups and three bands which occupied intermediate sites. Two of the intermediate groups, Red and Green, occupied home ranges contiguous to that of the lowland group; New Red, New Green, and the stumptail groups had home ranges which overlapped that of the upland group. A limited number of interactions were also observed between marked groups and three unmarked groups designated by geographic location as River, Hill and Spur groups.

Results

Initiation of Daily Activity

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

I observed the egress of tamarins from sleeping trees on 35 days. The average time of egress was sunrise time plus 11.7 min, with a standard deviation of ± 22 min. Available light at that time of morning varied with the cloud cover and the density of vegetation surrounding the sleeping tree, but was sufficient in all cases for observation of the exiting animals. Extremely early and extremely late times of activity initiation appeared to be roughly correlated with conditions which influenced the cessation of activity on the previous day. For example, when heavy rains caused the tamarins to cease their movements in mid-afternoon, activity began earlier the next morning. Conversely, when the tamarins foraged after sunset, they tended to become active somewhat later the following day.

Cessation of Activity

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

Total Activity Time

Average activity time (min) of the lowland group for 26 wet season days was 676 ± 62 SD. Daily activity time ranged from 426 min, for a day when heavy rain fell from 14.10 h until dark, to 731 min. Total activity time for 14 days in the early wet season (May–July) did not differ from activity time observed for 12 days during the late wet season (August–November); $F = 0.113$, $p > 0.75$). Rainfall, which was fairly evenly distributed within and among days, did not suppress activity in any one time period. A comparison of the total activity time for each of 3 dry season days with mean wet season total activity time using a technique for comparing single observations with means of samples [Sokal and Rohlf, 1969] indicated no significant differences ($p > 0.1$ for all tests).

Quantification of Daily Activity

A summary of daily activity during 2-hour time blocks is presented in table I. Linear distance travelled was the activity criterion. The highly significant χ^2 value ($p < 0.001$, 6 d.f.) indicates that distance travelled over time periods was not proportional to the available time within periods. A definite activity pattern is apparent – tamarins travelled significantly farther than one would expect during the early morning hours, began to reduce activity in late morning, experienced a lull in activity during midday, and resumed rapid travel at significantly higher rates during the late afternoon and evening hours. This activity pattern (which is at variance with the observations of Moynihan [1970]), and its significance will be discussed.

Measurable amounts of rain fell on 21 tracking days. The loss of foraging time due to rain which fell between initiation and cessation of activity averaged 15 min/day. This is an underestimate of the total effect. It does not account for activity time lost when rain retarded the initiation of activity or hastened its cessation. Heavy rain, and prolonged light rain, depress tamarin activity.

Table 1. Activity pattern of the Panamanian tamarin, *S. oedipus*, based on linear distance travelled during hourly periods over 26 wet season days

Hourly time period	Proportion of total time, P_e	Expected linear distance, m	Observed linear distance travelled, m	χ^2 values	Proportion of observed distance, P_i	'Family' of 95% confidence intervals on P_i
05.00-07.00	0.062	3,323	3,898	98.842	0.073	$0.070 < P_1 < 0.076^{**}$
07.00-09.00	0.175	9,379	9,452	0.568	0.176	$0.172 < P_2 < 0.180$
09.00-11.00	0.180	9,647	8,865	63.390	0.165	$0.161 < P_3 < 0.169^*$
11.00-13.00	0.180	9,647	7,495	480.056	0.140	$0.136 < P_4 < 0.144^*$
13.00-15.00	0.180	9,647	9,202	20.527	0.172	$0.168 < P_5 < 0.176^*$
15.00-17.00	0.171	9,165	9,830	48.252	0.184	$0.179 < P_6 < 0.189^{**}$
17.00-19.00	0.052	2,787	4,853	1,531.524	0.090	$0.087 < P_7 < 0.093^{**}$
				2,244.159 = χ^2		

* Observed proportion significantly lower than expected proportion ($P_i < P_e$).

** Observed proportion significantly higher than expected proportion ($P_i > P_e$).

Table II. Sleeping trees of the Panamanian tamarin: tree species and frequency of usage

Tree species	Number of trees used 'n' nights						Total trees	Total nights
	Nights							
	1	2	3	4	5	9		
<i>Anacardium excelsum</i>	5	2	1	3	1	0	12	29
<i>Spondias mombin</i>	2	0	0	0	0	1	3	11
<i>Cassia</i> sp.	1	1	0	1	0	0	3	7
<i>Luehea seemanii</i>	0	0	1	0	1	0	2	8
<i>Cupania</i> sp.	0	1	0	0	0	0	1	2
<i>Ficus</i> sp.	1	0	0	0	0	0	1	1
Dead trees, vine covered	1	1	0	0	0	0	2	3
Total	10	5	2	4	2	1	24	61

Characteristics of Sleeping Trees

Tamarins of the lowland group were observed in their sleeping trees on 61 occasions. At least seven tree species were used as sleeping trees; many were used repeatedly. On six of the 26 days of radio-tracking, the lowland group returned to the same sleeping tree which it had left that morning. A summary of tree types and frequency of usage is presented in table II; the locations of night sleeping trees are plotted in figure 1. Three sleeping trees of the upland group were also discovered. One site was in the top of a royal palm, *Scheelea rostrata*; the two other sites were representative of the two types of sites described below.

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

Patterns of Movement within the Home Range

The travels of the lowland group within its range were not random; they appeared to be influenced by a number of factors. The foremost were territorial behavior and distribution of food resources. As noted in figure 2, a total of

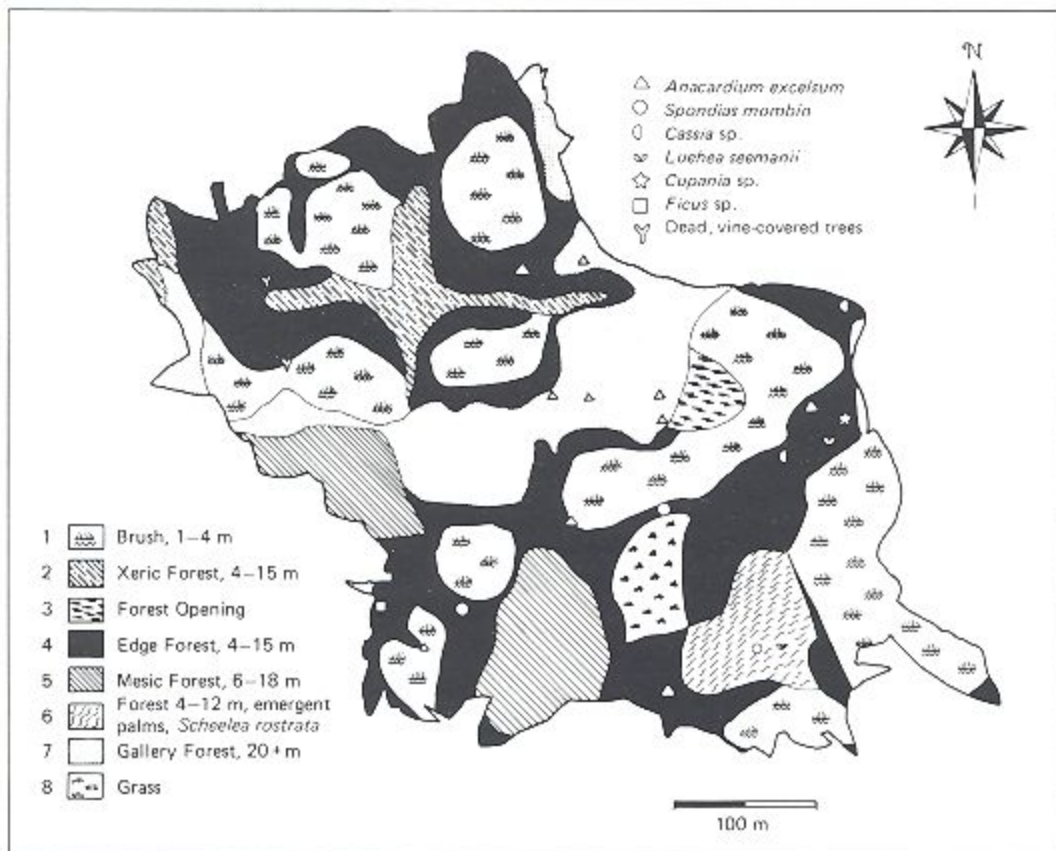


Fig. 1. Distribution of habitat types and sleeping trees within the home range of the lowland group.

approximately 13% of the lowland group's home range (territory) was overlapped at four locations by four other social groups. Of the four groups, three were observed to engage frequently in social altercations with the lowland group; only one agonistic encounter was recorded between the lowland group and the fourth group. On 19 of the 26 days monitored, the lowland group entered, or passed within, vocalizing distance of at least three of the four areas of overlap which it contested with these three groups. This observation is not incidental; the lowland group often travelled rapidly to areas of overlap, and usually two of the four areas were visited from early to mid-morning, the time of most territorial disputes. On 6 of the remaining 7 days, the lowland group visited the

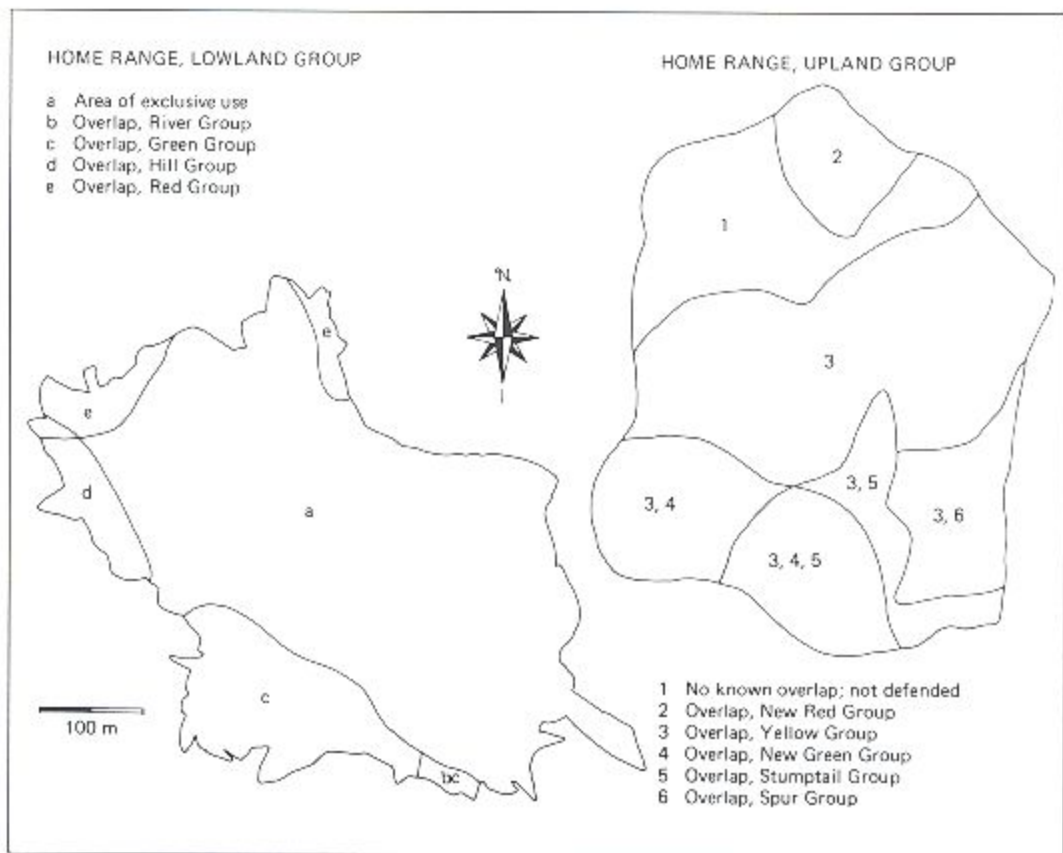


Fig. 2. A comparison of home range size and degree of overlap of a group of tamarins inhabiting a lowland area and a group inhabiting an upland area.

areas of overlap of two of the three groups. On 1 day in 26, the group visited only one area of overlap.

Availability of food also influenced movements. Marked changes in movement patterns were noted when *Anacardium excelsum*, *Lacistema aggregatum*, and a wild grape, *Vitis* sp., came into fruit. The response to the bulbous pedicels above the fruits of *A. excelsum* during the late dry season, a time of fruit scarcity, was particularly impressive. For several weeks the movements of the group appear to be highly correlated with the distribution of fruiting *A. excelsum* in the home range. The distribution of suitable sleeping trees may also influence movement.

Table III. Daily path length and home range size for selected neotropical primates

Species	Path length/day km	Home range size ha	Reference
<i>Saguinus oedipus geoffroyi</i>	2.06 ± 0.40 (S.D.)	26–32	Dawson [present study]
<i>Saimiri oerstedii</i>	2.5–4.2	17.5	Baldwin and Baldwin [1972]
<i>Saimiri sciureus</i>	–	14.3	Thorington [1968a]
<i>Cebus capucinus</i>	1.6+	85.2	Oppenheimer [1969]
<i>Alouatta villosa</i>	0.18	80–120	Carpenter [1934]
<i>Alouatta villosa</i>	0.29	14.4–20	Chivers [1969]
<i>Callicebus moloch</i>	0.57	0.4	Mason [1968]

Daily Travels within the Home Range

The mean linear distance or path length travelled per day was 2,061 m, with a standard deviation of 402 m. Mean path length travelled per hour was 183 m (600 ft). The mean travel distances (the distance between the two extreme locations on a given day, defined by Mason [1968]) was 468 ± 66 m. The mean area of the home range encompassed by the daily path travelled was 9.4 ± 0.6 ha. Thus, approximately 36% of the home range was encompassed by the group's movement on any given day. Path distance travelled in the outer one-half of the home range did not differ from path distance travelled in the inner one-half of the home range, $\chi^2 = 0.006$, 1 d.f., $p > 0.9$. Mean daily path length and home range size are compared with those of other neotropical species in table III. Tamarins can, however, travel much faster than this. A single radio-tagged animal from the upland group travelled more than 950 m over a 1-hour period, and the lowland group once travelled 221 m in 6 min en route to a sleeping tree, a rate of 2,210 m/h.

Differential Habitat Usage as Measured by Time Spent within Habitats

The home range (= territory) of the lowland group was divided into eight habitat types (see fig. 1). Time spent within each habitat type is summarized in table IV. The significant χ^2 value ($p < 0.001$, 7 d.f.) indicates that the time spent in the various habitats was not proportional to habitat area. Low brush (0–4 m) and forest edge (4–15 m) were used significantly more than expected on the basis of habitat area, while xeric forest, mesic forest (open canopy, 6–18 m), sparsely forested openings, and areas of grass were used significantly less. The

Table IV. Habitat utilization by *S. oedipus*: differential habitat utilization determined by time spent in eight habitats during 26 wet season days

Habitat No.	Area Ja	Proportion of total area Pe	Time expected (number of 15 min readings)	Time observed (number of 15 min readings)	χ^2	Proportion of observations Pi	95% 'family' of confidence coefficients on Pi
1	7.25	0.274	319	375	9.830	0.323	0.285 \leq P ₁ \leq 0.361**
2	1.21	0.046	53	36	5.453	0.031	0.017 \leq P ₂ \leq 0.045*
3	0.21	0.008	9	3	4.000	0.002	0.000 \leq P ₃ \leq 0.004*
4	9.28	0.351	408	540	42.706	0.464	0.423 \leq P ₄ \leq 0.505**
5	4.63	0.176	205	45	124.878	0.039	0.025 \leq P ₅ \leq 0.053*
6	0.74	0.028	33	33	0.000	0.028	0.014 \leq P ₆ \leq 0.042
7	2.55	0.097	113	131	2.867	0.113	0.088 \leq P ₇ \leq 0.138
8	0.54	0.020	23	0	23.000	0.000	no confidence limits possible
					212.734 = χ^2		

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

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

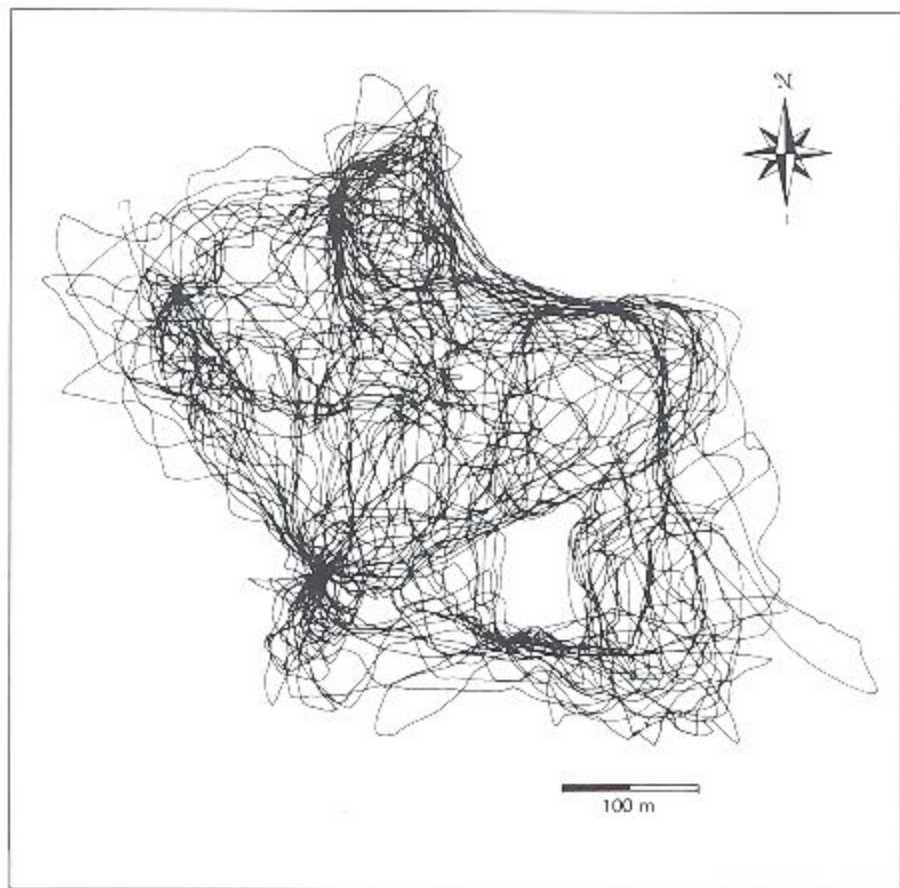


Fig. 3. Cumulative movements of the lowland group over approximately 500 h of radio-tracking.

habitat which included vine-covered trees with emergent palms (*Scheelea rostrata*), and the gallery forest of *Anacardium excelsum* were used in proportion to their area.

A χ^2 contingency test indicated that time spent within the seven utilized habitats was highly dependent on the day monitored ($\chi^2 = 418.189$, 6 d.f., $p < 0.01$). Daily variation in habitat usage resulted primarily from the existence of pattern in the travels of the tamarins, rather than differential usage within habitats. Since their travels encompassed only about one-third of the home range of a given day, some habitat types of limited area were not represented in many

daily samples, thus producing enormous χ^2 values. I considered sample sizes for both time and distance analyses to be sufficiently large to ignore variation due to travel patterns and to consider the accumulated data as independent samples representative of habitat usage.

Cumulative time spent in the outer one-half of the home range was not significantly different from cumulative time spent in the inner one-half of the range ($\chi^2 = 0.804$, 1 d.f., $p > 0.1$). Thus, there was no apparent tendency to use central areas of the home range more than peripheral areas. A single sample test [Sokal and Rohlf, 1969] was used to compare time spent within each habitat during each of 3 dry season days with the mean time spent in each habitat over the wet season. No significant differences were evident, with $p > 0.1$ for all comparisons.

Differential Habitat Usage as Measured by Distance Travelled within Habitats

In figure 3, the paths of group travel for the entire study period are recorded as lines. The patterns of usage in this figure are further elucidated by the information in table V, where the distance travelled within each habitat type is compared with the expected distance travelled per habitat type, based on the hypothesis that distance travelled per habitat type is proportional to habitat area. The significant χ^2 value ($p < 0.001$, 7 d.f.) indicates that habitat usage as estimated by distance travelled among habitats was not proportional to habitat area. Less travel distance was logged in habitats two, three, five, and eight than expected, while more distance was logged in areas four, six and seven than expected. The distance travelled in area one was proportional to the area of that habitat type in the home range. A χ^2 contingency test (7×26) indicated that the distance travelled within given habitat types was highly dependent on days sampled ($\chi^2 = 34$, 713, 6 d.f., $p < 0.001$). Again, as indicated above, this variation was due mainly to patterns of tamarin travel rather than differential usage within habitat types. As with the time analysis, the significant value of the contingency test was judged to have no effect on the validity of the habitat utilization analysis.

The Lowland Group vs. the Upland Group: A Comparison of Home Range Size and Utilization

Home range size and the degree of home range overlap with other tamarin groups are presented in figure 2. The lowland group defended its 26 ha home range as a distinct territory; during the wet season about 13% of its territory was

Table V. Habitat utilization by *S. oedipus*: differential usage determined by distance travelled among eight habitats during 26 wet season days

Habitat No.	Area ha	Proportion of total area P_e	Expected distance travelled m	Observed distance travelled m	χ^2	Proportion of observations P_i	95% 'family' of confidence coefficients on P_i
1	7.25	0.274	14,709	14,544	1.865	0.271	$0.266 \leq P_i \leq 0.276$
2	1.21	0.046	2,458	1,760	198.482	0.033	$0.031 \leq P_i \leq 0.035^*$
3	0.21	0.008	434	111	240.011	0.002	$0.002 \leq P_i \leq 0.003^*$
4	9.28	0.351	18,815	24,528	1,734.438	0.458	$0.452 \leq P_i \leq 0.464^{**}$
5	4.63	0.176	9,399	3,771	3,369.931	0.070	$0.067 \leq P_i \leq 0.073^*$
6	0.74	0.028	1,508	1,824	66.106	0.034	$0.032 \leq P_i \leq 0.036^{**}$
7	2.55	0.097	5,179	7,056	680.077	0.132	$0.128 \leq P_i \leq 0.136^{**}$
8	0.54	0.020	1,090	0	1,090.111	0.000	no confidence limits possible
					$7,381.021 = \chi^2$		

* Observed distance travelled significantly lower than expected ($P_i < P_e$).

** Observed distance travelled significantly higher than expected ($P_i > P_e$).

overlapped by the home ranges of other groups. The home range size of the upland group during the first 6 months of the wet season encompassed an area of about 32 ha. During the late wet season and the dry season its home range included this area and at least 11 additional ha. This area was not defended, but was rather shared with five other groups through spatial and temporal segregation.

During the first 6 months of the wet season, the upland area appeared to support higher densities of tamarins than the lowland area. By extrapolation from tamarin densities on the lowland and upland home ranges, density figures of approximately 27 tamarins/km² were obtained for lowland sites and approximately 36 tamarins/km² for the uplands. It must be kept in mind that these figures result from data for only two sites and must be regarded cautiously. They do, however, offer an objective estimate in support of my subjective impressions regarding population densities in the two habitat types.

Discussion

The Use of Time and Space

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

Before proceeding, it is necessary to define two terms which will appear in the discussion. The first, home range, is defined as 'The area in which an animal normally lives, exclusive of migrations, emigrations, or unusual, erratic wanderings' [Brown and Orians, 1970]. For the second term, territory, this paper will follow the usage suggested by Noble [1939] and Burt [1943], which is any area

defended against encroachment by extra-social-unit conspecifics. Definitions, such as that suggested by Schoener [1968], which require that the territory be an area of exclusive use to the occupant, are not flexible enough to account for the frequent acts of trespass which occur on the periphery of large territories.

Daily Activity Patterns

Moynihan [1970], in describing the habits of *S.o. geoffroyi*, observed that, 'unlike other diurnal monkeys with which I am familiar, and most other diurnal mammals and birds in the same habitats, these tamarins do not become active at, or very shortly after, dawn. In the wild they are never seen moving around until at least a quarter of an hour after it has become light. In most cases, they apparently do not get up until approximately three quarters of an hour, or more, after full light.' He also observed that 'It is only approximately one hour or half hour before sunset that they gradually stop feeding and drift off in the general direction of their sleeping trees.' He further states that with this unusual activity pattern '... one wonders if the animals do not become torpid or semitorpid at night.' Other observations regarding apparent torpor or semitorpor in this species are summarized by Hershkovitz [1977, pp. 739, 797].

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

If, for example, one approaches the animals 10–15 min after their arrival at the night's sleeping tree, they maintain their formation, and, if they respond to the observer's presence at all, they turn their heads groggily, stare at the observer, and then resume their former huddled posture. The same response can be elicited in the early morning hours.

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

Moynihan [1970] advanced the idea that this activity pattern is adaptive in that it temporally removes the tamarins from competition for insects with flycatchers, which forage extensively and intensively during crepuscular periods.

While this view may have some merit, flycatchers tend to specialize on smaller insects and flying insects, which are more difficult for tamarins to obtain and probably prohibitively 'expensive' in terms of the tamarins' energy budget. Furthermore, given the temporal segregation of the flycatchers and tamarins and the difference in the type of insects utilized, I find his suggestion that the similarities between many flycatcher calls and the vocal repertoire of the tamarins represent social mimicry to be unlikely. On the contrary, similarities between flycatcher and tamarin vocalizations are probably the result of the convergent evolution of vocalization frequencies which are most efficient in the general habitat occupied by both forms. If the vocalizations of the two forms were broadly overlapping in time, one would expect to find distinctly different types of vocalizations occurring in order to prevent the reception of extraneous auditory signals by either form.

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

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

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

Quantification of the Daily Activity Pattern and Behavioral Attributes

Upon examining table I, it is apparent that tamarins travelled significantly farther than expected during the first 2 h of the morning. The relatively longer distances logged are partially attributable to the tamarin's predilection for feeding on insects at this time of day. On the majority of days monitored, foraging began at or very near the sleeping tree; usually in areas of low, brushy vegetation, but occasionally in the tops of *Anacardium excelsum*, 20 m or more above the ground. On other days, the tamarins travelled 100–200 m as a group and then began foraging after having passed other areas which appeared to be equally as productive as the area in which they began foraging. Upon leaving the sleeping trees, the monkeys began to forage individually and to move as a loose group through the forest. Group scatter at this time was usually 40–70 m. Foraging was generally extensive rather than intensive, hence the longer path length. Insects appeared to be the primary objective during at least the first half hour of the activity period, although fruit was taken occasionally. Approximately an hour after leaving the sleeping tree the emphasis in foraging activity shifted to fruits. Contact calls (the 'long whistle' of Moynihan [1970]), which were commonly heard early in the time block became less frequent as the tamarins reduced their group scatter. During the latter portion of this period, and the beginning of the next, the monkeys were often seen eating fruit in single trees and concentrated food patches. On the majority of days monitored, the group began to move as a unit toward areas of home range overlap between 06.45 and 08.00 h. These movements added, in part, to the significantly higher movements per unit time before 07.00 h.

Most of the behavior involving intergroup territorial defense occurred between 07.00 and 10.00 h; the major part of the distance travelled to areas of intergroup conflict was accomplished between 07.00 and 09.00 h on 20 of 26 days. While foraging for both fruits and insects occurred en route to areas of

overlap, the path of travel was much more linear than during the early morning hours. Upon reaching areas of overlap, the group often devoted much of its time to foraging. In two areas, *Spondias mombin* and *Inga* sp. were common and, during their fruiting seasons, were attractive sources of fruit.

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

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

Marking behaviors, i.e., 'sit rubbing' and 'pull rubbing' [Moynihan, 1970], and especially the former, appeared to be more frequent in areas of overlap than in other parts of the home range. However, since thick brush in all areas made observations of the animals difficult, comparable quantitative data were not obtained. Scent marking, primarily by 'sit rubbing', both preceded and followed agonistic confrontations. Sit rubbing also occurred in the absence of the opposing group. Pull rubbing, as Moynihan [1970] indicates, is rare except in the more intense behavioral situations such as those involving overt conflict, or possibly, the sudden appearance of a terrestrial predator. Pull rubbing was observed only four times: twice following encounters involving physical contact with members of the other group, and twice when the observer appeared to be the stimulus.

Marking at territorial boundaries was usually initiated by the dominant (i.e. reproductive) female. The tamarins tended to perform their rubbing behaviors

on protruding knots, stubs, and rough bark rather than on smooth branches. No evidence was found for the existence of fixed, customary territorial markers or sign posts. While differences of opinion exist regarding the function and information content of scent marking behaviors [Epple, 1967, 1972; Epple and Lorenz, 1967; Moynihan, 1970], my observations indicate that they are an integral component of territorial behavior.

By approximately 10.00 h the tamarins had begun moving out of areas of low brush and into the shade. (Thorington [1968b] observed the same tendency in *Saguinus midas*.) On 12 days the tamarins travelled less than 200 m from an area of overlap before slowing their pace and engaging in intermittent resting and foraging activities; on 10 days the group travelled relatively rapidly across their home range to another area of overlap before their cadence of activity diminished. On 19 of the 26 days midday activity revolved around the stands of *Anacardium excelsum* and the large, shady trees in habitat 4. While activity did not cease between 10.00 and 15.00 h, path distance was significantly shorter than expected due to frequent periods of quiescence and to less directionality in group movement. Individuals and subgroups foraged sporadically between rest periods, during which the tamarins sat relatively motionless in the trees or very occasionally sprawled full length on a branch. Autogrooming and allogrooming behaviors were seen more frequently during these hours than during the remainder of the day, with the possible exception of the first few minutes following periods of rain, when autogrooming was a common, and possibly obligatory, comfort behavior.

On most days the tempo of activity began to increase at about 15.00 h. Travel from this time until entering the sleeping tree was directional and relatively rapid, which resulted in significantly longer distances travelled over the last 2–4 h of the day. While insects were taken during the late afternoon and evening, most travel seemed oriented toward fruit sources. The animals frequently travelled 100 m or more in five or fewer minutes and then spent 15–30 min in a fruit tree. The path followed during the late afternoon did not appear to be random; it appeared to be directed by the ultimate goal, the sleeping tree, and the location of fruit trees. That a given sleeping tree was the ultimate goal was indicated by: (1) the direct nature of the route of travel; (2) the fact that former sleeping trees and other presumably suitable trees were passed en route; (3) the fact that individual sleeping trees were often used on several successive nights, and (4) the rapidity of group movement over the last 100–300 m before arriving at the sleeping tree. The rapid movement to sleeping trees, the direct movement between fruit trees, and the brief interludes of

multidirectional foraging for insects, are responsible for the significantly higher rates of travel evident in the ultimate and penultimate time periods.

Sleeping Trees: Location and Associated Tamarin Behaviors

When the locations of sleeping trees (fig. 1) are compared with the map showing areas of home ranges overlap (fig. 2), it is apparent that most sleeping trees are located in the northeastern portion of the home range, while the remainder occur near areas of group overlap. Since apparently suitable trees are located throughout the area, this clustering of sites is not readily explained. One might surmise that the location of sleeping trees is dependent upon a number of factors, such as patterns of territorial travel, temporal variations in the availability of food, and differential densities of competitors and predators. However, no strong evidence exists in support of any of these factors.

Sleeping trees, in 22 of 24 cases, were either much higher than the surrounding vegetation, lacking extensive vine connections with other trees, or both. This lack of physical connection with the surrounding strata might lessen the probability of detection by nocturnal, arboreal predators such as felids and snakes which Hershkovitz [1977] suspects as 'the probably enemies of consequence'.

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

The existence of 'nests' may be important in the epidemiology of trypanosomiasis, with which these tamarins are heavily infected [Sousa et al., 1974; Sousa and Dawson, 1976]. The 'nest' interiors which may serve as moist refugia for insects during the dry season, harbor a variety of insect life. While no triatomine bugs were encountered in the five 'nests' examined, the existence of these refugia, and a documented history of periodic visitation by the tamarins suggest that such a vector-host relationship is feasible. This situation merits further study.

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

Upon reaching the sleeping tree the monkeys huddled together either on the 'nests' or within a tangled mass of thick leaves or vines. The tails were held forward and curled close to the body, the sleeping position described by Moynihan [1970]. Their heads were oriented downward and toward the center of the huddle, thus obscuring the white crest. Small infants were carried on the ventral sides of group members. This series of behaviors would seem to have the effect of rendering the animals less conspicuous while reducing individual heat loss through huddling. Moreover, when huddled together as a unit, tamarins form a compact ball about half a meter in diameter, a structure which has a very un-tamarin-like appearance. Upon first seeing such a huddle, I actually thought that it was a termite nest. If other 'predators' perceive the huddle in the same manner, this may be an example, as Moynihan [1976] suggests, of crypsis or protective mimicry. Even if the huddle were perceived as animal, the visual size of the prey might deter the tamarins' smaller predators, particularly those with no experience with the sleeping configuration.

If the tamarins were disturbed within approximately 10 min of assuming the huddling posture, they usually left the tree. On 3 nights I unintentionally disturbed the group while trying to get close enough to see them. On these three occasions the huddle veritably exploded, with tamarins exiting in all directions. In each case the troop regrouped and settled into another sleeping tree within 15 min. In two other instances the reproductive (alpha) female left the group and moved slowly away, at the same time uttering low volume, high pitched, single notes of about a second's duration. After I followed her away from the sleeping tree, she returned to the group. This behavior pattern appears to be analogous to the wing-dragging displays of female birds protecting a brood. Both behaviors are probably effective in predator avoidance.

In the morning tamarins began moving in the sleeping tree at least 10 min before leaving it. Few vocalizations were uttered until after they had left the tree. Tamarins sometimes left the tree singly; at times two or three or the entire group left as a unit.

Patterns of Home Range Usage

That patterns of home range usage exist is evident from even a cursory examination of the preceding figures and tables. The salient factors which may

influence these spatial and temporal patterns include population density, territorial behavior, thermoregulatory behavior, antipredator behavior, foraging behavior, temporal and spatial distribution of resources, and cover types. Upon comparing the travels of the lowland group (fig. 3) with figure 2, which depicts those areas of the lowlands group's territory which are overlapped by other groups, the relationship between movements and territoriality is obvious. When the accumulated travels of the lowland group (fig. 3) are compared with the map depicting cover types in the group's home range (fig. 1) the relationship between cover type and usage is also apparent.

Daily Travels in the Home Range

The daily path length of *S. oedipus* in this study, when compared to known path lengths of other neotropical primates (table III), was second only to that of the squirrel monkey, *Saimiri oerstedii*. Both forms are insectivorous and frugivorous; the long daily path lengths reflect the longer distances necessary to obtain animal protein. The path length of the white-faced capuchin, *Cebus capucinus*, which is primarily frugivorous but somewhat insectivorous [Eisenberg et al., 1972] occupies an intermediate position. Howlers (*Alouatta palliata*) and the ti-ti (*Callicebus moloch*) are primarily frugivorous and folivorous [Carpenter, 1934; Mason, 1966]; their shorter daily path lengths reflect the nature of their less demanding diets.

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

Differential Utilization of Habitat Types

Chapman [1929] and Enders [1930, 1935] wrote that this tamarin preferred areas of second growth, and the latter author indicated that they were common in areas of low, brushy vegetation not inhabited by other primates. Moynihan [1970] stated that this callitrichid had a pronounced preference for the vegetation along the edges of taller forests. He further refined this general statement by noting that *S. oedipus* prefers to inhabit the 'vicinity of the edge' rather than 'the edge itself'. Moynihan also indicates that extensive areas of tall forest are not favorable for tamarin populations, citing as evidence the inverse relationship between forest succession and tamarin abundance on Barro Colorado Island in the Panama Canal Zone.

The above authors based their opinions on habitat usage by tamarins on visual observations made while gathering natural history and behavioral data. I chose to quantify habitat usage in order to provide additional, more definitive information regarding habitat utilization. The reader is referred to figure 1 for a breakdown of the lowland group's home range by habitat; the cumulative travels of the group are plotted in figure 2. Tables IV and V present data on time spent and distance travelled in each of eight habitat types as indices of habitat usage.

Areas of low brush and forest edge, as expected from natural history observations, were used to a greater extent than their availability in the environment would dictate. While path distance travelled in low brush was not greater than expected, the time spent within the area was significantly greater than expected. These values reflect the usage pattern for this habitat: intensive, multidirectional foraging. Areas of forest edge were used extensively for foraging activities, resting and grooming areas, and as primary arteries of travel. Intensive use of edge vegetation in foraging may reflect the greater abundance and diversity of both fruits and insects which commonly occur at such ecotones [Odum, 1971]. The abundant vines and the high foliage density also provide readily accessible escape cover from predators, a characteristic described and appreciated by Moynihan [1970].

The gallery forest of *Anacardium excelsum* was an important habitat in the daily activities of the lowland group. These tall evergreens were used extensively to escape solar radiation during the heat of the day. Some foraging for insects occurred in the upper levels of this habitat during the early morning hours and on several evenings; when the trees were in fruit during the latter part of the dry season and the early wet season, the fleshy pedicles above the fruits were preferred foods. This evergreen gallery forest was also an important source of insects at this time. The importance of *A. excelsum* as a sleeping tree influenced early morning and late evening movements within this habitat, which resulted in higher scores for both time spent and distance travelled within the habitat.

Habitat six, an area which, save for the abundance of emergent royal palms (*Scheelea rostrata*), resembled the forest edge habitat, was utilized heavily in foraging for insects and also as a staging area for disputes with the River Group, which occupied a home range to the south of this habitat type. The tamarins foraged widely in the palm crowns, and frequently used the fronds as arboreal runways. Thus my observations disagree with those of Moynihan [1970], who stated that this tamarin avoided palms and other monocots. The trapping records of Telford et al. [1972], who commonly captured this species on the ground in clumps of *Heliconia* sp., also cast doubt on the validity of Moynihan's observation.

Four habitat types were avoided by the lowland group. These included areas of open, seasonally deciduous forest, areas of open forest on mesic sites, a sparsely forested opening, and the grass which bordered roads and former ammunition bunkers. The forest habitat types which were avoided held one characteristic in common — their canopies were open, with a scarcity of vines. Productivity of tamarin foods in such areas may be lower than in denser forest types. Additionally, these areas may not have provided sufficient escape cover. That areas of grass were not used is surprising, since they abut the edge vegetation commonly used by tamarins and contain high densities of orthopterans, a preferred food item. Tamarins (which do forage on the ground occasionally, particularly during the dry season) could easily dash into the grass, capture several insects, and then return to the adjoining cover. One instance of such foraging activity was observed in a small strip of grass bordering an old road in another part of the study area. However, the increased risk of predation, and, particularly, increased vulnerability to aerial predators, may make the use of large areas of grass undesirable.

On the basis of the above findings, the 'ideal' mix of tamarin habitat appears to be areas of low brush and vine-covered 'edge' vegetation interspersed with taller, nondeciduous trees. The former habitat types provide both food and cover; the latter provides night roosts and shelter from the sun during the midday hours. Thorington [1968b] recognized the importance of this mixed habitat type in his observations of *Saguinus midas* in Guyana.

The Lowland Group vs. the Upland Group — a Comparison of Home Range Size, Home Range Utilization, and Territoriality

Bates [1970], in a review of territorial behavior in primates, stated that 'territorial relations between primate groups are far from universal, even among those species which do establish territories'. Struhsaker [1967a, b], in his study of the vervet monkey (*Cercopithecus aethiops*), found that home range and territory are functions of vegetational composition and distribution rather than group size. The validity and widespread applicability of the concept are recognized by Altmann [1974], who states, 'Home range overlap depends primarily on those essential resources with the most restricted spatial distribution; it will be low in relatively uniform habitats and will be extensive if several essential resources have very restricted distributions.' The temporal restriction of resources is also important, and I submit that the word 'temporal' may be substituted for the word 'spatial' in the above quote. For example, in Jolly's [1972] study, *Lemur catta* groups which had formerly lived in discrete, well-

defended territories, adopted a system of time-space segregation in response to a scarcity of food resources during a severe dry season.

In this study, the differences in the degree of overlap between the upland and lowland home ranges are striking. The entire home range of the lowland group was defended as a territory; hence the small degree of overlap. The home range of the upland group, on the other hand, was widely overlapped by five groups. Territorial defense, when defined as the defense of an exclusive area [Schoener, 1968], did not occur. Rather, the upland group appeared to defend the integrity of the area around the group at a given point in time rather than a fixed, geographical territory.

One might further differentiate between the use of space by the two groups by observing that the travels of the lowland group conformed to regular patterns of home range usage, while those of the upland group appeared to be more random. The size of the upland group's wet season home range exceeded that of the lowland group, which implies that wet season resources in the upland area, while possibly more abundant when considered as a whole, were less available to individual animals, thus necessitating widespread foraging. When resources became less available during the late wet season and the dry season, the upland group expanded its home range by at least 11 ha and wandered widely. Semimadic behavior on the part of upland groups was commonly observed in the late wet season and the dry season. In contrast, the telemetered lowland group, and other groups inhabiting lowland areas, maintained intact territories and patterns of spatial usage through this time of resource scarcity. DeMoor and Steffens [1972] observed similar contrasts in habitat usage between vervet monkeys (*Cercopithecus aethiops*) living in gallery forests and those inhabiting a sandy hillside.

The key to this disparity in usage patterns between upland and lowland groups appears to lie in the temporal distribution of resources. As Janzen and Schoener [1968] indicate, lowland and mesic areas along streams support relatively stable quantities of insects throughout the year, while the abundance and diversity of insect populations and communities, respectively, on upland sites may undergo seasonal oscillations of great magnitude, reaching a low in both parameters during the dry season. The abundance and diversity of fruit resources appear to undergo similar seasonal fluctuations.

The territorial pattern of usage exemplified by the lowland group is the expected pattern of usage for a territorial primate inhabiting a relatively stable, uniform habitat [Altmann, 1974]. The efficient exploitation of predictably stable, low-density food resources which occur in large patches, together with

the advantages accrued by living in an exclusive area, make territoriality a feasible utilization strategy for *S. oedipus* in lowland areas.

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

Differences in the temporal equability of home range sites available to tamarins have consequences beyond those mentioned above. While group sizes of upland and lowland groups do not differ, the tenure of subdominant animals of both sexes may be of significantly shorter duration in upland groups [Dawson, 1976, 1978]. Higher levels of emigration and immigration account for the major portion of the difference. Additionally, upland groups seem to exhibit lower natality rates and reduced infant survivorship when compared to their lowland counterparts [Dawson, 1976; Dawson and Dukelow, 1976].

Anderson [1970], in a consideration of ecological structure and gene flow in small mammal populations, divided potentially-suitable habitats into two categories: survival habitats and colonization habitats. In survival habitats, resources are relatively stable throughout the year, social group compositions are stable, infant survivorship is relatively high, and territoriality is practiced. In colonization habitats, resources are temporally discrete, social group's compositions are unstable, infant survivorship is relatively low, and time-space segregation is the modus operandi of subgroup segregation. In this context, tamarins in lowland sites may be thought of as inhabiting survival habitats, while those in upland areas may be thought of as inhabiting colonization habitats.

Anderson [1970] characterized the function of the survival component of the population as 'maintaining the ongoing population in both the ecological and genetical senses', and the function of the colonization component as 'a test of the full range of ecological and genetic variation under all of the accessible variations of the fundamental niche of the species', while, at the same time, providing for the dissipation of excess animals. Populations of tamarins inhabiting r-environments in Panama's dry tropical forest may also benefit from the exchange of animals and their genes between the two disparate habitat categories.

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