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Among Neotropical monkeys, members of the subfamily Pitheciinae, with three genera and eight species, are among the least known with respect to their ecology and behaviour (Hershkovitz, 1972, 1979; Napier, 1976).

All pitheciine species are similar in being medium-sized (1.5-3.6 kg), diurnal, arboreal, and frugivorous; however, there are some major differences among their social structures. For example, the bearded sakis, *Chiropotes*, and uakaris, *Cacajao*, live in multimale troops (Fontaine, 1981; van Roosmalen et al., 1981; Ayres, 1981), whereas the sakis are reported to live in smaller monogamous groups ranging from 2 to 6 individuals (Izawa, 1975; Muckenhirn et al., 1975; Buchanan et al., 1981; Happel, 1982).

Several accounts in recent literature (e.g. Muckenhirn et al., 1975; Moynihan, 1976; Neville, 1976; Hernandez-Camacho & Cooper, 1976; Mittermeier & Coimbra-Filho, 1977; Ayres & Milton, 1981; Ayres, 1981; Freese et al., 1982) provide basic information on the genus *Pithecia*, especially regarding population density and general aspects of the ecology in their natural habitats. Others (e.g. Fooden, 1964; Izawa, 1975; Izawa & Yoneda, 1981) provide information on diets of *P. pithecia*, *P. monachus* and *P. hirsuta* through analysis of stomach contents of wild shot specimens. More recently, Buchanan et al., (1981), Mittermeier & van Roosmalen (1981), Fleagle & Mittermeier (1980) and Happel (1982) collected more detailed information on the general aspects of the ecology and behaviour of *P. pithecia* in Surinam and *P. hirsuta* in Peru.

The geographical range of the Guianan Saki (*Pithecia pithecia*) is confined to the north bank of the Amazon River west of the Rio Negro as well as the coastal forests of northern Brazil (Amapa Territory) and the Guianan countries (Hershkovitz, 1979), an area of approximately 1.350.000 km². *P. pithecia* is the most sexually dichromatic

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species in the genus. Males are uniformly black with the contrasting facial mask and the front part of the neck ranging from pale white or yellow to dark brown (perhaps varying geographically). The females are predominantly dark brown dorsally and paler ventrally. The females of this species are quite similar to both sexes in *P. monachus*. Six adult males collected by INPA and FSESP biomedical programs had mean body weights of 1.97 kg and body lengths of 358 mm. The females (n=3) weighed 1.59 kg and were 330 mm in length (Table 1).

Study Site and Methods

This research was carried out in a forest reserve belonging to the Tropical Hotel, located on the left bank of Negro River near the Tarumã-açu Tributary. The area is roughly 30 km west of Manaus, comprises a little over 20 hectares and is completely surrounded by a 2m high fence which protects it against intruders and hunting. The area is bounded by the Rio Negro to the south, the grounds of the Tropical Hotel to the east and secondary forest to the north and west, separated by marginal dirt roads.

The climatic data for the Ducke Forest Reserve (INPA/CNPq), 24km northeast of the city of Manaus (Ribeiro & Villa Nova, 1979), probably applies as well to the study site. The average annual rainfall is 2,478mm. According to Thornthwaite's (1948) water balance method, this region is characterized by two distinct seasons. The wet season, from December to June, has an average of 970 mm of water excess; and the dry season, from August to the middle of November has an average of 28 mm water deficit in the soil.

Five physiognomic vegetation types are distinguished in this area (Figure 1). A) Logged forest, about 35%, characterized by absence of emergent trees which had probably been removed by selective logging. Remaining trees range from 20 to 30 m height. B) Campinarana (6%) characterized by white sand soil, with cover lower than that of the former. C) Old secondary forest (45%): the original forest had been partially removed and the area is characterized by small trees, shrubs and lianas. This vegetation has a low biomass and never exceeds 15 m in height. D) The remaining 2% consists of patches characterized by the abundance of palms.

The monkey population of the study site in 1981, consisted of eight *P. pithecia* and one or two groups of *Saguinus bicolor bicolor*.

In October 1980, approximately 9 km of trails were established, dividing the whole area into 50 m x 50 m quadrats to provide better access to the monkeys and facilitate data quantification. The results described here were gathered during 45 days of research throughout 1981, but the bulk of it was obtained at the end of January and the beginning of August (18 days). In these periods, it was possible to contact the monkeys on 128 occasions, and each time they were located, we followed them for as long as possible. These sightings lasted from a few minutes to almost four hours. The monkeys were never habituated to the observers, but if the group was lost, it was possible to relocate them the same day.

Population Density and Structure

In 1981, the population of sakis in the study area consisted of two adult males, three adult females, one male and one female subadult (or young adult), and an infant female. Various combinations of individuals were sighted on 80 occasions during the course of the study (Table 2), and the population appeared to consist of three social groups of variable stability (Table 3). The most stable group was "A", consisting of an adult male, an adult female, and an infant female, born late 1980. Members of this family were invariably found together. Group "B" consisted of one adult male and two females (one adult and the other subadult or young adult). Although these animals were sighted less frequently than those in Group "A", they seemed to be a new group which had formed during the time of the study, probably of individuals from the other two groups.

The female "C" was probably from Group "B" since she was usually found with those individuals during the first period of observations. However, between the January observations and those in July, her time with male "C" increased from 8% to 24%. The male "C" probably originated in Group "A" since in the first period it was seen in 12% of the observations with this group while in the next period it was only seen in 5%. Another possibility for these changes within the population is the seasonality and availability of food in that area, but there are no data on the phenology of the trees. In any case associations between individuals were not uncommon and they have an apparently flexible social structure. Associations of 7 individuals (A + B + a female) were more common in the first half of the year.

The mean group size in the study area was 2.7 individuals. Another group of the species, observed in lowland primary forest at the Dimona Farm, 80 km north of Manaus, had three individuals. Other reports on group size for this species are given by Muckenhirn et al. (1975), Buchanan et al. (1981). These authors saw a total of 19 groups of this species in the Guianas and their mean size was 2.9 with a range from 1 to 5 individuals. It is likely that these authors may have seen occasional associations between groups, but the basic social unit, was the family composed of one adult male, one adult female and their offspring.

Freese et al. (1982) report 20 sightings of *P. monachus* with a mean group size of 2.8 and a range from 1 to 8 individuals. Happel (1982) reports 4 groups of *P. hirsuta* in Peru, with a mean group size of 4.5, ranging from 4 to 5 individuals.

Population density for the area was 40 individuals km² or 55-60 kg/km². This is a higher density than found at any of the six study sites surveyed by Freese et al. (1982) in Bolivia and Peru for *P. monachus*. It is also higher than those reported by Buchanan et al. (1981) and Muckenhirn et al. (1975) for *P. pithecia* in Surinam and Guiana. This is probably due to isolation of the study site and absence of other competing primates as well as the ability to conduct an accurate census of all individuals.

Diet

On 29 occasions, individuals of *P. pithecia* were observed feeding on vegetable

material. In 62% of the observations they were feeding on ripe mesocarps, 17% on immature seeds, 14% on flowers and on one occasion they were feeding on young leaves of *Trymato-coccus amazonicum* (Moraceae), and the shoots of another plant of the same family, *Cecropia scyadophylla*. Most of the mature mesocarps belonged to the palm trees, *Mauritia flexuosa* and *Oenocarpus bacaba*. In January and February, when fruits of the former are available, they fed mostly on this species, of which there were 8 trees in the whole area. In July and August, they seem to have a more varied diet, including both seeds and leaves. Flowers were only eaten in February from three different families: Bignoniaceae, Leguminosae and Passifloraceae (Table 4).

Because the animals never became habituated to the observers, there is a large chance of bias in our sample. First, it is based on spot observations, not time spent feeding. Secondly, fruits are more easily recorded in the sample because we could observe what had been eaten when the parts dropped to the ground. It is unclear whether they feed on animal matter. On one occasion after a monkey had left a tree, we found some empty pupae which had been opened a few minutes earlier. Fooden (1964) and Mittermeier (Buchanan et al., 1981) found only fruits in the stomach contents of *P. pithecia*, although Izawa (1975) and Izawa and Yoneda (1981) found leaves mixed with insects for two other species of this genus. Buchanan et al. (1981) document 22 feeding observations for *P. pithecia* in Surinam and found 54.5% feeding observations of seeds and 36% mesocarps. These authors also report flower eating for the species. Happel (1982) reports 16% of feeding bouts on leaves, 53% of ripe mesocarps and 18% of seeds (legumes and other fruits) for *P. hirsuta* in Peru.

Ranging Behaviour, Habitat use and Periods of Activity

The eight individuals of *P. pithecia* used an area of 13.5 hectares, or 67% of the total area available (Figure 2). The home range of Group "A" was between 8 and 9 hectares (Figure 3) and there was a considerable amount of overlap between this group and the other individuals of *P. pithecia*. The core area of group "A" was only 2.5 hectares.

It was never possible to follow the monkeys from sunrise to sunset. Our longest record of continuous contact was almost four hours during which the group travelled 635 m. Most of the time, however, the monkeys were fleeing from the observer. Sometimes the animals were spotted several times during the same day and on such occasions, we could estimate a day range length, which was found to be between 0.3 to 0.5 km.

To estimate the habitat preferences for the individuals in the area, we have used an index of habitat selectivity ("S") which was calculated as follows.

$$S = \frac{\text{Relative frequency of monkey sightings in that forest type}}{\text{How much of that forest type was available (\%)}}$$

Thus, higher values for "S" indicate areas that have been selected (Table 5.) The

results show that the sakis used the logged forest 1.5 times more often than they used the secondary forest. However, if we examine the selectivity, use of logged forest is 2.5 times greater because there was less logged forest available than secondary. The preference for the other two vegetation types does not differ much from that found for the secondary forest.

Buchanan *et al.* (1981) report a variety of different habitats for the genus including high forest, mountain savannah forest, liana forest, ridge and secondary forest. In the Voltzberg Nature Reserve in Surinam, 42.2% of the total observations (N=31) were in high forest, but they do not mention how much of each type of forest was available. Our data confirms that *P. pithecia* can live in a wide variety of habitats. Despite this potential to live in a wide range of vegetation types, they have a higher selectivity for less disturbed forest types.

Most activity occurs in the morning and early in the afternoon between 0555 to 1300 hs. In only 10% of the occasions were the animals seen active after 1300 hs. It is not clear, however, why they stop their activities so early, although it may be related to the limitation of resources due to the isolation of the area.

Interactions with the Pied Tamarin (*Saguinus bicolor bicolor*)

On several occasions Group "A" was seen passing near one of the groups of *S. b. bicolor*, although the two species were never seen in the same tree during our observations. There is a high degree of overlap between home ranges of these species, but the space used by *S. b. bicolor* is greater than that of *P. pithecia*. Also, the sakis preferred the central portion of the reserve while the pied tamarins could be seen in the new secondary patches. *P. pithecia* never made use of that vegetation.

Buchanan *et al.* (1981), Mittermeier and van Roosmalen (1981) and Happel (1982) report associations between *Saguinus* sp. and *Pithecia* and with other primate genera. On some occasions, these two genera were seen feeding on the same tree. It is possible that since both genera can make use of secondary growth forest and other similar habitat there is a higher probability of finding them together, but it is not as common a relationship as reported, for example, by Fleagle *et al.* (1981) for *Cebus apella* and *Saimiri sciureus*.

Reproduction and Parental Care

It is possible that the infant from group "A" was born in the end of November or December 1980. On November 20th we did not see an infant among the individuals of *P. pithecia*. When we renewed observations in January of the following year, however, we saw the female infant. No copulations were seen in this population. An infant is normally carried by the female until at least the end of the second or third month when it becomes partially independent of the mother; even though it is still unable to travel alone

for even short distances. Most of our observations were on group "A" because it was the easiest to follow. Since the adult could not flee without the infant, carrying it required them to move more slowly than the other group in the canopy. Because it was not as agile, it rarely came to the lower strata, but remained in the canopy where there are more branches and where locomotion is, therefore, easier for the infant.

On the first series of contacts, the distances from the observer were never less than 30-40 m. On these occasions, the adult male would remain in an intermediate position where it could see the observer, while the female and infant moved away some 50 meters. They would signal the male with a whistle and he would rejoin the group.

On other occasions the female and infant remained immobile, hidden in the canopy of the tree while the male moved up to 100 m away to attract our attention. Then the female would move away with the young.

On three occasions, the male was with the infant while the female was nearby, but he was never seen carrying the infant.

Locomotion

White and brown-face sakis (*P. pithecia*) are amongst the most spectacular leapers of all Neotropical primates (Fleagle & Mittermeier, 1980), as indicated by their common name of "monos voladores" (flying monkeys). During the course of our observations, we made notes on locomotor behavior of the monkeys and in late July and August made quantitative assessments of their use of different locomotor patterns.

Leaping is the most common locomotor pattern used by sakis and accounts for nearly 75% of their locomotor activity (Figure 4) when they are travelling about their home range, either in moving between food trees or fleeing potential predators. The leaping ability of the sakis enables them to exploit a wide range of forest types, where the arboreal supports may be horizontally discontinuous. In travelling, the sakis leap between all combinations of horizontal branches and vertical trunks.

Quadrupedal walking and running are much less common than leaping when the sakis are travelling. In general, they seem to be rather awkward quadrupeds, probably because of their relatively long legs.

Sakis rarely use any type of suspensory behavior. They occasionally climb up lianas, vines and various small tree trunks. Between leaps, the monkeys frequently use a series of rapid hand holds to change direction or to pull up on top of a branch, an activity that is probably responsible for the reports of "brachiation" in this genus. We never saw any extended bouts of purely bimanual progression.

We have less quantitative data on locomotion during feeding and on habitual postures. Like most primates (e.g. Fleagle & Mittermeier, 1980; Fleagle, 1980), sakis seem to rely less on leaping and more on quadrupedal walking when they are feeding rather than travelling. Sakis use both seated postures and frequently vertical clinging postures when feeding and resting. The latter are particularly common on lianas and

vertical tree trunks (Figure 5).

These observations in Brazil are virtually identical with those of the same species in Surinam (Fleagle and Mittermeier, 1980; Buchanan *et al.*, 1981) which portray these animals as prolific leapers. Mappel (1982), however, describes *P. hirsuta* in Peru as being more quadrupedal, although leaping did account for almost one third of this author's observations. Earlier reports on *Pithecia* as slow sloth-like animals almost certainly are based on the animal's frequent habit of hiding from observers, viewed as potential predators, or quietly slipping away through tangled vegetation.

Discussion

In many aspects, our observations of *Pithecia pithecia* from Manaus agree with those of others who have studied this species elsewhere (Buchanan *et al.*, 1980; Fleagle & Mittermeier, 1980; Mittermeier & van Roosmalen, 1981). The data suggest they are small, saltatory frugivores which live in a variety of forest types where they seem to frequent the understory and lower canopy levels. In gross diet, general dental features and digestive tract *Pithecia* resembles *Chiropotes* (Fooden, 1964; Hershkovitz, 1977). The two genera of Pitheciinae differ, however, in body size, social organization, habitat preferences, canopy use and locomotion. In contrast to *Pithecia*, *Chiropotes* lives in larger groups of up to 26 individuals (which can break down into smaller foraging units); is largely restricted to *terra firme* primary forests; prefers the middle and upper levels of the main canopy; and is almost exclusively quadrupedal (Ayres, 1981; van Roosmalen *et al.*, 1981; van Roosmalen & Mittermeier, 1981). How are these differences functionally interrelated in the different strategies used by these genera for exploiting the same Amazonian region?

The small individual size, small group size, leaping, understory use, and broad preferences of *P. pithecia* are almost certainly interrelated. Arboreal primates which frequent the understory and lower canopy levels are usually excellent leapers because this part of forest usually has few horizontal branches, but many vertical supports such as tree trunks and lianas, which can best be visited by leaping across horizontal gaps (Fleagle, 1978; Fleagle & Mittermeier, 1980; Fleagle, 1983). Leapers also seem to do better in secondary forest for similar reasons (Fleagle, 1980). At the same time, mobility and visibility are likely to be somewhat restricted in this milieu. As small monkeys living in small groups, *Pithecia pithecia* can subsist on fewer resource units spread thinly throughout forest. Likewise, they can find sufficient suitable resources in a variety of habitats.

Bearded sakis, *Chiropotes*, in contrast, travel quadrupedally in large groups searching for massed food supplies. They cover large home ranges (up to 300 hectares). They use the middle and upper canopy levels in primary forest, which enables them to move rapidly along fairly continuous horizontal networks of branches and also permits considerable intergroup visibility on those occasions when larger groups break up into smaller units.

These differences are most apparent during the period when there is a shortage of potential foods (Alencar et al., 1979). In the first period of our study, equivalent to the beginning of the wet season, the sakis tended to feed on ripe mesocarps of fruit rich in protein and fat such as *Mauritia flexuosa* (Aguilar et al., 1980) and larger associations were more common in this period. In Aripuanã (MT, Brazil) *Chiropotes albinus* fed at the equivalent time of the year on fruits such as *Astrocaryum vulgare*, *Caryocar villosum* and *Onychopetalum amazonicum* (for which they have the highest selectivity) which are rich in fat and protein as well (Ayres, 1981). In other periods, seed predation increases for *Chiropotes albinus* while *P. pithecia* has a more diversified diet, including young leaves, shoots and flowers.

As Happel (1982) reported, one of the most interesting features of *Pithecia* is that there is absence of territoriality in a monogamous primate. Territoriality among animals is related to the extent to which food sources and mates are defendable. In *Pithecia*, the question still remains because the population studied in this case could be a single group, since we found a great flexibility in their social structure. Usually members of genus *Pithecia* are not found continuously throughout the forest; they seem to have a clumped distribution in certain sections of the terra firme. A study of more than one of these clumps is obviously needed in order to clarify if *Pithecia* is or is not an exception among monogamous primates.

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Table 1. Body weight and length of wild shot *Pithecia pithecia* in the Brazilian Amazon by the parasitological and virus research programmes of INPA and FSESP.

Sex	Age	Body Weight (kg)	Head & Body Length (mm)	locality
M	?	?	230	Manaus
M	?	1.47	334	Manaus
M	Ad.	1.76	351	Manaus
M	?	1.38	306	Manaus
M	Ad.	1.65	330	Trombetas
M	Ad.	1.95	345	Trombetas
M	Ad.	2.50	390	Trombetas
M	Ad.	2.15	390	Trombetas
M	Subad.	1.55	365	Trombetas
M	Juv.	0.39	210	Trombetas
M	Ad.	1.80	340	Trombetas
F	?	1.25	292	Manaus
F	Ad.	1.77	352	Manaus
F	Ad.	1.75	330	Trombetas
F	Ad.	1.26	310	Trombetas

Table 2. Group size and composition for the population of *Pithecia pithecia* living in a 20 ha forest, west of Manaus, on the left bank of rio Negro (1981).

Unit	Adult male	Adult female	Subadult male (*)	Subadult female (*)	Infant male	Infant female	Total
'A'	1	1	-	-	-	1	3
'B'	1	2	-	-	-	-	3
'C'	-	-	1	1	-	-	2

(*) = or young adult.

Table 3. Associations between groups and individuals of *Pithecia pithecia* in the reserve on the left bank of the rio Negro west of Manaus (only 1st sight observations were used in this sample).

Association	Jan-Feb. no. obs. (n=25)	Frequency (*)	Jul-Aug. no. obs. (n=55)	Frequency (*)
'A'	10	40	12	22
'B'	2	8	7	13
'C'	2	8	7	13
'C'-M	0	0	8	15
'A'+M	3	12	3	5
'B'+ 'C'	0	0	6	11
'A'+F	0	0	5	9
'A'+ 'B'+F	3	12	0	0
'B'+F	2	8	1	2
'C'-F	3	12	3	5
'B'+ 'C'-F	0	0	1	2
'A'+2F	0	0	1	2
2M	0	0	1	2

M = adult or subadult male; F = adult or subadult female.

Table 4. Foods and feeding frequency of *Pithecia pithecia* in the study site on the left bank of the rio Negro, west of Manaus, Amazonas, Brazil in 1981 (n=29 obs.).

Species	Family	Part eaten	Freq.	Habit	Height	Month(s)
<i>Mauritia flexuosa</i>	Palmae	Mature mesocarp	8	tree	25	Feb., Mar.
<i>Oenocarpus bacaba</i>	Palmae	Mature mesocarp	5	tree	8	Aug.
Species nº 1 (NI)	Bignoniaceae	Flower	2	liana	12	Feb.
Species nº 2 (NI)	Bignoniaceae	Young seeds	1	liana	7	Jun.
<i>Passiflora</i> sp.	Passifloraceae	Flower	1	liana	6	Feb.
<i>Inga</i> sp.	Leguminosae	Mature mesocarp	2	tree	12	Jan., Jul.
<i>Clitoria amazonica</i>	Leguminosae	Flower	1	liana	5	Feb.
<i>Maximiliana</i> sp.	Palmae	Mature mesocarp	1	tree	4	Feb.
<i>Couma utilis</i>	Apocynaceae	Mature mesocarp	1	tree	12	Jul.
<i>Simphonia</i> sp.	Guttiferae	Young seeds	3	tree	13	Jul.
<i>Trymatococus amazonicum</i>	Moraceae	Young leaves	1	tree	6	Jul.
<i>Qualea retusa</i>	Vochysiaceae	Young seeds	1	tree	15	?
<i>Cecropia scyadophylla</i>	Moraceae	Young shoots	1	tree	6	Jul.
<i>Bellucia</i> sp.	Melastomataceae	Mature mesocarp	1	tree	7	Jul.

Table 5. Selectivity of *Pithecia pithecia* for four different vegetation types at the reserve, on the left bank of the rio Negro, west of Manaus, Brazil.

Type of vegetation	Absolute frequency (sightings)	Relative frequency (%)	Total disponible	Selectivity ('S')
Logged forest	117	0.58	0.35	1.66
Secondary forest (old and new)	76	0.38	0.27	0.67
Campinarana (white sand)	7	0.03	0.06	0.50
Palhal (Palm patches)	2	0.01	0.02	0.50
TOTAL	202	1.00	1.00	-

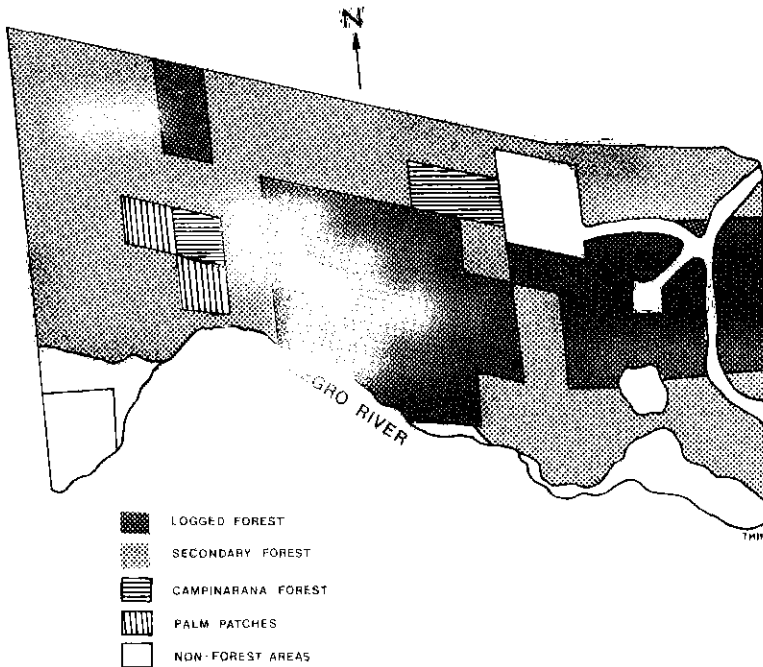


FIG. 1 - Study site and the distribution of five physiognomical vegetation types in the area.

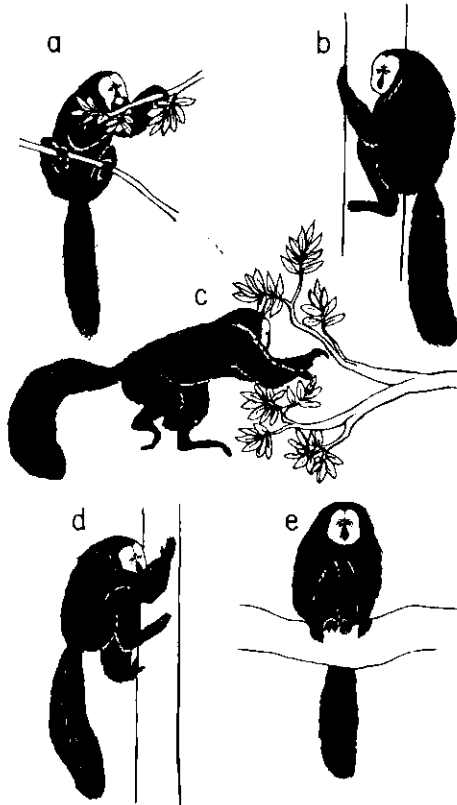
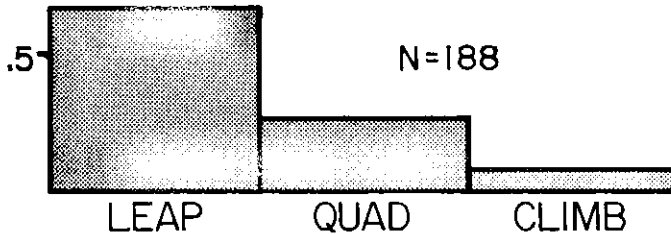


FIG. 4 - Typical locomotion and postural activities in *Pithecia pithecia*. a) Sitting and feeding on a branch. b) "Vertical clinging" on a trunk. c) Leaping into foliage. d) Climbing up a vertical trunk. e) Sitting on a bough.

BOUTS OF LOCOMOTION DURING TRAVEL



DISTANCE TRAVELED

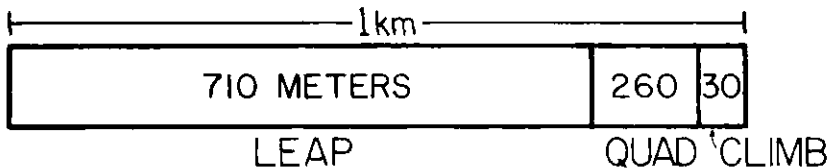


FIG. 5 - Quantitative analysis of the locomotor behavior of *Pithecia pithecia* showing percentage of locomotor bouts devoted to leaping, quadrupedal walking and running, and climb and the contribution of each of these locomotor activities to each kilometer of travel.

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