5. SOCIAL ORGANIZATION

5.1. **Introduction**

The social organization of spider monkeys is quite unsual among primates and thus far only chimpanzees have been found to exhibit a somewath similar system (Azuma and Toyoshima, 1962; Reynolds and Reynolds, 1965; Goodall, 1973; Sugiyama, 1973; Bygott, 1974; Wrangham, 1975). The similarities between spider monkey and chimpanzee organization is discussed in chapter 7.

Spider monkeys live in *social groups, networks* or *communities* (Carpenter, 1935; Klein, 1972; Klein and Klein, 1975; Cant, 1977). Klein and Klein (1975) defined a social group of spider monkeys as 'a network of animals that usually interact peacefully with one another, while different groups are separated from one another by agonistic interactions'. For *A. paniscus* a more comprehensive definition is used. A social group of spider monkeys is here defined as an established number of animals, that all use the same area ('home range') and usually interact peacefully with one another, with only the adult males acting territorially and respecting clearcut boundaries. According to this definition groups are separated from one another by agonistic interactions conducted by the males, mainly by means of calling behavior and with considerable distance between opposing animals. Very occasionally, a sort of boundary conflict was observed. It was initiated by one or more males near the boundary and consisted of very agitated long calling and barking. This usually caused a rush of nearby subgroups towards the spot. During these rare incidents, its was not possible to observe individuals of both groups at the same time because of the distance between opponents, but probably visual contact also took place between the two groups high in the canopy or in emergents. Males of different groups were never observed attacking one another, but this may happen. Carpenter (1935) reports on few instances of fighting males, and collected several specimens showing large scars on hands, shoulders and head.

In A. paniscus, females usually stay within the boundaries of a group's range but occasionally visit members of neighboring groups for periods ranging from several hours to about one full day, sometimes even staying overnight with members of adjacent groups. These visits appeared to be undertaken particularly by females with newborn infants, and they seemed to involve showing the infant to the neighboring group. At these times, several members of the resident group were seen clustering around mother and infant, touching and sniffing the infant carefully. Agonistic behavior by any member of the resident group towards the visitors was never observed during these visits. Once, in the late afternoon, I followed two females and a juvenile-3 male over more than one kilometer outside the home range, where they contacted some members of the adjacent group and stayed overnight with them. The journey was initiated by the leading female after she heard a male of the adjacent group repeatedly giving long calls far away. When crossing the group's range boundary, they left behind another female with a juvenile-2 and a male, previously belonging to their subgroup. In this particular case no newborn infant was involved. This behavior may be explained as visiting one or more relatives since there are indications that emigration may take place, especially in the case of young females.

5.2. **Group Size, Group Composition and Age Classes**

One of the most striking characteristics of spider monkey social organization appears to be that all members of a given group can never be observed in the same place and at the same time. At the end of the field period, the study group consisted of 18 animals: thre adult males, eight adult females, one subadult female, tour juveniles (one juvenile-3 male, one juvenile-2 male, two juvenile-2 females), and two infants (one infant-1 female, one infant-2 male). The largest subgroups ever observed in the study group contained nine individuals, and consisted of either three males, four females and two juveniles, or of two males, four females and three juveniles. Two other groups that were regularly encountered in the Raleighvallen-Voltzberg Nature Reserve contained 15-20 individuals, of which three or four were adult males. The overall impression is that the study group can be regarded as an average group according to group size and group composition.

For *A. paniscus*, age classes are distinguished in the field and differentiated on the basis of size and dependence on the mother. Compared with data given by Klein (1972) for *A. belzebuth*, by Eisenberg

(1976) for *A. fusciceps* and *A. geoffroyi,* and by Cant (1978) for *A. geoffroyi,* dependence on the mother in infants and juveniles appears to be prolonged in feral *A. paniscus.*

Infants are clearly divided from juveniles by their invariably being carried by the mother during progression. Infant-1 (I1) animals cling to the ventrum of the mother and range from zero to six months of age. Infant-2 (I2) animals ride on the back of the mother and range from six to 12 (or even 15) months of rage. In the intermediate phase, for about two weeks, infants were seen clinging at the lateral side of the mother during progression. Infant-2 animals become more and more independent in locomoting, while the mother rests. They usually start to eat solid food but are still highly dependent on the mother for nourishment. The color of the coat in infant *A. paniscus* is the same as in adults, but naked face is paler. The skin around the eyes and on the muzzle is more darkly pigmented and gradually changes to light pink in juveniles or subadults and to pinkish or bright red in adults.

Juveniles usually locomote independently during progression, but stay permanently with the mother and are still nursed. Three size classes are distinguished. Juvenile-1 (J1) animals are 12 (or 15)-24 months of age. They are usually independently locomoting. However, when they seem to be fatigued (as when the group is traveling with increased speed) or during aggressive display of subgroup members they still may ride on the mother's back. Also, gaps between adjacent tree crowns are usually crossed with the help of the mother, who may bridge the gap with her body or leap across the gap with the young juvenile on her back.

Juvenile-2 (J2) animals are 24-36 months of age, and are able to keep up with a fast-moving subgroup. They were never observed riding on the mother's back and bridging was observed only very rarely. Eisenberg (1976) reports that in captive *A. fusciceps* and in free-ranging *A. geoffroyi* of this stage, juvenile males show an increasing affiliation with subadult and adult males. This pattern of affiliation was also observed in wild *A. paniscus*, but Klein (1972) did not observe it in feral. *A. belzebuth.* When meeting with other males, many times juvenile males (but never juvenile females) were observed mutually embracing, pectoral sniffing and swiffing each other's scrotum. Weaning usually takes place at the end of the juvenile-2 stage, although suckling behavior was also observed in juvenile-3 males. Weaning in *A. belzebuth* is estimated to occur between two and three years of age (Klein, 1972), and in captive *A. fusciceps* Eisenberg (1976) observed intermittant suckling until 18 months of age.

Juvenile-3 (J3) animals are 36-50 months of age and stay with the mother most of the time. They play mainly with juveniles of about the same age or with adults. Juvenile-3 animals were ofter observed taking the initiative in leaving a food source and traveling in front of a subgroup in some parts of a route, that had been followed one or more times before. Juvenile-3 males start to share male long-calling and develop their own long call by trial and error.

Subadults are 50 to about 65 months of age. Female subadults were observed to stay almost permanently with the mother, even after the mother had given birth to an infant. Subadult males, however, were never observed to form a prolonged association with mother and infant, and they seemed to range independently from the mother. Subadults could be distinguished from adults by their face color and pigmentation and by their denser fur.

5.3 Group Range and Day Range Length

The annual home range of the spider monkey group in the Voltzberg study area covered 255 hectares, of which 220 hectares offered suitable habitat in the form of high forest, high mountain savanna forest and pina swamp forest. The perimeter of the group's range was determined for a greater part by natural boundaries, such as open granite flats, rocksavanna, low forest and liane forest. In areas where the range bordered the ranges of adjacent groups, it appeared to be clearly defined and non-overlapping.

Few estimates of home range size are available from other areas. Dare (1974) noted a range of 100-115 hectares for the *A. geoffroyi* group reintroduced on Barro Colorado Island. Klein and Klein (1976) estimated ranges of about 260-390 hectares with 20-30% overlap for *A. belzebuth* in La Macarena National Park in Colombia.

Travel distances from day to day were highly variable for *A. paniscus* in the Voltzberg study area, depending on the subgroup size and composition, the weather and the season, and the distribution patterns of particular food plants. Straight-line distances between the consecutive food sources and sleeping trees used in one day could range from 500 meters (e.g., for a solitary ranging male or non-leading female during the long dry season) to 5,000 meters (e.g., for a subgroup led by a female during the long wet season). Klein (1972) gives minimal day ranges from 500 to 1,800 meters, and estimates the upper range of straight-line distances to be as large as 4,000 meters. For *A. geoffroyi* on Barro Colorado Island the upper range is given as 3,000 meters (Richard, 1970).

5.4. Grouping Behavior

Members of a spider monkey group associate in temporary *subgroups* or *parties* of changing composition and variable size. As a criterion for determining which individuals belong to a particular subgroup or party, mutually interdependent actions in feeding and traveling were used. For example, one female usually travelled about 50 m behind a subgroup that consisted of a minimum of one male, one female and one juvenile. She kept her distance because of agonistic interactions with the male (in particular when feeding on the same food source), but was nonetheless considered part of the subgroup. Also, when a party split but both subgroups obviously kept in visual and/or auditory contact while traveling from one food source to another, and following slightly different routes, all animals were considered to belong to one subgroup during that period.

As stated before, several females can easily be recongnized as leading a subgroup and determining daily itineraries and activity patterns of the subgroup as a whole. These females usually leave the sleeping tree first, travel in front of the subgroup most of the time, always feed on the food sources that determine the route that is taken, and initiate most activity patterns. They appear to possess a better knowledge of available food sources within the 'core areas" than other adults. To this end, they follow the constantly changing phenological picture by frequently monitoring different food plants to determine stage of flushing, flowering or fruiting. Regularly, in particular during the late afternoon, leading females were observed checking certain food sources in order to incorporate them into the itineraries of the days or weeks to come. While the female conducted these activities, the rest of the subgroup associated with this female could be observed traveling towards a well-known food source or sleeping tree nearby. When the leading female was accompanied by a juvenile, the offspring might follow her, or play in the meantime with another juvenile or adult, or remain with the traveling members of the subgroup. Figure 39 shows travel paths determined by a leading female, while she lead the frequently changing subgroup on consecutive days (i.e., on February 11, 12, 13 and on February 15, 16, 17, 18, 1978).

The route taken by a leading female seemed to be preplanned and highly economic, and used the shortest possible connections between consecutive food sources (as shown in figure 39). Doubling-back rerely took place, and when it did, it seemed to be caused by confusion (e.g., after meeting and joining with anothe subgroup and following a route determined by the other leading female). By constrast, solitary or non-leading females seemed to be incapable of planning an economic route along a large number of food sources without making some loops and using certain important and well-known food sources repeatedly. Also, knowledge of available food sources and their exact locations appeared to be restricted among these animals, and resulted in a less varied diet (during the period in which they were on their own) that was mainly composed of foods from particular food sources wellknown to most or all members of the group. For males and nonleading females it would appear to be advantageous to regularly join subgroups led by a female in order to learm, through conspecific cueing (Kiester and Slatkin, 1974), about food sources avaible at the moment.

In total, four leading females could be recognized in the study group, and three of them were permanently accopanied by a juvenile at the end of the field period. One leading female did not have offspring. Most observations were of two leading females, one with a juvenile-3 male and one with a juvenile-2 female, that used partly overlapping core areas with the camp situated about in the center during most of the year. The combined core area was situated roughly between B8 and B20 (fig. 40). In addition to the two leading females and their associated juveniles, two males and two nonleading females without offspring (one of them gave birth to an infant at the very end of the field period) were encountered most frequently in this area.

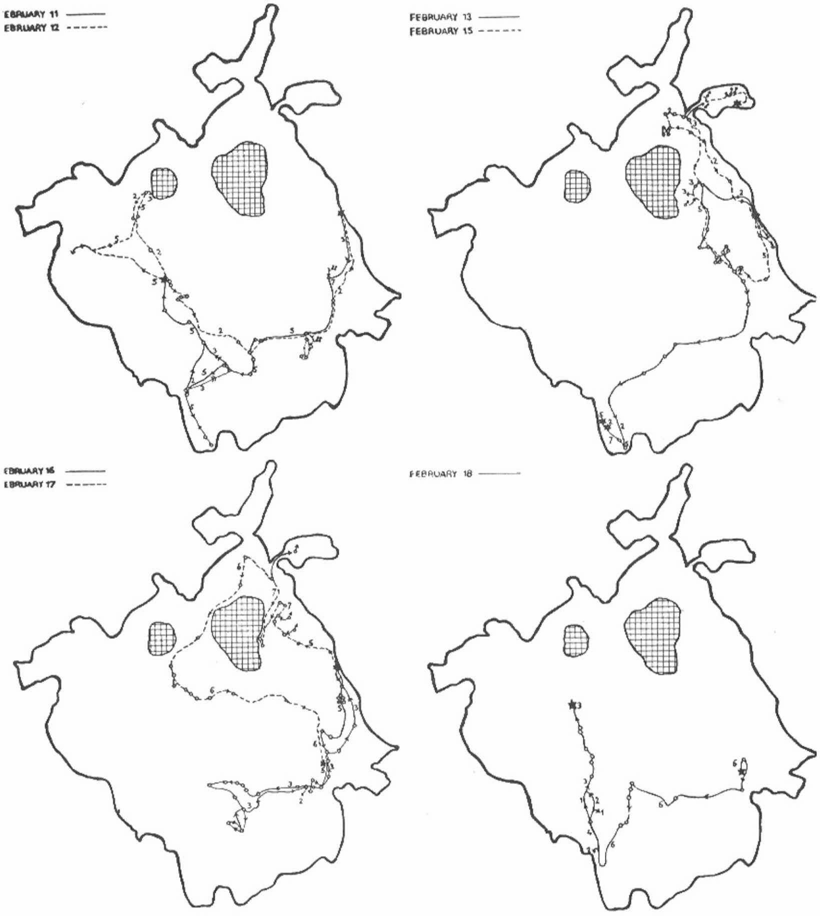
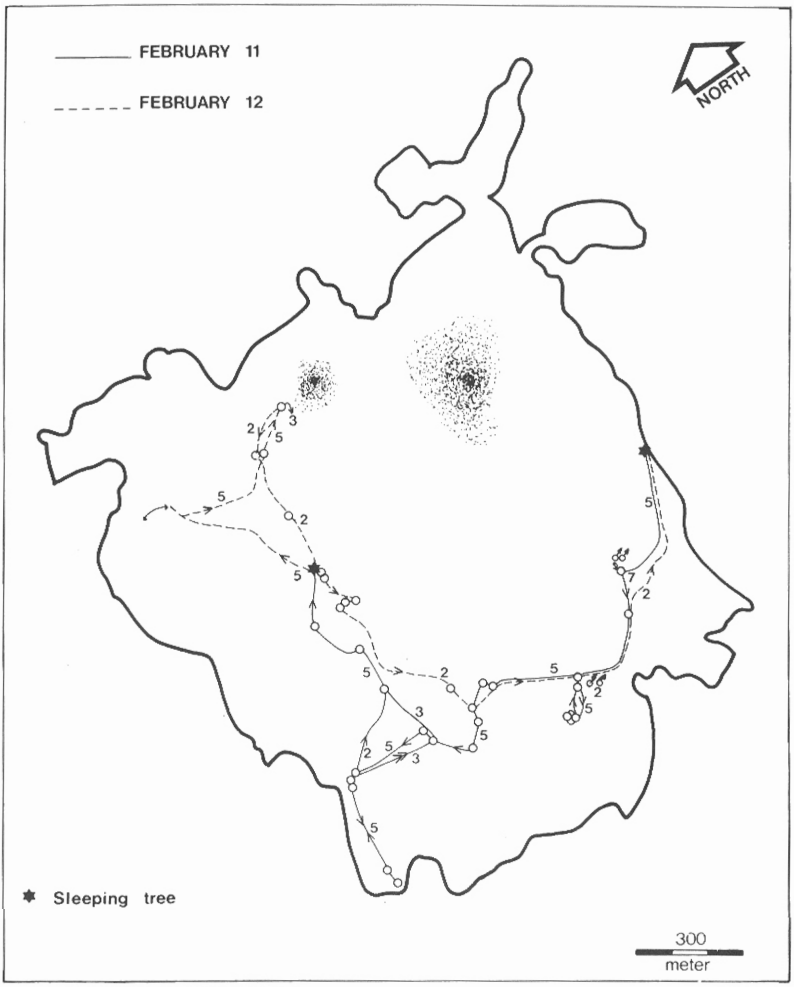
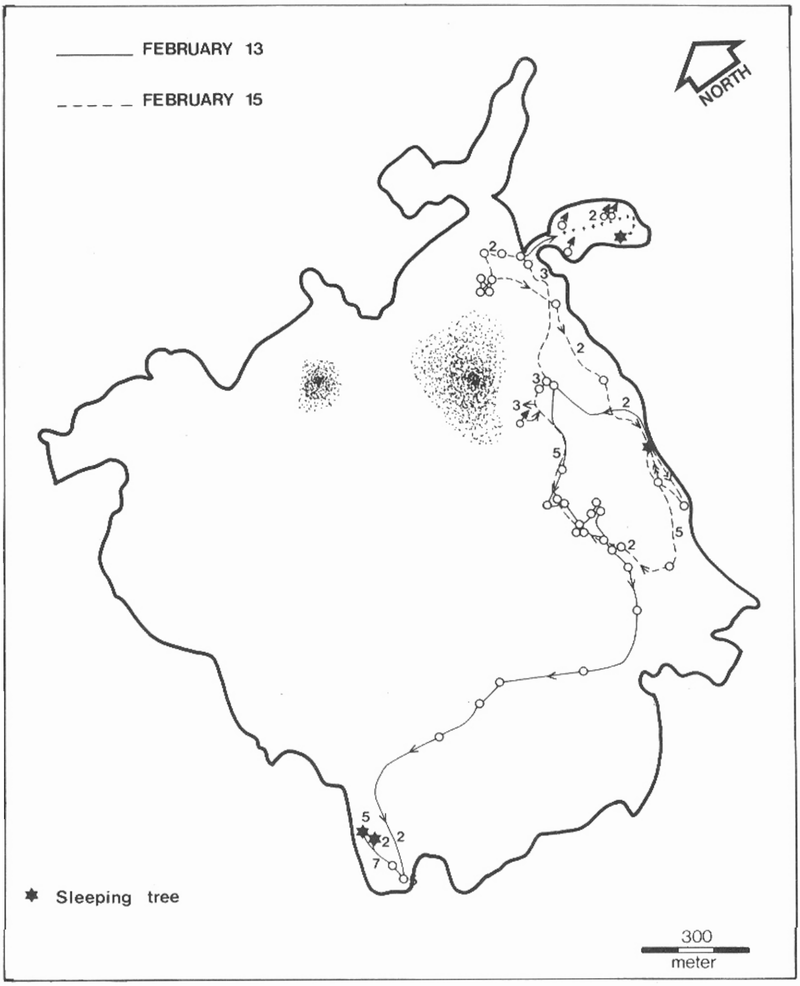


Figure 39 Daily travel paths and the pattern of temporary associations with the female (with juvenile) leading the frequently-changing subgroup on February 11, 12, 13, 15, 16, 17 and 18, 1978. Subgroup size, food plants and sleeping trees used are indicated. See for details figures 3g A,B, C, and D.

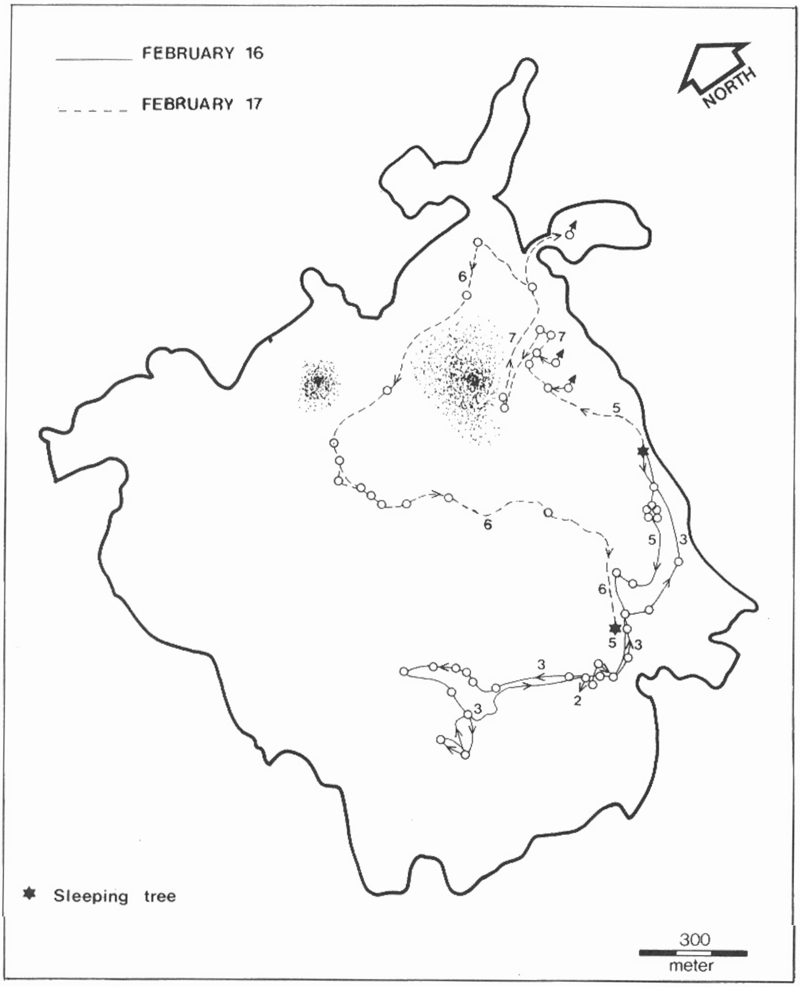
In table XI, monthly association patterns between and with both leading females of the B8-B20 set are given by calculating the percentage of total observation time for four categories of subgroup composition: 1) no leading female(s) in the subgroup; 2) one leading female in the subgroup; 3) both leading females in the subgroup; and 4) one or more leading females in the subgroup. Observations were spread evenly over all six adults. For this purpose, a juvenile



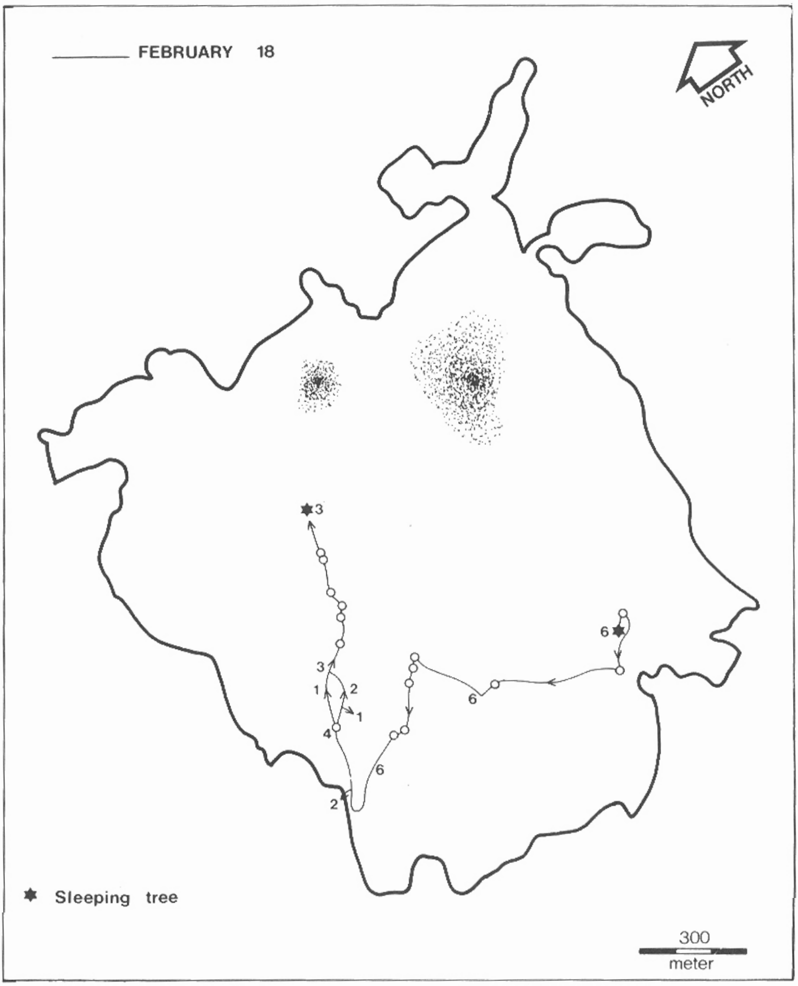
and its mother are considered a single unit. Thus, in these calculations six adults are involved: two leading females, two non-leading females and two males. The figures, given in table XI, clearly show a tendency for adults to assemble into subgroups containing at least one leading females thoughout the year, except for the months July and August (39.0 and 40.5%, respectively) which represents a period of food scarcity (table X). The tendency is strongest from April through June (between 94.1 and 96.6%), a period of food excess (table X).



In table XII, all subgroup sizes and compositions observed in the study group during one year of intensive study are listed and their frequencies are expressed in terms of cumulative observation time (minutes) and percentage of total observation time (i.e., 1,061 hours). For this purpose, infants were considered together with their mothers as long as they were not fully independently locomoting during travel (i.e., from birth to about 12—15 months of age). Subgroups of three or less individuals were observed slightly more frequently than subgroups of four or more individuals (53.3 and 46.7%,



respectively). A subgroup of three individuals was observed most frequently (28.0%), followed by subgroups of two and four individuals (19.1 and 18.6%, respectively). Solitary ranging animals were seen with a frequency of 6.2%, but they may be underestimated because of their being harder to detect. Subgroups of five, six and seven individuals made up for 12.7, 9.0 and 6.2%, respectively, whereas subgroups of more than seven individuals only made up for 0.24% of total observation time.



The subgroup composition most frequently observed was the combination ♂ ♀+J (18.5%), followed by that of ♂ ♀ ♀+J (12.3%). The subgroup compositions ♀ +J (8.9%) and ♀ ♀ +J (8.6%) were also common. Solitary ranging males were observed with the same frequency (i.e. 3.1%) as solitary ranging females with or without an infant but, as stated before, these frequencies may be regarded as underestimated. The combination male — non-leading female was observed with a frequency

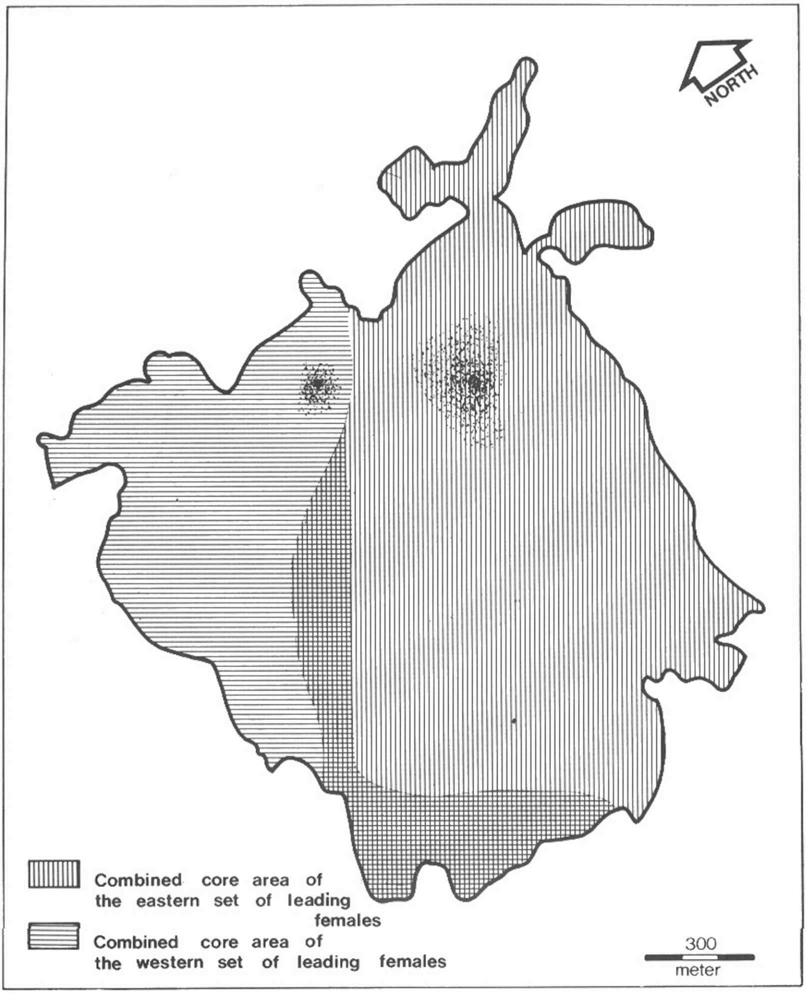


Figure 40 Distribution of combined core area of both sets of leading females within the spider monkey group range. The combined core area of the western set of leading females corresponds with the core area of male ♂2, the combined core area of the eastern set of leading females corresponds roughly with that of male ♂1 and male ♂3. Male ♂3 was found most frequently in the core-area overlap zones where every group female could be encountered regularly.

of 6.1% and mainly involved a receptive female. A subgroup consisting of at least one male together with other animals was observed with a frequency of 70.9%. A subgroup of only two males made

Table XI. Monthly variation in frequencies of four different subgroup categories composed of individuals ranging mainly within the B8-B-20 area, the combined core area of one set of leading females, selected because it belonged to the best studied section on the spider monkey group. Six adults are involved: two leading females, two non-leading females, and two males (male ...1 and ...3). For the sake of determining association partterns between and with leading females, juveniles were considered together with their mothers (both mothers were leading females). High monthly observation time figures from October through March are due to an assistant simultaneously gathering data on subgroups formed by fission from the focal subgroup.

Month	Frequency of subgroups containing				Total observation time in minutes
	O	One	Two	One or more	
	leading	female(s)			
January	23.7	57.7	18.7	76.3	7,775
February	27.1	39.6	33.3	72.9	9,562
March	17.4	51.7	30.9	82.6	8,565
April	3.4	57.9	38.7	96.6	4.690
May	2.2	67.5	30.3	97.8	3,000
June	5.9	90.8	3.3	94.1	3,804
July	61.0	39.0	0.0	39.0	2,218
August	59.5	40.5	0.0	40.5	2,288
September	22.9	72.5	4.6	77.1	2,260
October	19.7	62.0	18.3	80.3	8,018
November	23.9	41.8	34.3	76.1	11,244
December	9.1	72.5	18.4	90.9	6,750

up for 3.9%, whereas a subgroup of only three males was seen only in other groups in the Raleighvallen-Voltzberg Nature Reserve. Subgroups containing at least two males together with other animals were observed with a frequency of 15.7%, whereas a large subgroup including all three males was observed in only 0.2% of total observation time.

Since spider monkeys are large animals that feed predominantly on mature, relatively nutritious fruits not produced in large amounts simultaneously by a particular food plant, subgroup size has to be restricted to avoid competition in a given food plant. Theoretically, subgroup size in spider monkeys will be positively correlated with food patch size. In table XIII, all subgroup-size classes observed in the study group and the percentage of total observation time for each size class are given for each month of the year. To make the figures easier to interpret, subgroups-size classes have been reduced to two in table XIV: subgroup of more than three and subgroups of three or less fully independently locomoting individuals. Subgroups

Table XII. Mean size frequencies of independent, aged and sexed subgroups during a full year observation. For this purpose, infants were considered together with their mothers, as long as they were not independently locomoting during travel. I = Infant, J = juvenile, S = subadult

Subgroup		Cumulated observation time in minutes		%Total observation time (1,061 hours)	
Size	Composition				
1	♂	1,959	3,962	3.1	6.2
	♀±I	2,003		3.1	
2	♂,♀	3,869	12,134	6.1	19.1
	♀+J	5,649		8.9	
	♂,♂	2,492		3.9	
	♀,♀	124		0.2	
3	♂,♀+J	11,753	17,798	18.5	28.0
	♀,♀+J	5,445		8.6	
	♂,♂,♀±I	25		0.04	
	♂,♀,♀±I	485		0.8	
	♀,S♀,♀±I	90		0.1	
4	♂,♂,♀+J	3,396	11,816	5.3	18.6
	♂,♀,♀+J	7,836		12.3	
	♀,♀,♀+J	350		0.6	
	♀+J,♀+J	234		0.4	
5	♂,♀+J,♀+J	4,206	8,077	6.6	12.7
	♀+J,♀+J,♀±I	2,654		4.2	
	♂,♂,♀,♀+J	1,128		1.8	
	♂,♀,♀+J,♀±I	89		0.1	
6	♂,♂,♀+J,♀+J	1,497	5,742	2.4	9.0
	♂,♀+J,♀+J,♀±I	3,888		6.1	
	♂,♀,S♀,♀+J,♀±I	252		0.4	
	♂,♂,♀,♀,♀+J	105		0.1	
7	♂,♂,♀,♀+J,♀+J	3,687	3,927	5.8	6.2
	♂,♀,♀+J,♀+J,♀±I	240		0.4	
8	♂,♂,♀,♀,♀+J,♀+J	15	15	0.02	0.02
9	♂,♂,♂,♀,♀,♀+J,♀+J	158	173	0.2	0.2
	♂,♂,♀,♀+J,♀+J,♀+J	15		0.02	
		+ 63,644			+ 100.0

were smallest during the first part of the long dry season, a period of food scarcity (particularly of mature fruits), with significant minima in July, August and September (26.8, 18.4 and 4.6%, respectively, for subgroups of more than three individuals). In contrast, subgroups were largest during the peak of the long wet season when an excess of mature fruits existed (table X), with significant maxima in April and May (77.2 and 65.4%, respectively, for subgroups of more than three individuals). During the rest of the year, figures are relatively constant and subgroups of more than three individuals range from 35 to 45%.

In a subgroup of four or more independently locomoting animals following an itinerary determined by a leading female, rarely did more than three animals feed at the same time on one particular food source. In general, this only occurred when a sleeping tree also provided ample, food or when a large-crowned flowering or flushing tree offered enough space to feed at ease together. While the leading female with her offspring was feeding on a particular, usually primary, food source, one or more other animals (i.e., particularly non-leading females) could be seen searching for or feeding on nearby food sources, sometimes of less high quality. They often entered the food plant chosen by the leading female when the other animals were resting or moving to the next food source. In this way, the itineraries followed are the same for all subgroup participants. Also, non-leading females and males can learn about important food sources and their location, information that they will need when they are solitary or associated with one or more non-leading female(s) and/or male(s). Clearly, this foraging pattern can be followed only when food supply is high and fruiting food plants occur in relatively high densities, making it likely that another food source will be in the vicinity of the one chosen by the leading female. During the present study, this condition appeared to be fulfilled particularly in April, May and June, when trees of *Guarea grandifolia, Protium neglectum, Protium polybotryum, Tetragastris altissima* and *Tetragastris panamensis* were fruiting abundantly. These species had overall densities of respectively 214, 148, 103, 777 and 133 full-grown trees per square kilometer (table I) and locally reached much higher densities.

Table XIII. Monthly variation in size frequencies of independent subgroups, expressed as the percentage of total observation time per month for size classes of one to nine individuals. High monthly observation-time figures from October through March are due to an assistant simultaneously gathering data on subgroups formed by fission from the focal subgroup.

Month	Number of individuals per subgroup									Total obs.time in min.
	1	2	3	4	5	6	7	8	9	
January	19.4	8.8	36.9	15.2	4.2	14.5	0.9	-	-	7,869
February	4.7	43.2	14.6	4.2	22.5	7.7	3.1	-	-	9,584
March	17.1	3.0	37.8	11.0	7.9	13.0	10.0	-	0.2	8,578
April	3.4	0.1	19.3	38.5	8.8	15.1	14.8	-	-	4,690
May	1.0	21.4	12.2	46.2	8.2	3.5	7.5	-	-	3,000
June	5.2	29.5	19.8	41.6	3.1	0.8	-	-	-	3,834
July	2.9	45.7	24.6	26.8	-	-	-	-	-	2,218
August	10.5	24.1	47.0	18.4	-	-	-	-	-	2,288
September	0.0	45.9	49.5	-	4.6	-	-	-	-	2,260
October	7.6	5.5	45.5	13.1	15.5	3.6	9.2	-	-	8,053
November	7.3	21.9	24.6	10.2	15.9	9.6	9.0	0.1	1.4	11,619
December	7.4	3.8	44.6	23.6	13.9	6.7	-	-	-	7,002

Table XIV. Monthly variation in size frequencies of two classes ($\leqslant 3$ and > 3 independently locomoting individuals) of independent subgroups, expresses as the percentage of total observation time per month and the percentage of the total number of observed nightly subgroup sizes per month in the same size classes.

Month	%Total observation time per subgroup-size class		Total observation time in minutes	%Total night observations per subgroup-size class	
	$\leqslant$ 3 ind.	> 3 ind.		$\leqslant$ 3 ind.	> 3 ind.
January	65.1	34.9	7,869	62.5	37.5
February	62.5	37.5	9,584	60.0	40.0
March	57.9	42.1	8,578	50.0	50.0
April	22.8	77.2	4,690	25.0	75.0
May	34.6	65.4	3,000	20.0	80.0
June	54.5	45.5	3,834	37.5	62.5
July	73.2	26.8	2,218	100.0	0.0
August	81.6	18.4	2,288	100.0	0.0
September	95.4	4.6	2,260	100.0	0.0
October	58.6	41.4	8,053	60.0	40.0
November	53.8	46.2	11,619	60.8	39.2
December	55.8	44.2	7,002	77.0	23.0

Two of the four leading females in the study group were intensively studied. Throughout the year, they used mainly the area between the parallels on B8 and B20. The other two leading females used the area between the parallels on B1 and B10, within the perimeter of the group's range (fig. 40). In addition to the strip between B8 and B10, an important area of overlap between the core areas of both sets of leading females could be found to the south of the B-axis, between B10 and B18. In this area, every member of the group could be encountered regularly. The non-overlaping areas were not exclusively used by the respective set of leading females with their associates, but seemed to be most familiar to them. The most intensively studied set of females using the area between B8 and B20, visited the second area (between B1 and B10) more frequently than the second set of females visited the first (i.e., the area between the parallels on B10 and B20, and to the north of A15). This was especially true during October and November when preferred food (i.e., mature, relatively nutritious fruits) was still scarce. The eastern subgroups were foraging regulary for infructescenses of *Philodendron* spp., fruits of *Ecclinusa guianensis* and flush leaves of *Ceiba pentandra*, foods which more often were present in the second area.

Leading females of each set usually exploited different but partly overlapping core areas within their general range. The core-area overlap appeared to grow with increasing food supply. In times of food scarcity (i.e., from July through September), one leading female of the eastern set almost exclusively exploited a core area situated between the B8 and B15 trails, and in particular to the south of the B-axis, whereas the other almost exclusively used a core area between the B15 and B20 trails, and in particular to the north of the A15 trail. Each core area covered about 100 ha. In times of food excess (i.e., during April and May) this set of leading females used almost all of both core areas combined, covering about 200 ha. The western set of leading females exploited a combined core area of about 120 ha.

Looking at subgroups containing both leading females of the eastern set together with one or more of the other four adults ranging mainly within this area, the following frequencies were observed: 18.7% (January), 33.3% (February), 30.9% (March), 38.7%

(April), 30.3% (May), 3.3% (June), 0.0% (July), 0.0% (August), 4.6% (September), 18.3% (October), 34.3% (November) and 18.4% (December) (table XI). During the first part of the long dry season (i.e., July - September), a period of food scarcity, both leading females almost never joined into one subgroup. In contrast, at the end of the long dry season, a peak of joining can be seen. One reason for this pattern of association may be the abundance of large crowned flushing and flowering food plants (e.g., *Ceiba pentandra, Vataireopsis speciosa*) and several Bignoniaceae) in November. These offer enough food and space for relatively large subgroups to feed together (table XIV; 46.2%, four subgroup sizes of more than three independently locomoting individuals). A second reason may be the already mentioned regular visits of both leading females, often together in one subgroup, to the core areas of the western set. Roughly similar frequencies of joining are reached from February through May when supply of mature fruits was high and several important food species fructified abundantly. An absolute peak of joining can be seen in April when an excess of mature fruit was most obvious (table X). Food supply in October, December and January was moderately high (consisting partly of flush leaves and flowers), resulting in medium frequencies of joining (i.e., about 18%).

Considering the conspecific-cueing concept in foraging, as described above, the following question may arise: What mechanism governs the decrease of mean subgroup size in times of food scarcity, and when would it be most advantageous for males and non-leading females to learn about available food sources from leading females by joining their subgroups? Leading females of a set each seemed to prefer regular contact through merging of subgroups when food patch size and distribution allowed foraging in relatively large subgroups. The reason for this association pattern may be merely a social one. These females and particularly their offspring seemed to enjoy very much one another's company. When in the same subgroup, the juveniles spent much time playing together. The exchange of knowledge of available food sources does not seem of importance for leading females. This may be demonstrated by the way both females of a set acted after merging subgroups. At these occasions, they alternately determined subgroup activity patterns and frequently separated into two subparties for short periods of time. Each female led part of the subgroup along slightly different itineraries before merging again. For the sake of foraging success, leading females obviously do not need one another. Therefore, no agonistic behavoir is needed to force them into exploiting different core areas in times of food scarcity. With this in mind, it may be interesting to note that already in June when food supply still was fairly high (table X), both leading females of the B8-B20 set assembled into one subgroup with a frequency of only 3.3% (table XI). This pattern may be explained by the following. For optimal exploitation of different, barely overlapping core areas in July, leading females may have to begin early to monitor future food sources in these areas. It may require some time to learn and memorize all food sources about to become available in a smaller but previously less frequently visited area. The above argued mechanism of leading-female core-area splitting alone already will drastically decrease mean subgroup size during the period of food scarcity. Males and non-leading females may join a leading-female subgroup or form small subgroups with one another. By calculating the monthly frequencies for each category of subgroup composition (table XI), it appears that subgroups of one or more individuals without a leading female were found much more frequently in July and August (61.0 and 59.5%, respectively), than during the rest of the year. Whether this association pattern of males and non-leading females results after increased agonistic behavior from leading females is not fully clear. Regular overt aggression was observed by males towards non-leading females and juveniles. This occurred especially when they fed at the same time on one food source with restricted food supply. Some overt aggression was observed in July by a leading female towards the younger male within her subgroup. Aggressive behavior by a leading female toward a non-leading female was observed very rarely but was severe when it did occur. In this context, it may be adequate to note that a comparable type of appeasement behavior as performed mutually by males when meeting one another after some time, occasionally was observed in females. It was initiated by the non-leading female when meeting a leading female, and was attended with pectoral sniffing and mutual embracing.

5.5. Male Behavior

The study group included three adult males, an old male (♂1), one of middle age (♂2) and a young male 6-7 years of age (♂3).

When meeting one another after some time, male spider monkeys belonging to the same group perform a kind of greeting ceremony composed of mutual embracing and pectoral sniffing usually followed by mutual sniffing of the scrotum. Greeting behavior among males invariably appeared to be initiated by the lower-ranking male, and it may be regarded as appeasement behavoir. The old male (♂1) was the highest ranking, followed by male ♂2, male ♂3 and a juvenile-3. It seems that dominance relationshps among spider monkey males are largely determined by age.

Adult males were never observed outside the perimeter of the group's range, and usually (but not exclusively) ranged within certain core areas. The older males, ♂1 and ♂2, each used approximately the combined core area of a set of leading females, the eastern and western set, respectively. The young male (♂3) alternately used both male core-areas but more often could be seen within the eastern area, and particulary within the overlap zones (i.e., the areas to the south of the B-axis and between the B8 and B10 trails) (fig. 40).

Each adult male appeared to prefer joining a subgroup of one or more group members (70.9% of total observation time), especially when it contained one or more leading females (60.0%). The males usually associated with each female of a set, or more specifically with a certain leading female. For example, male ♂2,was observed most frequently in a subgroup led by the mother of the juvenile-3 male, whereas male ♂3 alternately joined a subgroup led by a female of the eastern set or, less often of the western set.

Both male ♂2 and male ♂3 were seen visiting the male ♂2 core area more often than the reverse, and such visits took place especially in the second part of the long dry season. In this period, the three males repeatedly came together with other group members in an emergent tree of the species *Hymenaea courbaril* (fig. 41, no. 38), which apparently functioned as a meeting place. On these occasions, the largest subgroups were observed and ranged from seven to nine independently locomoting individuals. The adults rested in the huge crown for hours, whereas the juveniles played with one another and/or with adults. Otherwise, the three adult males of the study group were observed together only during the very rare territorial boundary conflicts with members of the adjacent group to the south. These conflicts started with one adult male becoming agitated and starting to perform long calls. In cooperation with one or more females, he performed siamang-like barking duets. These caused an invasion of subgroups from the vicinity, whereas the members of the other group responded with similar behavior at the other side of the boundary. High up in the canopy or in emergents, the males of both groups were probably in sight of one another at a distance of about 100-200 m, acted very upset and performed an aggressive display for a considerable time. The males shook branches and broke off twigs, branches and even dead boughs, and uttered long calls ("whoops") and barks in cooperation with one or more females ("ook-barking"; terms derived from Klein, 1972). Several times, the males were observed performing reassurance behavior by mutually embracing and pectoral sniffing or by briefly touching one another's back, shoulder or arm with the hand. These territorial conflicts, always initiated by a male, were very rare and were heard among other groups in the Raleighvallen-Voltzberg Nature Reserve only a few times during this study. The rarity of territorial conflicts between groups may be explained by the relatively few high forest boundaries with adjacent groups. Most of the study group's range boundaries were formed by geographical barriers, such as liane forest and open granite areas.

5.6. Calling Behavior

Only male spider monkeys perform long calls or "whoops". On the forest floor, these long calls are audible at a distance of 800-1,000m. High up in emergent trees, long calls can be heard over approximately 2,000 m, whereas from the top of the Voltzberg (240 m) calling males can be located at distances of 3,000-4,000 m. Assuming that the spider-monkey sense of hearing is at least as good as that of humans, spider monkeys in an emergent crown should be able to hear every intragroup long call. The longest distance between two points within the perimeter of the home range amounts to 2,400 m.

Long calls by the different males of the study group could easily be recognized individually by their sound frequencies, and both the number and length of intervals between notes.

At least five types of male long call are distinguished, sounding similar superficially but performed in different behavioral contexts:

1. **Morning Long Call (MLC):** Performed usually once or only a few times during the period of increased foraging activity (i.e., between 6.00-7.30 h), and as a rule answered by one or more males of the same group. It seemed intended to inform males (and other group members) of one another's location and direction of travel. Estrous females were also attracted using this call.

2. **Evening Long Call (ELC):** Performed usually only once, just before or after the male entered a sleeping tree. It seemed intended to inform all group members of the location of the sleeping site selected for the night. Nearby parties could therefore be attracted to join and form larger units. When more males were associated in a subgroup, usually only one of them gave the ELC. An ELC usually was not answered immediately by other males. The males seemed to perform ELC's at different times, since they usually did not simultaneously settle for the night. In addition, ELC's were not given every day. For example, the males kept silent when it was raining. Also, ELC's were heard less often during the long dry season.

3. **Food Long Call (FLC):** Food long calls could be given throughout the day, in particular just before or during feeding on an important, usually primary food source that probably was well-known to most or all members of the group. In most cases, FLC's were not answered. They seemed to be used for spacing purposes. The performing male often was part of a relatively large subgroup and merging of subgroups usually did not take place after a FLC. These calls seemed intended to inform other monkeys that a nearby food source was being depleted at that moment, and therefore might better be dropped from a leading-female's foraging route.

4. **Contact Long Call (CLC):** Contact long calls could be given by a male just after leaving or loosing contact with a subgroup, perhaps in an attempt to influence the direction of travel chosen by the female leading the subgroup. Sometimes the male attracted the subgroup and joined it again, but usually he seemed not to succeed. This behavoir could be observed, for example, when a male left a subgroup in order to contact another one nearby, but after meeting the second group decided not to join it. It could also occur when the subgroup led by a female took one of two possible routes. In that case, the male could stay for a while at the junction of both potential routes, giving CLC's repeatedly.

5. **Alarm Long Call (ALC):** Alarm long calls could be given all day by males, especially when upset by the presence of a large carnivore (e.g., a jaguar) or an unfamiliar human intruder, by alarmed terrestrial animals on flight (e.g., tinamous, quails, trumpeters, curassows, agoutis, deer, peccaries), or by combinations of these factors. Also, they could be performed during long-distance agonistic behavior towards one or more adult males of a neighboring group. ALC's were combined with "ook-barking", usually performed in cooperation with one or more adults, and sometimes lasted for more than an hour. After calling, most adults remained very unstable for a while and the slightest incident could cause repetition of the behavior. For example, the observer could cause the aggressive display to be directed towards him by simply stepping on a dead branch, even if he did not play a role in initiating it. ALC's seemed intended to attract nearby subgroups to share in an aggressive display, and were never answered by calls from other subgroups belonging to the same group.

During the first part of the long dry season, long calls were heard only occasionally. Spacing may be optimal when males are relatively silent, especially considering the small day ranges and the drastically decreased energy budget in this period of food scarcity. As it was for the observer, it probably was also much more difficult for individual spider monkeys to encounter subgroups at any given time. The aggregating component of male long-calling behavior is therefore of mimimal importance in this season. It seems to be more important during more favorable periods when day ranges are much larger and the energy budget is increased considerably. Moreover, during the long dry season the available food sources are usually quite different from those offered during the rest of the year, and are of the kind that make quick depletion unlikely. Ripe fruits of *Apeiba* spp. and *Dimorphandra pullei* are important food sources that are present for long periods, whereas foods such as flush leaves and flowers are usually widely dispersed and available in large quantities for a short period (table I.). During the months of July and August, males and non-leading females in particular could be seen remaining for an entire day or more within a small area that offered only a few of these food sources, and much of this time was spent resting. The decreased energy budget may be explained not only by the decline of overall food supply but also by the dietary shift, with flush leaves and flowers constituting a considerable part of the diet. The proportion of time spent on feeding and moving is negatively correlated to the proportion of foliage in the diet (Clutton-Brock, 1977).

5.7. **Sleeping Behavior**

The tendency to aggregate in sleeping trees is illustrated in table XIV. The percentage of nights spent together is given for two subgroup-size classes consisting of ... 3 and ... 3 independently locomoting individuals. Comparing these percentages to day figures, a strong tendency to aggregate in sleeping trees can be noted only in May and June. A strong tendency for spacing is demonstrated in July, August and December when food supply is more limited (table X).

A spider monkey group uses many sleeping trees during the year but only a few are important throughout the year. Few trees have the permanently open crown preferred in a sleeping tree (e.g., *Hymenolobium* spp., *Parkia pendula* and *Vochysia tomentosa*). Strategic location within the perimeter of the home range or core area may also play a role and the size of the food supply to be found in the vicinity of the sleeping tree during most of the year is also important. In total, 43 different sleeping trees were used by membres of the study group (fig. 41). The following species contributed the greatest number of sleeping trees: *Buchenavia capitata* (ten trees), (*Vataireopsis speciosa* (five trees), *Couratari stelata, Hymenolobium petraeum* and *Hymenolobium flavum* (four trees each), and *Parkia pendula* (three trees). Ranked according to the number of nights spent in trees, the following species were most important: *Hymenolobium flavum* (31), *Vochysia tomentosa* (16), *Newtonia suaveolens* (12), *Buchenavia capitata* (ten), and *Vataireopsis speciosa* (eight).

Spider monkeys seemed to use the following criteria in selecting a sleeping tree:

1. The tree has to be an emergent, not only determined as such by its absolute height but also by its relationship with the environment. The crown has to be completely free from the canopy beneath and is entered by swinging or leaping across a gap from the periphery of an adjacent crown or by ascending the huge trunk using

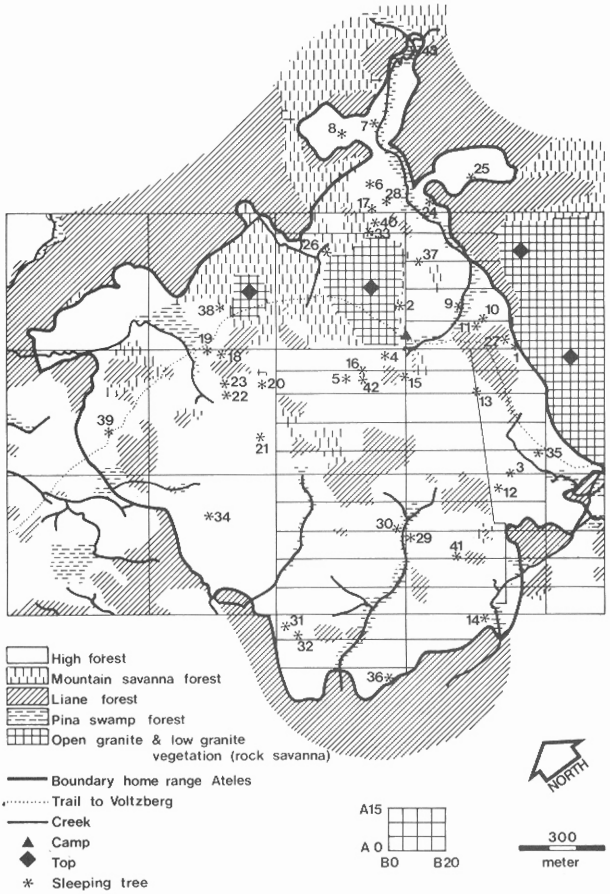


Figure 41 Location and species of sleeping trees used by members of the spider monkey group in the Voltzberg study area:
1. *Hymenolobium flavum* 2. *Hymenolobium petraeum* - 3. *Enterolobium schomburgkii* - 4. *Couratari stellata* - 5. *Buchenavia capitata* - 6. *Vochysia tomentosa* 7. *Buchenavia capitata* 8. ***Parkia pendula*** - 9. *Dimorphandra multiflora* - 10. *Buchenavia capitata* - 11. *Cedrelinga catenaeformis* - 12. *Newtonia suaveolens* - 13. Hymenolobium petraeum - 14. *Parkia pendula* - 15. *Buchenavia capitata* - 16. *Vataireopsis speciosa* - 17. Hymenolobium flavum - 18. *Ceiba pentandra* - 19. *Parkia nitida* - 20. *Buchenavia capitata* - 21. *Buchenavia capitata* - 22. *Buchenavia capitata* - 23. *Buchenavia capitata* - 24. *Couratari stellata* - 25. *Parkia pendula* - 26. *Couratari guianensis* - 27. *Vataireopsis speciosa* - 28. *Vataireopsis speciosa* - 29. *Couratari stellata* - 30. *Vochysia tomentosa* - 31. *Vataireopsis speciosa* - 32. *Vataireopsis speciosa* - 33. *Hymenaea courbaril* - 34. Hymenolobium petraeum - 35. *Hymenolobium petraeum* - 36. *Hymenolobium flavum* - 37. *Hymenolobium flavum* - 38. *Hymenaea courbaril* - 39. *Buchenavia capitata* - 40. *Dimorphandra multiflora* - 41. *Buchenavia capitata* 42. *Couratari stellata* - 43. *Qualea dinizii*.

stems of lianes, epiphytes and/or aerial roots. In particular, emergents at edges of natural clearings, granite outcroppings, low forest or liane forest are preferred for sleeping.

2. A broad, open crown that has small leaves, is currently leafess or is in early flush, is preferred.

3. The crown has to be structured with more or less horizontal branching. Spider monkeys seem to prefer almost horizontally forked branches for long resting postures, usually sleeping stretched out in a reclining posture or in a more or less asymmetrical sitting posture.

4. The tree has to be located strategically in respect to the foraging grounds of the late afternoon and the morning of the next day. Spider monkeys seem to be very hungry after awakening and prefer to have one or more important food sources situated near the sleeping tree, providing a good breakfast at the start of a day's itinerary.

5. A particular sleeping tree that provides the monkeys with a source of food may be given priority. This may be in the form of fruits, flowers or flush leaves of the sleeping tree itself, or edible epiphytes and/or lianes growing in its crown. When edible flowers or flush leaves are on the tree the monkeys prefer to consume these during the late afternoon, just before choosing their sleeping branch for the night.

Predation at night seems to be the only reasonable explanation for the strong selectivity in choice of sleeping trees fulfilling the first three criteria mentioned above. Another indication may be the fact that spider monkeys acted very upset and issued trilling squeaks when they were encountered in a sleeping tree late at night, probably being unable to identify the intruder on the forest floor. Occasionally, these specific vocalizations were heard at night near the camp, perhaps as a reaction to disturbance by a terrestrial carnivore or herbivore near the sleeping tree. All subgroup members, except infants, were scattered over a sleeping tree crown with preference for the center and the upper part, and always on branches. Each monkey appeared to possess its own sleeping branch, at least in frequently used sleeping trees. By using slender perches in open and isolated crowns, the monkeys would be readily awakened by a felid or other predator climbing the tree. During the present field study, predation of spider monkeys was never observed. However, a young infant in the study group died for an unknown reason. Daytime predation probably does not present a problem for spider monkeys. Several times, spider monkeys were feeding in the periphery of open crowns with a harpy eagle (*Harpia harpyja*) flying in the vicinity, but in no way did they seem to be restrained by the bird's presence. Juveniles kept on feeding in vulnerable sites, and only once was a short branch-shaking display performed to scare off this large raptor. Some other observations may be mentioned in this context. Juvenile spider monkeys were observed curiously following tayras (*Eira barbara*) at very short distances for brief periods. Many hairballs and dung samples from the jaguar (*Panthera onca*) living in the area were found on trails and bare granite and were analyzed (Van Roosmalen, in prep.). They appeared to contain only nails, hair and bones of terrestrial animals. It is interesting to note that spider monkeys appeared to become particularly upset by alarmed terrestrial animals on flight, such as tinamous, quails, trumpeters, curassows, agoutis, deer, peccaries and tapirs. Ocelots (*Felis pardalis*) were living in the area, and once an ocelot was fighting with two tayras on the forest floor. A male spider monkey descended to about 10 m above the fighting animals and barked at them. An ocelot might be able to catch a juvenile spider monkey at night and even if this occurred only once per spider monkey generation, strong selective pressure for use of safe sleeping trees probably would be maintained.

Spider monkeys are very courageous animals, apparently not afraid of any day-time intruder, including man (unless they have prior experience with guns). On first contact with human intruders, spider monkeys usually perform a branch-shaking and branch-breaking aggressive display directed towards the intruder. Apart from this, the males may give long calls or perform "ook-barking" in cooperation with one or more adult females. Other subgroups may join the aggressive display. Dead branches and even boughs, preferably those right above the intruder's head, are selected and broken off. This display may also be performed when detecting a large felid walking on the forest floor.

5.8. **Reproductive Biology and Sexual Behavior**

According to Eisenberg (1976), spider monkey females giving birth to an infant will pass into a lactation anestrus for a period of 15.3-24 months. The data gathered in the Voltzberg study area, however, indicate a lactation anestrus for a period of about three years. An infant born in October 1974 was regularly nursed until September 19, 1977. A month later, its mother came into estrus for the first time. Another female gave birth to an infant in January 1975, and nursed it until December 1977. This female came into estrus again on January 22, 1978. Several females of *A. paniscus* in Surinam were nursing a juvenile-2 or even a juvenile-3. Old juveniles were nursed only few times a day (mean duration of two minutes), usually while resting in a sleeping tree before nightfall. These few nursing bouts seemed to be sufficient to keep the mother in anestrus. The difference between the data from Eisenberg (1976) and the data collected on feral spider monkeys in Surinam may be explained by species specific differences or by the fact that social weaning for young spider monkeys in captivity is much earlier than in the wild.

Female spider monkeys coming into estrus show a tendency to manipulate, inspect and rub the clitoris. The duration of sexual receptivity in Surinam spider monkeys ranged from 8-10 days. The interestrus interval lasted an average of 15 to 17 days. This agrees with the cyclical uterine bleeding of adult female spider monkeys described by Goodman and Wislocki (1935) as occurring every 26 to 27 days.

In captivity, spider monkey gestation has been calculated at 226 to 232 days (Eisenberg, 1973). The interbirth interval is a function of the duration of lactation and the number of estrus periods needed for successful conception. Interbirth intervals in captive *A. fusciceps* ranged from 22.8-31.5 months (Eisenberg, 1976). The range for *A. geoffroyi* is 17 to 45 months (Dare, 1974), 22 to 45 months (Eisenberg, 1976), or 28-36 months (Milton, 1981). Interbirth interval in feral *A. paniscus* in Surinam appeared to be four years (range: 46-50 months). These comparisons include only cases in which the mother reared her young to social weaning.

In *A. paniscus*, one of the leading females was seen copulating at least 11 times, spread over eight successive estrus periods.

Another leading female was seen copulating at least seven times spread over three estrus periods. Successive estrus periods of five females belonging to the study group given in figure 42. Unfortunately, at the end of the field period, the two most intensively-studied females had not yet become pregnant. Another female was lost after five successive estrus periods. The fifth female belonging to the western set of leading females copulated at least once with both male ♂1 and male ♂3 but regular contact was not maintained later in the study.

Klein (1971) suggests that captive *A. geoffroyi* and feral *A. belzebuth* in Colombia do not exhibit a discrete birth season. In contrast, Eisenberg (1976) indicates that *A. fusciceps* in captivity shows a tendency towards two birth peaks and suggests estrus synchrony. In addition, Milton (1981) presents evidence for seasonality in the distribution of births of *A. geoffroyi* on Barro Colorado Island. In Surinam, *A. paniscus* appeared to show a birth peak in the period November-February, from the end of the long dry season through the short wet season. None of six females shot by hunters in Lely Mountains in the period February-April 1976 contained a fetus (Mittermeier, 1977). Figure 42 shows estrus synchrony in four out of five *A. paniscus* females in Surinam in the period October 15 to at least April 26. The female giving birth to an infant on April 17, 1978 lost her previous infant in 1977, a fact that may explain asynchrony in estrus compared with the other females.

An estrus season from the end of the long dry season onto halfway the long wet season appears to agree with the seasonal variations in food patch size and grouping behavior as described earlier in this chapter. During the period of food scarcity, it should be unfavorable for females to come into estrus because of reduced frequency of encountering males and high energy demands of early pregnancy.

Males appeared to maintain consortship with receptive females usually not for the entire estrus period but at least for periods of time ranging from one to three days and nights. Also, consortship between two males and a receptive female was observed in *A. paniscus* and lasted as long as three days and nights. Female advertisement was observed prior to all copulations (N=27) and involved both leading and non-leading females. The receptive female always

The mean duration of observed complete copulations was 10 minutes (N = 5). During copulation a female is very active, brings one hand to her abdomen, moves continuously to and fro on the branch on which copulation takes place, shakes her head restlessly, and regularly looks over her shoulder into the male's face. Her lips are protruded and the eyes half-closed. Sometimes, the female rubs the male's upperleg or back with one hand. At the moment of ejaculation, the female may move a couple of meters with the male hanging behind her. Then the animals separate. In general, three or four copulations take place each day during a female's estrus period.