A Preliminary Field Investigation of the Yellow Handed Titi Monkey, Callicebus torquatus torquatus, in Northern Peru*

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REPPINTED FROM

PRIMATES

A JOURNAL OF PRIMATOLOGY

PUBLISHED QUARTERLY BY

JAPAN MONKEY CENTRE

INUYAMA, AICHI, JAPAN

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ABSTRACT. A three month field study was conducted on *Callicebus torquatus* near the Nanay River in northern Peru. Data were collected primarily by the time sampling method. Information on daily movement, vocalizations, population density, and social behavior is presented. The titi monkeys we studied have a family unit pattern of social organization, territoriality accompanied by vocal activity, and a home range of about 20 hectares. There is a high degree of parental investment in care of the infant on the part of the adult male.

INTRODUCTION

In 1964 and 1965 Dr. WILLIAM MASON conducted the first field study of a titi monkey, Callicebus moloch (MASON, 1966, 1968). MASON demonstrated three distinguishing features of the titi: a family unit pattern of social organization, territoriality accompanied by extensive vocal activity, and a relatively small home range. MASON's study was conducted in Socay Forest, an isolated 6.9 ha tract in Eastern Colombia. C. moloch has the smallest home range (0.5 ha) of any diurnal primate thus far studied (Jolly, 1972). No other field studies of Callicebus have been published, so it is difficult to determine to what extent the behaviors observed in Socay Forest were the result, in whole or in part, of the isolation and limitation of the small forest tract. The following report provides field data on a titi monkey from another location where the arboreal habitat is continuous for hundreds of km².

A family unit type of social structure is relatively rare among diurnal primates; yet, pair bonding may be the result of retaining a phylogenetically primitive anthropoid trait (EISENBERG, MUCKENHIRN, & RUDRAN, 1972). The study of another species of Callicebus, in a different habitat, will lead to a more complete understanding of the ecological correlates of this distinctive type of social structure. Callicebus torquatus does indeed share with C. moloch the three general behavioral features noted above, although there are important differences between the two species. The question is whether the differences between them are the result of differences in habitat, species, or a combination of both. The similarities, as well as the differences between the two species will become apparent in the brief report that follows.

^{*}A preliminary version of this paper was presented at the 73rd Annual meeting, American Anthropological Association, Mexico City, November, 1974.

THE STUDY SITE

The study site is in continuous virgin tropical rain forest in northern Peru, near the Nanay River, 30 km southwest of Iquitos, and about 4 km south of the *caserio* of Mishana (see Fig. 1). This is an area of black water streams, relatively poor in soil nutrients (JANZEN, 1974), which should be taken into account when considering the distribution of both its flora and fauna.

The study area is in the western Amazon basin, and the climatic conditions throughout the year are relatively constant compared to the lower Amazon. Annual rainfall in Iquitos averages over 2,500 mm and during the three months of the study the average daily rainfall at camp was 8.17 mm. Rain fell two out of every three days, with a maximum of 49.6 mm per 24 h period. Temperature ranged from a low of 15°C to a high of 32°C in the shade 1½ m above the forest floor. Average minimum night temperature was 20.5°C and average daily maximum was 27.3°C. Relative humidity reached 100% every night and fell to an average daily low of 83.0% at 14:00 h. The amount of daylight varied during the three month study from 11.90 to 11.98 h. Sunrise occurred between 5:56 and 6:02 and the sun set between 17:52 and 17:58 h.

The terrain consists of gently undulating hills, interspersed with small streams, supporting several types of vegetation. We have adopted the local Spanish terminology for the vegetation zones. A more complete description of the flora at the study site, together with a division of the major vegetation zones into subtypes, is available elsewhere (Revilla, 1974). A discussion of the relationship of *Callicebus torquatus* to the vegetation is presented elsewhere (Kinzey, 1977).

On the tops of the hills the vegetation is referred to locally as "varillal". Varillal is noninundated forest with relatively little ground cover, a lower story (up to 10 m in height) of short slender trees, and a middle story (from about 15 to 25 m) consisting of a dense closed canopy including the crowns of such trees as Rheedia (Guttiferae) and Eugenia (Myrtaceae). The upper story consists of occasional emergent trees (up to 30 or 35 m) such as Clarisia (Moraceae) and Hymenaea (Leguminosae), with

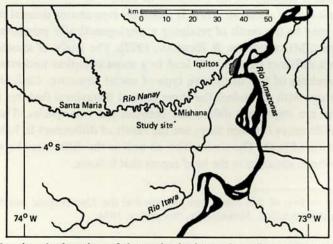


Fig. 1. Map showing the location of the study site in northern Peru, Departamento Loreto.



Fig. 2. Section



Fig. 3. Section of

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Callicebus torquin the Amazonas observe any sexua male and female i adult male is sligh

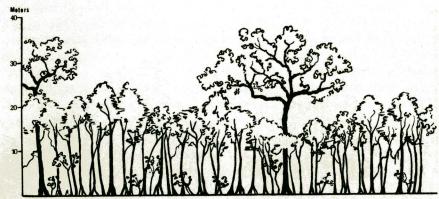


Fig. 2. Section of Varillal.



Fig. 3. Section of Irapayal.

undivided trunks for most of their height (see Fig. 2). Palms are virtually nonexistent in the *varillal* and the variety in species of trees is so great that no one single species could be said to be typical of this vegetation zone.

Along the edges of the streams, at the bottom of the hills, the vegetation is *irapayal* after the predominant woody plant in the area, the irapay palm (*Lepidocaryum*). *Irapayal* consists of a tremendous undergrowth of young irapay palms and lianas, a discontinuous canopy of irregular height, seldom reaching more than 25 m, and no upper story emergents. The ground is damp and may be temporarily inundated after heavy rains (see Fig. 3).

On the slopes, between the *irapayal* and the *varillal*, lies the *palmal*. As in the *irapayal* the ground tends to be damp (but never inundated), the undergrowth is heavy, and the canopy is irregular and discontinuous. There are occasional emergent trees, and there is a large variety of palms including ungurahui (*Jessenia polycarpa*), aguaje (*Mauritia*), casha-pona (*Socratea*), and shebon (*Scheelea*) (see Fig. 4).

Callicebus torquatus is the larger of the two partially sympatric species of Callicebus in the Amazonas River basin (Hershkovitz, 1963). Although Hershkovitz did not observe any sexual dimorphism in size or pelage, there is a slight difference between male and female in canine size (Kinzey, 1972). We also have the impression that the adult male is slightly larger than the adult female in the troop we studied. The pelage

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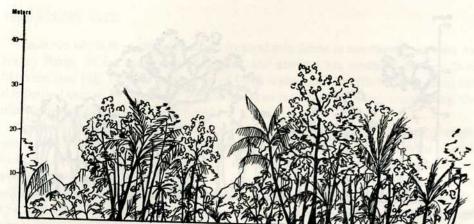


Fig. 4. Section of Palmal.



Fig. 5. Adult male Callicebus torquatus torquatus. Note the light colored hands and throat patch.

is rather uniformly reddish black, although the tail is blacker than the body. Two contrasting areas of coloration are a whitish to buffy colored throat patch and yellowish hands (Fig. 5). The throat patch does not extend like a collar around the neck, but occurs only on the ventral side of the neck. In the color of the hands *C. t. torquatus* contrasts with *C. t. medemi* from southern Colombia which has black hands. The third subspecies, *C. t. luqens* from Venezuela, northern Brazil and eastern Colombia, however, also has whitish or yellowish hands. The infant animal we observed has relatively longer hair, particularly noticeable in the tail which therefore appears more "fluffy." Otherwise the pelage of the infant is indistinguishable from that of the adults.

Other primates in the study area include Callicebus moloch, Saguinus fuscicollis,

Pithecia monachus, and Aotus trivirqatus. Cebuella pygmaea (KINZEY, ROSENBERGER, & RAMIREZ, 1975) and Saimiri sciureus occur within 5 km of the study area, primarily in inundated forest. Other primates, Alouatta seniculus, Ateles belzebuth, Lagothrix lagothrica, Cebus apella, and Cebus albifrons are said to have occurred near the study area within the last decade but have disappeared from the lower Nanay as a result of hunting pressure. Ateles may well be entirely absent from the Nanay River although the other species do exist 200 km up river (FREESE, 1975). Callimico goeldii was observed near Mishana several years ago (SOINI, 1972).

METHODS

We collected data in the study area from 4 June, 1974 through 25 August, 1974. A single troop (Group I) of three *C. torquatus* was studied intensively from 25 June through 18 August. Data were recorded simultaneously on all three members of Group I, which consisted of an adult male, an adult female, and an independently locomoting male infant. The infant fed himself (except for periodic suckling), and we estimated its age to be between four and eight months. We observed Group I on 25 days, totaling 138 h, and we followed its path of movement for more than 10 km. Observations were made from as early as 5:55 to as late as 17:45 h, and for as long as 10.9 h in any one day. The troop was observed for six complete days (see Tables 2 & 3) from dawn until it settled in a sleeping tree for the night.

Data were collected by time sampling (CROOK & ALDRICH-BLAKE, 1968; CHIVERS, 1974). Every five minutes the activity of each animal in the troop was noted, as well as its position in relation to the habitat and in relation to the other animals in the troop. The activity was recorded in one of four exclusive categories as "feeding," "locomoting," "resting," or "animal not observed." Summaries were then prepared for each animal, for each day, for each type of activity, for each vegetation zone, and for each level of the forest canopy. In addition, note was taken of other incidental behaviours in between the five minute samples, such as the time of entering and leaving each feeding tree. We noted each type of food eaten, marked each feeding tree, and in virtually all cases obtained a sample of each food eaten.

The troop was active for slightly less than 10 h every day, from the time of first movement to the time the group entered the night sleeping tree. The alert period ("the time from first movement to last," CHIVERS, 1974) was slightly more than 10 h, since the group always groomed intensively in the sleeping tree before settling down for the night. In order to standardize the measurement of activity for each day, the "day" was arbitrarily taken as 10.00 h. Thus, a "day" consisted of 120 time samples for each animal, or 360 individual time samples for the troop. All percentages of daily activity were based on these time samples. The time sampling began with the first movement of the first animal away from its sleeping position in the morning and ended arbitrarily 10.00 h later with from 5 to 60 min of "resting" including grooming at the end of the day.

Utilizing streams and trails as coordinating points an accurate map was constructed of the study area. Daily movement patterns of the troop were recorded by keeping compass bearings, and noting trail and stream crossings. By tracing these patterns on

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the map the path length and travel distance (MASON, 1968) each day were determined. All movement of the troop was based on measurement of movement of the adult male, since he was easier to follow than the female. Also, we did not trace the separate paths of the male and the female on every day.

The amount of time spent in each feeding tree varied from a few seconds to a maximum of 52 min. Feeding heights and tree heights were determined with an Abney level. There were limited numbers and kinds of trees in which all three animals remained feeding for 10 minutes or more. Such a sequence of time samples was called a "major feeding bout" and was defined empirically as any series of three consecutive time samples in which all three animals were feeding in the same tree, or the same species of tree.

Each food eaten was categorized as fruit, leaf, or insect. Each fruit was further classified on the basis of structure as berry, nut, soft seed, soft-fleshy (drupe or pome), legume, gelatinous aril, or palm. Leaves were further classified, whenever possible, as mature or immature. Insects were further classified, whenever possible, as hard (e.g., buprestid beetles), or soft (e.g., hymenoptera larva). All percentages of time spent eating were determined by counting the number of time samples.

RESULTS

(1) ONE DAY'S ACTIVITY

Following is a synthesis of our notes for July 24, 1974, to provide an example of the sequence of activities for an entire day.

At 6:00 (see Tables 1 a & b for time samples) all three animals are still huddled together where we left them last night, on a large horizontal branch, 23 m high in their sleeping tree. Dawn occurs at 6:01 local time. At 6:02 the female moves away from her sleeping place to another branch closer to the periphery of the same tree. (For the purposes of summarizing, the 120 time sample "day" begins with the next sample at 6:05.) Between 6:05 and 6:10 all three animals move out of the sleeping tree. The adult female is the first animal to move away from the sleeping position as well as the first animal to move out of the sleeping tree. She is quickly followed by the infant and the adult male. At the 6:10 time sample the female and infant are momentarily lost from view. By 6:12 the troop has traveled 10 m to a nearby *Clarisia* tree and begins a "major feeding bout."

(Typically the animals first stirred in their sleeping tree shortly before sunrise and moved out of the tree within 30 min. There was always at least one "major feeding bout" in the morning and generally the first occurred within an hour after dawn. If a feeding tree were not located near the sleeping tree, the group would move quickly after waking to a feeding tree. Once they moved to a tree 240 m away.)

The Clarisia (tree No. 61) is an emergent tree of 37 m height with a crown breadth of more than 20 m and a crown depth of about 10 m. The adult male and the infant feed in different branches a few meters from one another, while the adult female feeds at least 12 m away in the same tree. The foliage is dense, and although individual animals are lost from view occasionally, the constant dropping of nut shells easily identifies their locations.

Table 1a. One complete day's time samples of activities. Group I, Callicebus torquatus. July 24, 1974. Samples taken every five minutes. Some incidental data are included in footnotes. S=resting, F=feeding, L=locomoting, \$\preceq\$ =adult female, \$\preceq\$ =adult male, I=infant, *=animal not observed.

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¹⁾Begin "day"; ²⁾End "day"; ²⁾Major feeding bout; ⁴⁾Moving into sleeping tree, —) body contact, →) grooming.

Table 1b. Summary for day.

-	-	F	L	S	*	
Female	N	33	10	45	32	
	%	28	8	37	27	
Male	N	34	20	51	15	
	%	28	16	43	13	
Infant	N	37	23	51	9	
	%	31	19	43	7	
Total	N	104	53	147	56	
	%	29	15	41	15	

After feeding for 24 min, the troop moves 132 m to a liana, *Maripa*, which is only 67 m away by direct line. Here, beginning at 7:24, they feed on soft seeds for 46 min. Between 8:10 and 8:11 the troop leaves the *Maripa*. For the next two hours the troop meanders 55 m and eventually arrives at another major feeding tree, which is only 12 m from the Moripa in a direct line. During these two hours the female is about 15 m away from the male and infant, who remain within 5 m of each other. On several occasions a few young leaves are eaten by one or another of the animals, but most of the two hours is spent sitting in the middle story, "looking around," (for insects? for ripe fruit? or for predators?). At no time do the animals come into contact with one another, although the male is always very close to the infant.

At 9:57 we hear the hoot call (see "vocalizations") of another *C. torquatus* troop at some distance to the southeast (probably more than 200 m away and certainly outside the home range of Group I). The infant looks in the direction from which the call comes, but we do not observe any reaction to the call by the other two animals.

(Even when neighboring troops that might have been within the home range of Group I were heard to call, no reaction to their vocalizations was observed in our group (but see "vocalizations" below).)

At 10:16 the female moves into another liana, *Coccoloba*, and begins to feed. Within several minutes the other two animals follow suite. All three animals feed upon the purple liana berries until 10:47.

By 11:00 (midday by our definition: the middle of the 10 h day) the troop has moved 346 m from their sleeping tree. The morning has been heavily overcast. The animals appear to have been moving less than usual. The female moves off several times 30 to 40 m in some direction and the male does not follow. She then returns to within 10 or 15 m of the male, but soon moves in another direction. Since the path length is computed for the movement of the male, these additional movements of the female are not taken into account in the daily total.

(The path length covered by the middle of the day was less than the average path length of 417 m for the first half of the day. We have the impression that when the weather was heavily overcast and threatening, the animals tended to move less. More accurate data on cloud cover are necessary to confirm this. Although it was typical for the female to move first, followed by the male and infant, as she did this morning, it was not often that the male did not follow her. Whenever this happened, as on this day, the female returned and started off again in a new direction.)

The troop spends the remainder of the day alternately moving and resting, occa-

sionally feeding from the Cocco tree which is reathereafter the feinfant. They im three animals having. From then each other, and exactly the same ing (July 25), and during the night

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The daily activities are very small "unknown" categorioned on a 2:1 be "feeding" respectively procedure provide throughout the dapletely excluded a

Feeding activity in late morning, a sionally feeding upon leaves or berries, or foraging for insects. The path of movement from the *Coccoloba* is 250 m (compared with 160 m by direct line) to the new sleeping tree which is reached at 15:35 h. At 15:25 the male begins to groom the infant. Shortly thereafter the female moves into a nearby tree and is soon followed by the male and infant. They immediately huddle together with all three tails twined—the first time all three animals have been in contact since leaving their previous sleeping tree this morning. From then until we leave the troop at 16:25 all three animals take turns grooming each other, and frequently two or three tails are entwined. All three animals are in exactly the same position when we arrive back at the sleeping tree the following morning (July 25), and we presume that they have not moved from their sleeping branch during the night.

Three events occurred during the afternoon of July 24 which deserve special mention. Between 12:55 and 13:00 the infant came to the ground for 2 min 57 s. He appeared to be "playing," running, and jumping in some leaves. During this time the male came to within two meters of the ground and watched the infant intently. This was one of only four times that we saw the infant come to the ground voluntarily during the nearly 140 h of study. (See further discussion of play behavior, under "intragroup relations".)

The second event occurred between 13:40 and 13:45. The infant moved away from the male, whom he had been close to all day, and moved closer to the female, eventually contacting her, nudging her ventrum, apparently trying to nurse. She rebuffed him. After moving away for a few seconds he returned and this time the female allowed him to nurse for 1 min 10 s. Nursing occurred one to three times each day for up to 1½ min duration each time.

A rather unusual event occurred at 14:20. For about two minutes the two adults were in contact and during the second minute the male groomed the female. Generally we did not see the two adults in contact during the day although the male and infant were often in contact for short bouts of grooming and /or play.

(2) Daily Pattern of Activity and Movement

The time samples of activity for the six days on which there are complete data are summarized in Table 2. Our general impression is that the infant spent more time moving and feeding than did either adult. The differences among the three animals in Table 2 are not statistically significant, however ($\chi^2=3.95$, p>0.05).

The daily activity followed a pattern that is summarized in Figure 6. Since the chances are very small that an animal was "locomoting" when it was lost from view (the "unknown" category in Table 2), the "unknown" time samples have been apportioned on a 2:1 basis (the approximate ratio of the known samples) to "resting" and "feeding" respectively, in order to produce the curves in Figure 6. We believe this procedure provides a more accurate estimate of the changing ratios of activity throughout the day. (Curves produced by data from which the "unknowns" are completely excluded are essentially similar in shape.)

Feeding activity reaches a peak in the early morning, falls off, reaches another peak in late morning, and another in the early afternoon. As feeding activity declines, the

amount of immediately increase in lo

Table 2. Time samples for six days summarized for Group I of Callicebus torquatus.

	Feeding	Locomotion	Resting	Unknown	
Adult female	24%	12%	47%	17%	
Adult male	24	13	50	13	
Infant	31	16	42	11	
Group average	26	13	47	14	

Table 3. Path length and travel distance of Callicebus torquatus, Group I.

Day	Path length (m)	Travel distance (m)	Path length Travel distance		
July 22	621	260	2.4		
July 23	919	390	2.4		
July 24	466	180	2.6		
July 25	689	298	2.3		
Aug. 7	800	299	2.7		
Aug. 8	608	319	1.9		
Mean \pm S.E.	684 ± 65	291 ± 28	2.4 ± 0.1		

Table 4. Percentage of time samples that all three animals in Group I are engaged in the same activity.

	, ,	les in which Is are known	Unknown*	Percentage of different activities					
Date	Identical activity	Different activity		All differ	♀ differs	3 differs	Infant differs		
July 22	59%	41%	25%	5%	41%	27%	27%		
July 23	51	49	32	12	30	23	35		
July 24	71	29	36	0	55	27	18		
July 25	66	34	36	0	65	19	16		
Aug. 7	64	36	14	3	32	35	30		
Aug. 8	63	37	23	9	56	9	26		
Average	62	38	28	6	44	23	27		

^{*}Percentage of time samples in which one, two, or three animals are engaged in unknown activity.

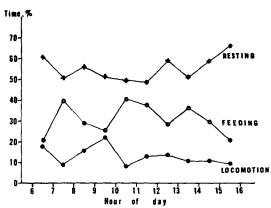


Fig. 6. Diurnal variation in activity pattern. Average for each hour of six days of time samples for all three individuals of Group I. Less than 5% of the activity after 16:00 hours is feeding and/or locomoting and has been excluded. "Unknown" time samples have been apportioned to "feeding" and "resting" as described in the text.

Fig. 7. Map of the on six complete of closed circles and Open rectangle is

amount of resting increases, and *vice versa*. There is a burst of locomotor activity immediately after dawn as the animals head for their first feeding tree, followed by an increase in locomotor activity between the two morning feeding periods.

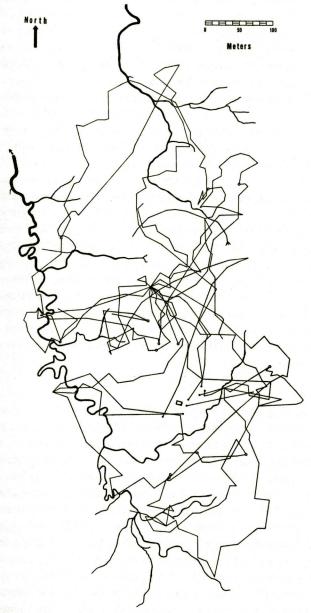


Fig. 7. Map of the home range of Group I of Callicebus torquatus, showing path of movement on six complete days and on parts of 14 additional days. Open circles indicate sleeping trees, closed circles indicate location of first contact on other days. Heavy irregular lines are streams. Open rectangle is the base camp.

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The paths traveled on all days or parts of days during which the location of the troop was plotted are shown in Figure 7. On six of these days the troop was followed for the entire day and these total daily path lengths are given in Table 3. The "path length" is the actual total path traveled by the adult male and the "travel distance" is the straight-line distance between the two most remote points in a day's travel (MASON, 1968). The average path length for a whole day was 684 m. We believe that the value of 684 m is actually an underestimate of the true average path length since on July 11, when we followed the troop for only part of the day, the path was 1,108 m in only 7½ h. Further, an estimate of the whole day's path length, based on adding half days (see below), is greater than 684 m.

As indicated in Figure 6, more locomotor activity took place in the first half of the day than in the second. The average path length for the first five hours of the day (N=9) is 417 ± 49 m; the average for the second five hours (N=9) is 300 ± 29 m. The resulting total of 717 m is greater (but not statistically so) than the average path length based on only six complete days of data.

The most frequent locomotor pattern seen in Callicebus torquatus was arboreal quadrupedalism. In only 0.1% of all time samples were animals on the ground. The majority of the time was spent in the middle story (52% of time samples). When the animals were in the lower story the most frequent activity (60% of time samples in the lower story) was resting. The most frequent activity in the upper story emergent trees was feeding (50% of time samples in the upper story). The majority of locomotor activity (66% of locomotion time samples) occurred in terminal branches as opposed to horizontal or vertical supports. Leaping, especially from the terminal branches of one second story tree to another was not infrequent. Leaping from one vertical support to another (6% of locomotion time samples) was also observed, during periods of feeding on berries in the lower story, provided that the support was small enough in diameter to grasp (KINZEY, 1977).

(3) SLEEPING TREES

The troop was observed entering its sleeping tree on 12 different occasions. In no case was the same sleeping tree used twice, even though on one occasion a tree was used that was within 15 m of a tree that had been used 10 days previously (see Fig. 7). The troop arrived at its sleeping tree as early as 15:35 h (on an afternoon when it was raining), and as late as 16:35 h, with an average time of 16:12 h. The animals always selected a horizontal branch of at least about 25 cm diameter, generally one of the first primary branches of an emergent tree. The height at which the animals slept varied from 17 m to 33 m, with an average of 25.1+1.4 m (N=12). More significant than the absolute height, however, was the height in relation to surrounding trees. In every case the animals slept on a branch that appeared to be just slightly above the surrounding closed canopy, with other branches of the tree above them (presumably allowing protection from flying predators). This position afforded the animals an excellent view of the surrounding jungle, and, since sound carries better above the tops of the trees than through the closed canopy, they were in a better position to hear vocalizations from neighboring troops, as well as to be heard themselves if they called at dawn. We were not able to determine any pattern to the location of sleeping trees; they

occurred both in the center as well as the periphery of the home range (Fig. 7). The troop left the sleeping tree in the moring between 6:05 and 6:26.

(4) DIET

A detailed description of feeding behavior is presented elsewhere (KINZEY, in press); the salient points are summarized here. The animals spent an average of 26% of their time feeding (see Table 2). Of the 2.6 h/day spent feeding, 65% of that time involved feeding on various kinds of fruits, 15% on leaves, and 16% on insects. During the remaining 4% of the time it was not possible to observe what the animals were eating. There was no significant difference among the three animals in percentage of time spent eating each kind of food. The kinds of fruits eaten varied considerably; however, there was one fruit that they ate nearly every day: the fruit of the ungurahui palm, Jessenia polycarpa. On the six complete days for which there are data (Tables 2 & 3), two "major feeding bouts" occurred in ungurahui palms on July 22, and one each on July 23, 25, and August 8. On August 7 they passed through an area with several ungurahui palms, but (according to field notes at 12:36 on that day) "They have been in an area of several ungurahui palms for 11 min and appear to have been looking for one with ripe fruit, but have not found one. Although the palm fruit in this area was eaten by the troop a month ago, there is no observable ripe fruit here now." On July 24 the troop spent most of the morning near a stream where we would have expected ungurahui palms, but we did not see any. Perhaps on that day there were such trees in the area, but none with ripe fruit. Of the 76 trees that the troop fed in during our study, 13 were J. polycarpa. All other species were represented by no more than four specimens each. Of 37 "major feeding bouts" during our study, 13 were in the ungurahui palm.

(5) VOCALIZATIONS

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Of the many vocalizations described by MOYNIHAN (1966) for *C. moloch* we tentatively identified four possibly homologous ones in *C. torquatus*: chuck notes, resonating notes, pumping notes, and chirrups. The chirrups were frequently uttered, during all times of day, probably by all three animals, and they seemed to be simply for localization among members of the troop. They were generally uttered in a slow series, very softly, so that they were often just barely audible at ground level.

A few chuck notes, followed by a long series of alternating resonating notes and pumping notes comprised a "song phrase" (MOYNIHAN, 1966) which could be uttered at daybreak (the dawn call of MASON, 1966), and/or later in the day as a group solidarity hoot call. We distinguish these two song phrases not only on the basis of time of occurrence, but also on the basis of differing positional behavior of the animals, and on possibly differing biological roles of the call.

The dawn call and the group solidarity call sound identical to us, (however, sound spectrographic analysis might reveal differences), and both calls probably express intragroup cohesion. Yet, following Marler's (1968) analysis, we feel that the two calls may function differently in their effect upon the spatial distribution of animals. We observed two group solidarity calls given by Group I and we did not see any attendant intergroup behavior. Similarly, we did not observe any intergroup activity

quently. (4)

following dawn calls, but MASON (1968) believed that in C. moloch the dawn call served as a distance maintaining mechanism. We did not hear the distance-maintaining "gobble" call so well described by MASON (1966) for C. moloch. The problem of spacing in relation to vocal communication requires considerably more data for adequate analysis.

Dawn Calls

When they occurred, dawn calls began shortly before sunrise. We listened for any audible dawn calls at or near camp on 47 mornings and calls were heard on only 31 (66%) of those mornings. They began as early as 5:29 and as late as 6:02, continued for two to seven minutes, sometimes until after sunrise. The average beginning time was 5:45 for the 31 dawn calls of various C. torquatus troops heard in the area near camp.

On 12 mornings we were with Group I at dawn. On only two (17%) of those mornings did the adult male utter a dawn call.

We could not detect any relationship of the dawn call to the location of other groups of titi monkeys or to the location of Group I within its own home range. For one dawn call, the troop was located at one of the four sleeping trees near the geographical center of the home range; for the other, the troop was located at one of the two sleeping trees at the northeast corner of the home range (Fig. 7). Other mornings, when the troop slept near these two trees, they did not utter dawn calls.

Perhaps the most remarkable aspect of the dawn call is the display that accompanies it. Both dawn calls were made solely by the adult male, and during the call he ran and leaped through the trees a distance of about 30 m. The female accompanied him, as though in a game of chase. The infant did not appear to play any role in the display. After the call was over, all three animals sat still for over an hour, most of the time in contact. The daily activity pattern that followed did not appear in any way different from that of a day on which a dawn call did not occur.

The distance over which the calls could be heard varied with the topography. We heard calls which we knew were as far away as 750 m; however, if the animals, or the listener, were in a valley or behind a hill, calls which were made by animals as close as 200 m were sometimes not heard. Although two or more listeners can locate a call by triangulating the angle from which it is heard, the muffling effect of jungle growth reduces the accuracy as distance increases.

There were no groups of C. moloch within calling distance of our camp, so on several mornings we listened for dawn calls about 750 m north of camp. On nine such mornings we heard dawn calls of C. moloch and on three of those mornings we also heard dawn calls of C. torquatus. The first dawn call of C. moloch occurred as early as 5:17 and as late as 5:37 with an average for the nine calls of 5:28. On the three days dawn calls of C. torquatus were also heard, their first calls were later than the first calls of C. moloch. These data for C. moloch discolor are in accord with those for C. moloch ornatus collected by Mason (1968) in which the earliest dawn calls occurred as early as 5:17.

Judging by our limited data on C. moloch together with the data of Mason (1966, 1968), the dawn calls of C. torquatus differ in the following ways from those of C. moloch. (1) They begin later in the morning, (an average of about 17 min later). (2)

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Vocal Interchan

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Group Solidarity Calls

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On one occasion, August 8, at 10:10 the male in Group I uttered a hoot call of 7 min 37 s duration. There was no elaborate display as with the dawn call, although before beginning the call the male lashed his tail violently as he sat apparently staring at the female 30 m away. During the call the male sat on a large horizontal branch without moving, except to lash his tail and once to turn around. A significant difference between this call and the dawn call was the behavior of the troop before and after the call. During the morning prior to 10:10, the infant had spent most of his time close to the female instead of the male. On several occasions that morning the female moved in a direction different from that of the male. Both these behaviors are unusual; it appeared to us that the group was not behaving as a cohesive unit. Following the male's call, the infant and male sat in contact for the first time since early that morning and, except for two brief nursing bouts at 10:59 and 13:50, the infant stayed close to the male the remainder of the day. The female appeared to stay closer to the male-infant pair than she had before 10:10; she did not move away in a direction opposite from theirs as she had done earlier in the morning. Because of this obvious change in behavior following the call we have termed it a "group solidarity hoot call" to emphasize the unification of the troop's behavior following the call.

Two similar calls were given by the male on July 12, at14:30. They were of much shorter duration (37 s and 60 s respectively, with a brief interval in between). They occurred after the female had been a long distance away from the male and infant for about half an hour, and missing from our view for part of that time. We did not hear her respond to either of his two calls. Half an hour later, the female (still missing from our view) called and the male and infant immediately ran about 80 m to where she was.

Vocal Interchanges

On two occasions we observed a vocal encounter between two troops of C. torquatus. The first occasion was on the morning of July 27. We heard a hoot call beginning at 7:20, about 200 m southeast of camp, near the edge of the home range of Group I. The call continued for four minutes. At that distance it was not possible to determine whether more than one animal, or even whether more than one group, was calling, but since the call was similar to the hoot call of the male in Group I, we assumed it was uttered by a single individual. We arrived at the group of five animals (Group II) shortly after the call had ended. At 7:37, while we were beneath Group II, another group (Group III) began to call from a point at least 20 m to the north; simultaneously, Group II moved south, and we followed them. That call lasted 2 min 40 s and although it sounded like more than one animal, we could not be certain. When this call ended there were a few moments of quiet, then from above us an animal in Group II began to call and that call lasted for slightly more than a minute during which time Group II continued to move south, and then turned west. After a few moments, Group III called again for about a minute. After this, the only vocalizations we heard were a long series of soft chirrups from individuals of Group II, resting above us.

These vocalizations lasted several minutes. Then, Group II moved again, to the west, and by 8:15 we had lost them.

The second occasion occurred on August 8 at 8:15. A neighboring group (IV) began a hoot call from at least 100 m west of our camp. The call lasted about a minute. After about a half a minute of silence Group I (which was at the south edge of the camp) responded with a call of 1 min 5 s duration. Group IV called again for about a minute and, after a brief interval, Group I called for 1 min 48 s. No further calls were heard from Group IV, but Group I, after 30 s silence called for 21 s, then 29 s silence, and a final call of 25 s. The entire interchange lasted less than 15 min, after which Group I remained in the same vicinity feeding for about half an hour. We did not observe any apparent movement of Group I away from the direction of the call of Group IV, and there was no elaborate visual display as in the dawn call.

These are the only two instances for which we have first hand information about intergroup encounters in *C. torquatus*. Neither time was there evidence of physical contact between members of the two groups, nor evidence that they were even in the same tree together. We heard several hoot calls from neighboring troops, similar to those described above, at various times of the day during the course of our study. We cannot be certain, of course, that hoot calls, heard from more than several hundred meters away, were not the result of intertroop confrontations like those described by MASON (1968).

(6) PREDATORS AND HAZARDS

A large predatory bird (Harpia?) was observed catching Callicebus moloch elsewhere in Peru (C. Freese, pers. commu.). In our study area we saw the Harpey eagle (Harpia harpyja) one time, but we did not observe the reactions of monkeys to this or to any other bird of prey. On numerous occasions large birds (parrots, vultures) flew over our troop but the monkeys appeared to ignore them. The potential effect of predators such as the Harpey eagle on monkey populations should not be underestimated, however. The one study of Harpia in its natural habitat (Fowler & Cope, 1964) noted that by far the predominant prey at two different nest sites were monkeys.

There were footprints of a large felid seen within the home range of Group I but, similarly, no evidence was seen of interaction with the monkeys.

Man is potentially the most successful predator of nonhuman primates. Hunters may have frequented the study area prior to 1972 when the conservation area was established, but since then hunting has been forbidden. Even where hunting does occur, *Callicebus* is not among the principal sources of food of rural hunters (NEVILLE, 1974).

There is a very high rate of tree fall in the area around the study site. This is probably because of the rather poor soil and very shallow root system of most of the trees, coupled with the strong winds that often blow. We heard the crash of at least one large falling tree virtually every day. When a large tree fell near the Group I infant, the male immediately uttered an alarm. The infant was far enough away from the falling tree that he was not injured.

Another potentially dangerous situation is the fall of an animal from a tree. On

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three occasions we saw the infant fall to the ground from as high as 30 m, but he always got up apparently unhurt. We never saw an adult animal fall.

(7) POPULATION DENSITY

The home range is roughly 750 m north-south by 400 m east-west (Fig. 7). The calculated area of the home range for Group I of *C. torquatus* is 20 ha. This is the area contained within a line connecting all the outermost points of the daily path lengths. If there were no overlap of home ranges and troops had contiguous boundaries this would be a population density of five troops/km² or about 15 animals/km² if the average troop size were three individuals. We observed adjacent troops of *C. torquatus* within the home range of Group I on three occasions. In no case did the adjacent troop move more than 100 m into Group I's home range, nor did it appear to do more than move straight into the range and then straight out again, in two cases following hoot calls. (In neither case did we see which group made the call.) We estimate that there is at most a 10% overlap in home ranges of adjacent troops.

The calculated home range of 20 ha represents less than three months of the year and thus underestimates what the home range would be on an annual basis. We were recently informed, for example (R. Castro, pers. commu.), that during November, 1974, Group I moved through an area of 15,000 m² (1.5 ha) which they had not previously utilized.

We counted three troops of *C. torquatus* near the study site with the following troop counts: three (Group I), five, and three. The average troop size thus appears to be between three and four individuals. This compares with the average value of five individuals per groop given by TOKUDA (1968) for *C. torquatus* along the Rio Putumayo in Colombia.

(8) INTRAGROUP RELATIONS

According to Mason (1966, 1968) Callicebus moloch is pair bonded, and C. torquatus also appears to live in pair-bonded groups, with strong intragroup cohesion. Intragroup cohesion is demonstrated by the high frequency of identical activity, of contact between animals at the sleeping site, and by the short interpersonal distance between animals within the group.

Simultaneous Activity

On each of the six days for which there are complete data, all three animals are engaged in the same activity in more than 50% of samples in which all animals are identified (Table 4). In 62% of samples for all six days the animals were engaged in identical activities. Of those time samples in which one or more animals were engaged in different activities, in only 6% was each of the three animals engaged in a different activity. In the remaining samples, the female was the animal most often engaged in an activity different from the other two. This reflects the fact that the male and infant were most often close together and engaged in similar activity, while the female was usually some further distance away, often feeding while the other two were resting, or vice versa. Of the 62% of samples in which all three animals were engaged in identical

Field Study of Calli

activities, 55% described resting, 31% feeding, and 14% locomoting. The samples in which all three animals were feeding simultaneously primarily reflected the major feeding bouts.

Contact Between Animals

As has been mentioned, the infant and male were together most of the time, while the adult female was apart from them much of the time. Rarely during the study were all three animals in contact, except in the sleeping tree. This did occur on July 22 when all three animals rested in contact for 35 min following the dawn call (see "vocalizations" above). On three other days, at 11:00, at 12:00, and at 12:45 all three animals were momentarily in contact during long periods of resting. This was related to the presence of a slight peak in "resting" activity between 12:00 and 12:55.

Except while in the sleeping tree, contact between the male and female was observed only once during the six days of complete time samples, at 14:20 for a brief grooming episode. The infant and female were only observed in contact when the infant was nursing. Several times every day the male and infant were in contact, either resting, grooming, or occasionally sitting with tails twined. On July 22, the day on which the most male-infant contact occurred, during 64% of resting time samples the male and infant were in contact. Although there were occasional male-infant contacts scattered throughout the day, 60% of the male-infant contact time samples occurred either between 6:00 and 6:55 or between 14:00 and 14:55. The morning contact always occurred immediately after a major feeding bout and the afternoon contact also occurred within one hour of a major feeding bout, and (in the afternoon, at least) was generally accompanied by grooming.

Analysis of inter-individual distances between animals of Group I will be presented elsewhere. Our general impression, however, is that most of the time during the day the male was closer to the infant than either of them were to the adult female. Sexual behavior was not observed.

Grooming

Grooming is an activity that occurred every evening in the sleeping tree. Grooming was never observed in the morning in the sleeping tree before the animals moved toward their first feeding. It occurred sporadically throughout the day between the male and infant as mentioned above. The bout of grooming at the end of the day generally involved mutual grooming among all three animals. We observed no apparent order of who groomed whom, although a more detailed analysis might reveal some pattern in the grooming activity. Autogrooming was not observed, although animals occasionally scratched themselves. The evening grooming bout lasted, off and on, for as long as $1\frac{1}{2}$ h, before the animals finally settled down in their sleeping positions for the night.

Play

Behavior which can best be described as play occurred several times in Group I. The infant played alone, and play occurred between the infant and the adult male.

On four occasions the infant came to the ground. One time he ran and jumped among the stilt roots of a tree for about 5 min; a second time he played on the ground for 20 min and even ran between the legs of one of us; the other two times he ran around

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(9) INTERGE

In contra most a con the more th of titi mon on the ground for 2 min 57 s and for 58 s. All four occurrences were in the afternoon, between 12:55 and 15:20. On two of these occasions the adult male came briefly to the ground; the other times he sat, near the ground, watching the infant. Although these terrestrial activities might be interpreted as something other than play, they were relatively uncommon, and provided exploration of a unique aspect of the environment. They did not appear to involve looking for, much less obtaining, any food item.

During the day when the male and infant were together their bouts of grooming were often interspersed with the infant's rolling around the limb of the tree, swinging below the branch momentarily, or grabbing the tail of the adult male. The male's behavior is best described in these situations as manifesting tolerance toward the infant. We did not observe any behavior on the part of the female, the male, between the infant and female, or between the two adults that we could describe as "play" behavior.

Role Differentiation

Although, as in *C. moloch*, there is no clear dominance within the troop, there is an apparent differentiation of roles between adult male and adult female. The role of the female appeared to be to lead the group throughout its daily ranging pattern. She was generally the one who went to look for new sources of food. She was virtually always the first one out of the sleeping tree in the morning, as well as the first one into the sleeping tree at night. She was usually the first one into any new feeding tree, and similarly the first one out of the tree at the end of the feeding bout. Nevertheless, the role of the male appeared to be that of directing activity of the group. This was evident particularly on the two days when he gave group solidarity calls. It was also evident in that virtually every day there was at least one occasion when the female moved off in one direction, looked back and observed that the male and infant were not following her, returned to within a few meters of him, and headed off in a new direction until the pair followed her.

The other obvious role of the male was to care for the infant. This was an extension of behavior common among platyrrhine primates (Callithricidae, Aotus and Callicebus), in which the infant at an earlier age was carried by the male except when nursing. When we first observed Group I the infant was already locomoting independently from its parents, but we presume that at an earlier age, as in C. moloch, he was carried by the adult male. At what age the infant ceases to remain close to the male, and whether a female infant would remain as close remains to be determined. It is interesting, however, that in the siamang, which is also pair-bonded, the infant (which was a female in the troop studied by CHIVERS, 1974) was also closest to the adult male most of the time.

(9) INTERGROUP AND INTERSPECIFIC RELATIONS

In contrast to the *C. moloch* groups studied by MASON (1966, 1968) there was almost a complete absence of intergroup activity in *C. torquatus*. On no occasion during the more than 130 h of observations did Group I come into contact with another troop of titi monkeys. We know that at least two, and probably four to six, troops had home

ranges nearby (and perhaps contiguous with or overlapping) the home range of Group I, because we observed other troops within their home range on two separate occasions, both when Group I was elsewhere in its range. On two occasions we observed vocal interchanges between troops of *C. torquatus* (see "vocalizations"), but the groups did not come into physical contact.

On three occasions we observed Group I in the same trees as a troop of Saguinus fuscicollis. On all three occasions the tamarins were lower in the canopy than Callicebus, moving in approximately the same direction, only diverting their direction amidst loud chattering after we were observed by them. Apparently even before we were observed, the tamarins were very noisy in contrast to the very quiet titis.

It certainly appeared advantageous to the titis for attention to be diverted away from them by the loudly chattering tamarins who were not only more vocal, but moved more rapidly at a lower, more readily visible, elevation. The two species were observed in close proximity for 10 min, 15 min, and 45 min on the three occasions. We could not determine how many tamarins there were; twice three were counted, and once four, but all three times we felt there probably were more than four individuals. On no other occasion did we observe interaction between *Callicebus torquatus* and any other mammalian species.

DISCUSSION

The data presented here, while still preliminary, are the first field data on the behavior of Callicebus torquatus. They indicate that while the two species are similar in being pair bonded, there are major differences in behavior between C. moloch and C. torquatus. Most of these differences appear to be interrelated and are perhaps due to smaller home range in C. moloch than in C. torquatus. It is now important to determine the size of home range of C. moloch groups outside of Socay Forest. According to Mason (1968) C. moloch in Colombia has a home range of about one half hectare, whereas Group I of C. torquatus has a home range of 20 ha, or roughly 40 times that of C. moloch. Related to this difference are the longer path length, much longer travel distance, and lower ratio of path length to travel distance in C. torquatus. Similarly, the relative frequency of dawn calls in C. moloch is probably related to the higher density of troops and the increased probability that two groups might be in close proximity to one another. MASON observed face to face encounters virtually every day; we did not observe any face to face encounters during our study, and only vocal interchanges, in which the two groups were at least 20 m apart. Another factor that may be related to the relatively small size of the home range in C. moloch is the limited number of trees that were used as sleeping trees. In contrast we never observed the group to sleep in the same tree twice, even though on three different nights they slept in trees whose trunks were within 35 m of each other.

Whether the difference in home range and the concomitant differences in behavior between the two species are the result of differences in habitat, rather than in species specific behavior, will have to await the study of *C. moloch* in an area of continuous tropical forest.

It may be enlightening to make some comparisons with other pair bonded primates,

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What is these pair is behavior c his own you knowledge sposing to tions dese such as the gibbon and siamang. CHIVERS (1974) has provided an excellent summary of the behavior of the siamang, Symphalangus syndactylus, in Malaysia. Despite the fact that the siamang is ten times larger, utilizes a completely different locomotor pattern, and is 65% folivorous compared to the titi, which is 65% frugivorous (both do eat leaves and fruit), there are some striking similarities in social organization and activity pattern. Both species are pair bonded, have an average troop size between three and four individuals, and have home ranges of similar size. (When data were collected over a five year period, however, the siamang had a home range nearly double that of our group of C. torquatus. Chivers, Raemaekers, & Aldrich-Blake, 1975.)

The spatial distribution of group members is similar in both species. The entire group generally feeds in the same tree. When either traveling or resting, groups of both species are dispersed over less than a 30 m area. Also, the daily path length (day range of CHIVERS) is almost identical (684 m cf. 698 m), when comparison is made with data for the wet season in the siamang-this season is similar to that in which we found Callicebus in terms of rainfall, cloud cover, humidity, and temperature.

There appear to be similar mechanisms for maintenance of territory. Both species maintain their territory with loud dawn calls, though in both cases the calls do not occur every morning and they both range near their borders frequently. Siamang chase neighboring groups out of their range, but we cannot be certain whether C. torquatus would do likewise if a group were contacted within its range. Both species sleep high in the canopy where visual and aural cues are picked up over a greater distance than in the closed canopy. Basic differences in anatomy dictate that Callicebus sleeps close to the trunks of trees on large horizontal branches, whereas the siamang sleeps in the terminal branches. Nevertheless, both locations are above the closed canopy and afford an opportunity to see and hear at dawn, whether or not conspecifics are impinging upon their home range.

Perhaps the most remarkable similarity between the siamang and the titi is the division of roles between male and female. In both species there is a high degree of group cohesion. Using a similar statistic the siamang group is involved in identical activity 73% of the time and the titi 62% of the time. Within the group the female has the role of leading the group, especially to sources of food, whereas the male coordinates and directs the activity of the group. In addition, the male stays close to the infant, whether the infant is male (this study) or female (CHIVERS' study). We have attempted to show that the adult male titi plays an active role in guiding and caring for the infant, which is an extension of paternal behavior observed in many platyrrhines beginning soon after birth. Among hylobatids the paternal assumption of care apparently begins later in infancy (Carpenter, 1940; Chivers, 1974) whereas in other catarrhines the infant is carried by the mother.

What is the significance of this division of labor between adult male and female in these pair bonded groups? What is the adaptive significance of the various correlated behavior convergences in these two primates? The greater the parental investment in his own young, the greater their chances of survival (TRIVERS, 1972). Perhaps the knowledge of paternity on the part of the adult male is an important factor predisposing to increased paternal care of the infant. We can only suggest that these ques-

tions deserve further consideration.

SUMMARY

A troop of three Callicebus torquatus, consisting of an adult male, an adult female, and a male infant, were observed in continuous tropical rain forest for 138 hours. Using the time sampling method of collecting data we determined that the group spent 26% of the observed time samples feeding, 13% locomoting, and 47% resting. During 14% of the sample time the animals were not seen. There were no significant differences in frequency of activities among the three animals. By following the group for six complete days and parts of 14 additional days we determined a home range of 20 ha, which is considerably larger than that previously determined by MASON for C. moloch. Vocalizations included dawn calls and group solidarity calls, neither of which occurred every day. Significant differences from C. moloch occurred in the timing and patterning of vocalizations. Most of the grooming took place late in the day, in the sleeping tree, for up to an hour and a half before the animals went to sleep for the night. All three animals took turns grooming each other. There was a marked differentiation of roles between the adult male and female. The former looked after the infant and coordinated activities of the group; the adult female led the group throughout its daily ranging pattern. The difference between observed behaviors in C. torquatus and those reported by MASON for C. moloch may be species specific, the result of differences in habitat, or a combination of both.

Acknowledgements. The field station at which this investigation was carried out was established under project AMRO-0719 on the conservation of Peruvian primates, sponsored by the Pan American Health Organization (PAHO) in cooperation with the Peruvian Ministry of Health. We are especially indebted to Dr. Pedro Acha, Chief of the Department of Human and Animal Health, PAHO, to the PAHO field consultants, Melvin Neville and Curtis Freese, and to Rogerio Castro of the Instituto Veterinario de Investigaciones Tropicales y de Altura (IVITA) who is the Peruvian director of the field station. Without their continuing and unselfish efforts in establishing and maintaining the field station, our study could not have been undertaken. Numerous people aided us in one way or another and we thank them all. In particular, for assistance in planning and preparation in Iquitos we thank Napoleón and María Castro, Erwin and Hilda Schreiber, and Curtis and Marge Freese. For assistance in the field we are indebted to Juan Revilla, Andrés Mármol, Marleni Ramírez, and our many friends in Mishana, especially our guides PABLO PIZARRO and RAMÓN RAMÍREZ. A special vote of thanks goes to our miraculous handyman and boatman, Antonio Rojas. We thank Juan Revilla, Robin Foster, and Sidney McDaniel for identification of plant specimens. We are grateful to AUDREY STANLEY for the illustrations. For critical and helpful comments on the manuscript we thank Curtis Freese, Melvin Neville, Mary Pearl, DAWN STARIN, and ROBERT SUSSMAN. The study was supported by grant FR-10067 from the City University of New York and by a grant from the Explorers Club, both to W. K.

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-Received September 22, 1975; Accepted March 12, 1976

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