Habitat preferences, diet, feeding strategy and social organization of the black spider monkey [Ateles paniscus paniscus Linnaeus 1758] in Surinam

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ABSTRACT (back cover)

HABITAT PREFERENCES, DIET, FEEDING BEHAVIOR AND SOCIAL ORGANIZATION OF THE BLACK SPIDER MONKEY, *ATELES PANISCUS PANISCUS*, IN SURINAM.

A Socioecological Field Study.

This monograph reports on a 26 month socioecological study of black spider monkeys (*Ateles paniscus paniscus*) in the Raleigh-vallen — Voltzberg Nature Reserve, Surinam. It recognizes the fundamental importance of food to the behavior and the regulation of population density for this primate. It clarifies the complex temporal and spatial effects of tropical rain forest food sources on the behavior of a group of spider monkeys, concentrating on food category, food plant identity and phenology, and quantity, density and dispersion of the most important food sources. In addition, the present study describes habitat choice, optimal feeding strategy and sexual behavior of the spider monkey, and discusses implications of diet for social behavior. This study is also fundamental to conservation. Specialized in eating mature fruits, the spider monkey is a very important dispersal agent for many trees and lianes, particularly canopy species. However, the spider monkey is probably the most vulnerable monkey species in Surinam and it is disappearing rapidly throughout the remainder of its range. Unfortunately, it is large and noisy and can be easily tracked and hunted. It is largely restricted to undisturbed high forest, and consequently habitat destruction has more effect on it than on most other species. Together with its slow reproductive rate (a female gives birth only once every four or five years), this means that the species is poorly adapted to recover from exploitation. In order to implement proper measures for conservation, data on forest type preferences, diet and social behavior of the species, or on closely related species, in undisturbed areas, such as the one described in this monograph, are essential tools for assessing the potential of proposed protected areas.

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4. Diet and Feeding Behavior

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ACKNOWLEDGEMENTS

1. INTRODUCTION

1.1. Background

The role of food as a basic determinant of social organization and behavior has been a much discussed topic in the recent literature on free-ranging primates (Chivers, 1977; Clutton-Brock, 1974; Rasmussen, 1979; Rodman, 1973, 1977; Wrangham, 1977, 1979). Unfortunately, the detailed autecological studies on undisturbed primate populations urgently needed for this investigation are few in number. One of the main reasons may be the fact that primatology and botany are a rare combination of skills. The floristic complexity of the oldest terrestrial ecosystem on earth, the tropical rain forest, surely plays a role as well. Recognizing this before starting the present field sdudy, I compiled all available data on fruits and seeds of woody plants of Surinam since it was known that all monkeys occuring in the country are at least partly frugivorous (Husson, 1957). Two years of research resulted in a book (Surinaams Vruchtenboek, 1977) with detailed descriptions of the fruits and seeds of about 1400 species of tree and liane. In most cases a drawing was included, in addition to general descriptions of leaves and inflorescences of the species, habit of the plant and habitat preferences. This book turned out to be a useful guide for identifying most food plants in the field. Feeding monkeys drop fruit parts and sooner or later complete fruits, sometimes with leaves attached, whereas trees and lianes usually drop their fruits in a certain stage of maturity, making the collecting of fruits much easier than that of flowers and leaves.

The identification of species in the field on fresh samples increases one's knowledge of the forest much faster than the usual way of collecting, preserving, shipping and, much later, identifying the samples. Knowledge of plants is of great advantage to studies of monkeys. Types and subtypes of forest are easier to recognize by determining and recognizing certain indicator species. One's understanding of the forest is better when one is no longer walking in a highly variable mass of trunks and stems. By fixing in one's memory special properties of individual trees of known species, one

becomes habituated to every part of the forest previously visited. All one's attention can be directed to the monkey's behavior. Also the phenology of forest plants can easily be studied by collecting all kinds of fresh fruit from the forest floor from month to month in successive years. In this way periodicity and length of fruiting period can be determined for many species, both at individual plant and species level.

Until recently, very little information was available on diet and habitat choice of *Ateles paniscus paniscus*. More is known about two other *Ateles* species, *A. belzebuth* and *A. geoffroyi*.C.R. Carpenter (1935) reported on a natural population of *A. geoffroyi* in Panama. He described the species as frugivorous. About 90% of the items consumed were said to be fruits. Little data on other food stuffs were reported by Carpenter. In 1969, Hladik and Hladik described feeding behavior, diet and quantitative and chemical analyses of many food items used by a group of *A. geoffroyi*, reintroduced to Barro Colorado Island, Canal Zone, in 1961. Since their study did not cover an entire year, it is difficult to interpret their results. Moreover, the monkeys lacked the traditionally developed knowledge of food and optimal feeding strategy as found in wild populations. Klein and Klein observed free-ranging *A. belzebuth* in the Colombian National Park, La Macarena, during one year (1967-1968). Among other things, they collected information on diet, feeding behavior, feeding heights and sites and social organization (1972, 1976, 1977).

The present study recognizes the fundamental importance of food both to the behavior and the regulation of population density for the black spider monkey in Surinam. It clarifies the complex temporal and spatial effects of food sources on the behavior of a group of spider monkeys, concentrating on food category, food plant identity and phenology, and quantity, density and dispersion of the most important food sources. In addition, this study describes habitat choice, optimal feeding strategy and sexual behavior, and discusses implications of diet for social behavior. This study is also fundamental from the viewpoint of conservation. *Ateles* is probably the most vulnerable monkey species in Surinam. It is large and noisy and can be easily tracked and hunted. In undisturbed areas, it usually reacts to a human intruder by performing a 'branch shaking and branch

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dropping display', which attacts other nearby subgroups. A hunter can wipe out most of the group with little effort. Moreover, *Ateles* is largely restricted to undisturbed high forest, and habitat destruction has more effect on it than on most other species. Another important point is its slow reproductive rate. A female usually gives birth only once every four or five years, meaning that the species recovers slowly from exploitation. In order to implement proper measures for conservation, data on forest type preferences and diet of the species that are to be protected, are needed since they are essential tools for assessing the potential of proposed protected areas.

1.2. Taxonomy and Distribution of Ateles

The taxonomy of the genus *Ateles* is the subject of some controversy. Kellogg and Goldman (1944) recognize four species of *Ateles: A. geoffroyi, A. fusciceps, A. belzebuth* and *A. paniscus.* Several recent authors (e.g. Hershkovitz, 1972; Groves, 1972; Moynihan, 1970, 1976), however, consider all *Ateles* conspecific and refer to them collectively as *A. paniscus* (the oldest available name). Recent studies indicate that there may be some 1 - 2 chromosome significant differences among the species recognized by Kellogg and Goldman (Heltne and Kunkel, 1975). Furthermore, an important contact zone between *A. geoffroyi* and *A. fusciceps* exists in eastern Panama and the species apparently hybridizes to some extent (Rossan and Baerg, 1977). Until further information becomes available, I prefer to follow Kellogg and Goldman (1944) and use the name *Ateles paniscus* in the strict sense.

The Surinam representative of the genus is *Ateles paniscus paniscus* (Linnaeus, 1758). It is found in lower Amazonia, between the Rio Negro and the Atlantic and north to the Guianas (Kellogg and Goldman, 1944), a range similar to that of *Saguinus midas midas, Pithecia pithecia, Chiropotes satanas chiropotes* and Cebus *nigrivittatus,* four of the other seven primate species occuring in Surinam. The second *A. paniscus* subspecies, *A. p. chamek,* is found in western Matto Grosso, eastern Bolivia and northeastern Peru and extends into Brazil as far east as the Rio Jurua, a southern tributary of the Rio Amazonas (Kellogg and Goldman, 1944). The other three species of *Ateles* are found from Southern Mexico to the southern reaches of the Amazon basin.

In Surinam, *A. p. paniscus* is almost entirely restricted to the interior. Like *Chiropotes s. chiropotes* and *Cebus nigrivittatus*, it just enters the old coastal plain in the western part of the country (fig. 1). Its is covered with long, glossy black hair. The naked face varies from light to dark pink and is sometimes lightly freckled (fig. 2). The eyes are usually brown, but some individuals have blue eyes. The female has a long pendulous, backward-directed clitoris, that immediately distinguishes her in the field. The scrotum of the male is black. The hair on the head in both sexes is long and directed forward, forming a peak over the eyes (fig. 3). Individual difference in face color and marking, eye color, hair tufts, hair length and physique make the animals readily recognizable in the field, even at great distances. *Ateles p. paniscus* is a large monkey. Three males in the British Museum had a meanisc head-body length of 545 mm (range: 515-580) and a mean tail length of 807 mm (range: 720-852); ten females had a mean head-body length of 540 mm (range: 490-620) and a mean tail length of 814 mm (range: 640-930) (Napier, 1976). Four females cited in Kellogg and Goldman (1944) had the following measurements: head-body length: 460, 418, 570 and 660 mm; tail lenght: 870, 920, 880 and 753 mm. Adult males usually are more heavily built, but sometimes extremely large females have been observed too. Five males weighed in Surinam had a mean body weight of 7.86 kg (range: 6.5-9.2) and seven females a mean body weight of 7.70 kg (range: 6.5-8.5) (Mittermeier, 1977).

1.3. Population Density and Biomass

Because of flexible grouping behavior in *Ateles*, accurate estimation of group size, group composition and population density is only possible if the members of a group are recognizable as individuals. In the Voltzberg area in Surinam, *A. paniscus* occurs at a density of 7.1. individuals or 6.3 independently locomoting individuals per km^2. When only the area of suitable habitat is considered, an economic density of 8.2, resp. 7.3 individuals per km^2 results. The figures from other areas vary considerably, but only the estimate of Klein and Klein (1976) is based on individually recognizable animals of a natural population. Muckenhirn, et al. (1975) estimate 2.4-6.2 individuals per km^2 for *A. p. paniscus* in Guyana; Heltne, et. al. (1975) give 2.0 individuals per km^2 for *A. p. chamek* in Bolivia; Klein and Klein (1976) give a density of 12-15 indi-
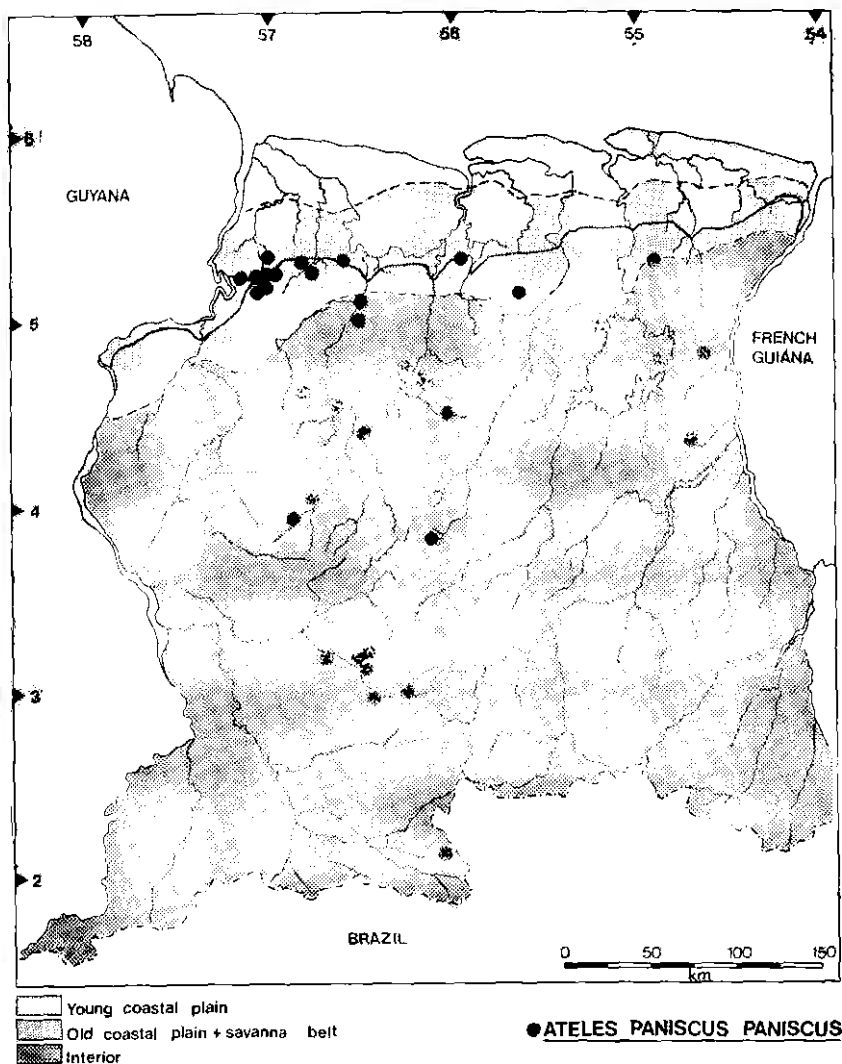
Figure 1 Distribution map for *Ateles paniscus paniscus* in Surinam. The central broken line marks the border between the coastal region and the interior. The area immediately to the north of this line is the old coastal plain, that to the south is the savanna belt. The dashed lines indicate the borders of the two areas. For the purposes of this study, the savanna belt is considered part of the interior, but it is actually a geological distinct region. *Ateles* occurs throughout the interior, but is rare in the savanna belt and only enters the old coastal plain in the extreme western part of the country.

Figure 2 Juvenile-1 *Ateles p. paniscus* from Surinam. The naked face is light pink and may be lightly freckled.

Figure 3 Adult female *Ateles p. paniscus* from Surinam (Photo by R. A. Mittermeier).

viduals of one year or older per km^2, and including infants 15-18 individuals per km^2 for. *A. belzebuth* in Colombia; Bernstein, et. al. (1976) estimate 9-14 individuals per km^2 in northern Colombia; Freese (1976) found 6-9 *A. geoffroyi* per km^2 in Costa Rica. In Guatemala, Coelho et al. (1976) estimated 45 individuals per km^2 and Cant (1978) 26 individuals per km^2. In Peru, Janson (1975) estimated 24 *A.p. chamek* per km^2.

The biomass for *A. paniscus* in the Voltzberg area in Surinam is calculated using the mean body weight data derived from Mittermeier (1977): 7.86 kg for males and 7.69 for females. The figures range between 0.4 and 0.5 kg/ha, depending on the home range size chosen (255 and 220 ha, resp.). Estimates from other areas are as follows: 0.07 (Eisenberg and Thorington, 1973), 0.2 (Heltne et al., 1975), 1.4-1.9 (Janson, 1975), 0.3-0.6 kg/ha (Muckenhirn, et al., 1975), 0.7 (Bernstein, et al., 1976), 1.5 (Coelho, 1976), 0.3-0.5 (Freese, 1976), 0.6-0.9 (Klein and Klein, 1976), and 1.4 kg/ha (Cant. 1978).

1.4. Climate

Surinam lies close to the equator and has a typical tropical climate. The mean annual temperature is 26.1°C (Lindeman and Moolenaar, 1959). Mean monthly temperatures vary only about 2.° during the year. A maximum is reached in September and October and a minimum in January and February. daily variations are greater and range from 21.0-31.6°C at 1.5 m in the rain forest. Temperatures at the top of the canopy are similar to those in clearings and range from 21.0-36.0°C. Personally collected data over two years at 1.5 m in the rain forest in the Voltzberg area show temperature maxima in September, October and November and minima in June, July and January (Fig. 4).

Relative humidity in the rain forest is highest in the early morning (95% or more), drops to about 82% during the middle of the day and reaches 95% again at dusk. In clearings and at the top of the canopy the daily range is greater and humidity may be as low as 40% in the middle of the day (Schulz, 1960; Hoogmoed, 1969).

Mean annual precipitation lies between 2,000 and 2,400 mm (Lindeman and Moolenaar, 1959) and is not evenly distributed

throughout the year. Usually, four seasons are recognized. A long wet season, usually beginning in mid-April and lasting until mid-July, with maximum rainfall in May or June. A long dry season begins in August and lasts until mid-November, October is, in the average, the driest month, but differs only slightly from September. The period from December to April can be divided into a short wet and a short dry season that vary considerably in length and intensity. The short wet season usually runs from December to mid-January or February, the short dry season from February to April. In abnormal years one of the two can be absent. In 1976, the long dry season lasted from August to 15 February 1977. Then, after a two-week wet period, a short dry season followed lasting six weeks, while the long wet season started about mid-April. Many trees dropped their leaves completely, giving a dead appearance to the mountain savanna forest. The long dry season is characterized by a monthly rainfall of less than 100 mm. October is the driest month with as little as 20 mm locally (Hoogmoed, 1969). May is usually the wettest, with precipitation that may exceed 400 mm locally. During the two years of observation in the Voltzberg area, the driest month was September with precipitation as low as 68 mm. The wettest month was May with 316 mm (fig 4).

The nights in the interior are mostly windless. Gales are rare. As elsewhere in the tropics the most violent winds are squalls. They occur during the transition periods (particularly in July and August) and may precede thunderstorms. During such squalls it is risky to walk through the forest. Old trees can be heard falling everywhere, especially during and just after heavy rainfall, and even younger vigorous trees may fall. This phenomenon of tree-fall is of great importance in the regeneration of primary forest.

1.5. Geology

The interior of Surinam is a part of the Guayana Shield, a formation of Precambrian age that is composed mainly of granito-diorites and granites. In central Surinam, a single remnant of the Mesozoic Roraima sandstones, the Tafelberg, has withstood erosion. The rocks in the interior are usually covered with deeply weathered ferrosiallitic/ferrallitic soils that vary from loamy sand to clay. Here one finds high upland forest. On shallow soils covering laterite caps and outcrops of unweathered granite, one finds more or less

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xeromorphic types of vegetation (Bakker, 1957). In some areas, such as the Voltzberg region, exposed unweathered rock can still be seen at the surface. These granite-inselbergs are mainly covered with lichens and algae, which cause weathering with high PH-values. The SiO_2, dissolved under these circumstances is deposited in the form of small, very resistant sheets. Together with the lichens and algae, the SiO_2 — sheets shut the granite off from deeper weathe-
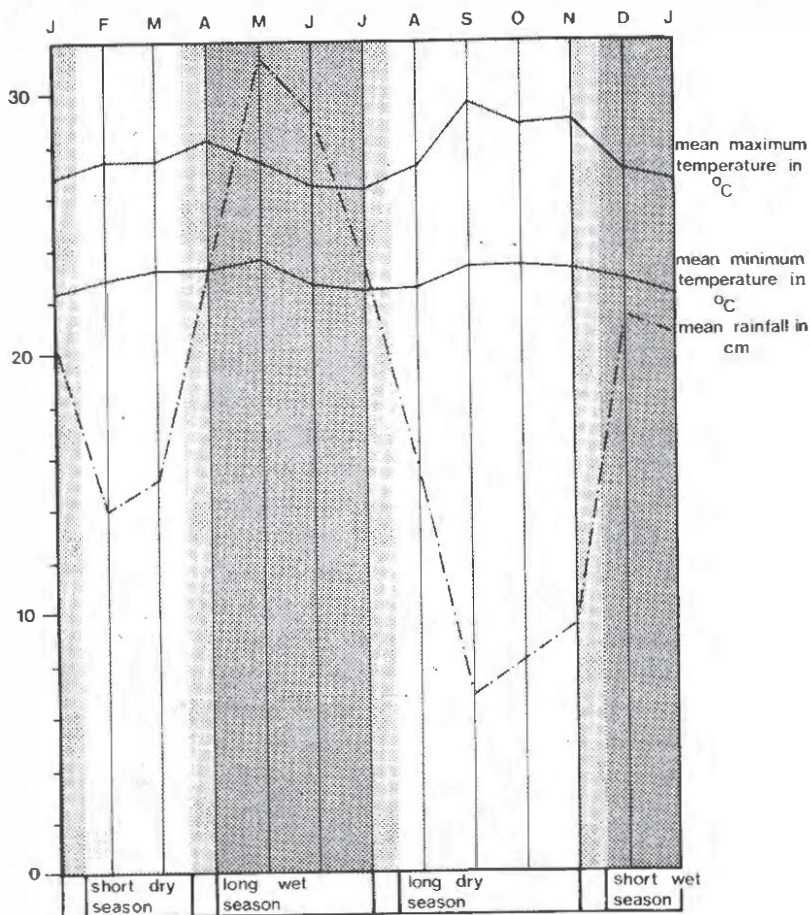
Figure 4 Climate of the Voltzberg study area during the present study, showing the monthly variations of mean maximum and minimum temperature at 1.5 m in the rain forest (full lines) and rainfall in a clearing (broken line). Data were collected from May 1976 to May 1978.

ring, a process which seems to be essential in the forming of inselbergs in the tropics (Bakker, 1957).

1.6. Topography

The coastal region of Surinam has almost no relief. In the interior several low mountain ranges are found, the highest peak being 1,280 m (Wilhelmina Mountains). Several plateaus, for instance the Brownsberg (514 m), are given mountain status in Surinam, as are isolated outcroppings such as the Voltzberg (240 m) and the Van Stockumberg (360 m).

Six major rivers dissect the country and for the most part flow from south to north. The Corantyn formes the border between Surinam and Guyana, the Marowijne divides Surinam and French Guiana (fig. 5). The lower reaches of the rivers are calm, but the upper reaches below 5.° N are broken by many rapids (e.g., the Raleighvallen-complex in the Coppename River near the Voltzberg).

1.7. Vegetation of Surinam

The Surinam coast primarily consists of mudflats covered by mangroves which are broken by occasional beaches. Behidind these lie large stretches of swamps, cut by sand and shell ridges running parallel to the coast. Moving further south, there is a belt of rain and marsh forests, then a narrow belt of white sand savannas and savanna forests, and finally the rain forests of the interior (Hoogmoed, 1969). The savanna belt, which begins roughly 25 km from the coast in the east and 80 km in the west, is not part of the coastal region and can be considered a division of its own or part of the interior. The interior is for the most part covered with high tropical rain forest broken by other forest types and small savanna enclaves. The largest of these is the Sipaliwini Savanna, which is located in the extreme south and connected with the larger Paru Savanna of Brazil (fig. 5).

1.8. Structural Description of the Forest Types found in the Raleighvallen-Voltzberg Region.

1.8.1. DRY EVERGREEN FOREST TYPES

Tropical Rain Forest

High rain forest. The range of forest types in Surinam covers Beard's (1955) categories of true tropical rain forest and evergreen seaso-

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nal forest. Since there is a continuum between the two categories, it is preferable to follow Lindeman and Moolenaar (1959) and Richards (1952) in using the term high rain or high forest, dryland forest to include the two Beard types.
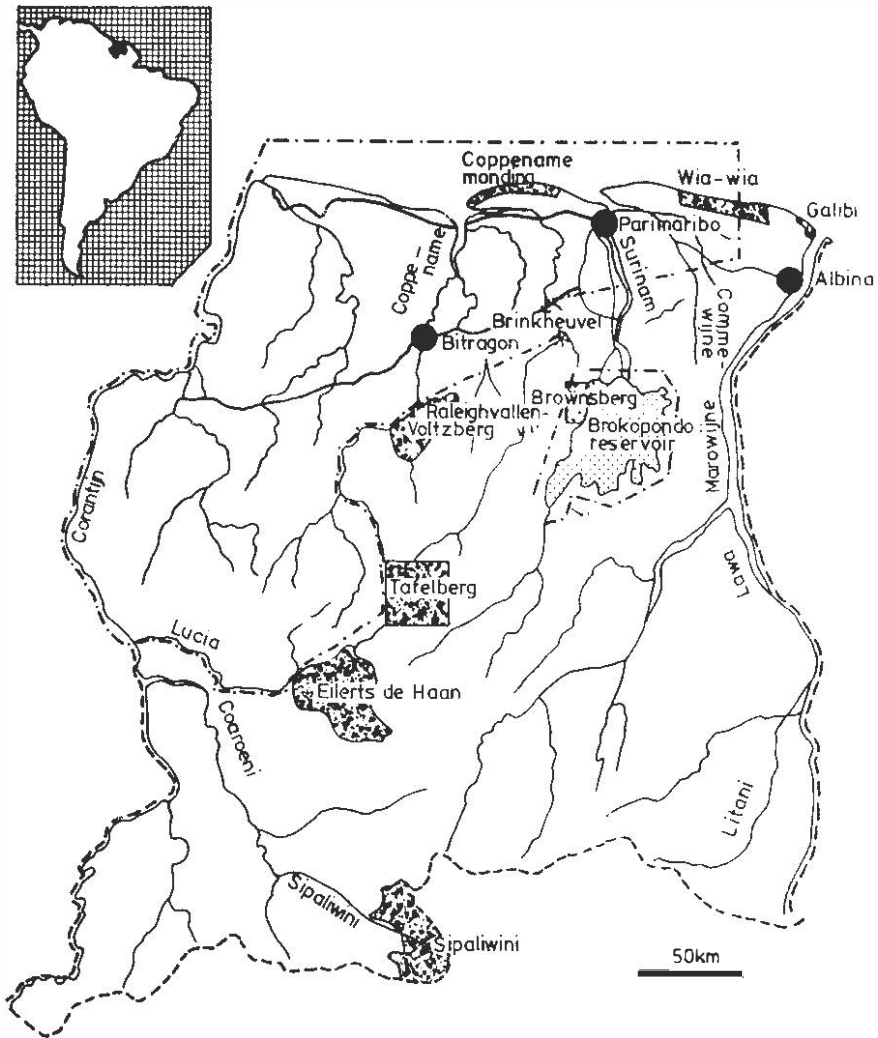
Figure 5 Map of Surinam showing the location of the Raleighvallen Voltzberg Nature Reserve and the other eight protected areas in the country.

High rain forest or high forest is found in areas not affected by seasonal flooding of rivers. The soil varies from loamy sand to clay, drainage is fair to good and litter decomposition is good. It is usually possible to distinguish three or four storeys in high forest. The upper storey consists of emergent trees which can reach 40-50 m and occasionally higher (in Surinam only *Cedrelinga cateniformis* reaches 60 m). Below the emergents is the canopy, which ranges from 15-30 m and can itself be divided into three categories, the upper part (25-30 m), the middle part (20-25 m) and the lower part (15-20 m). The understory consists of slender trees up to about 15 m, whereas saplings and undergrowth species make up the bottom 3 m.

In general, the crowns of the emergent trees are more wide than deep and spread over the top of lower trees around them. No lianes connect them with the canopy crowns. The canopy crowns are almost as wide as they are deep and are connected by many lianes, whereas those of the understory vary from long and narrow to tapering. Many species of liane (some important families are Bignoniaceae, Celastraceae, Convolvulaceae, Leguminosae, Menispermaceae and Moraceae) occur in high forest, but individuals of each species are usually widely dispersed. Epiphytes, including many Araceae and Orchidaceae, occur mainly in the crowns of trees. Stilt roots are rare, but buttresses are common. The herb layer is very open and consists mainly of broad-leaved forest grasses, small saprophytes and shrubby Rubiaceae Palms are common in high forest. *Oenocarpus bacaba* reaches the canopy, whereas *Astrocaryum, Attalea* and *Bactris* are found in the understory (Lindeman and Mooleneaar, 1959).

High forest is very rich in species and seldom shows any tendency to single-species dominance. The abundance of species makes it difficult to characterize high forest floristically. In the present study, the floristic composition of high forest and high mountain savanna forest in the Voltzberg region is partially analyzed by means of ½ ha plots, in which about all trees and lianes representing potential food sources for *Ateles* are plotted (Appendix). The most important vegetational attributes measured are number and distribution of the component plants. The most decisive criterion in the evaluation of relative importance of a species in a given forest stand is the number of individuals. Success in the struggle for existence is
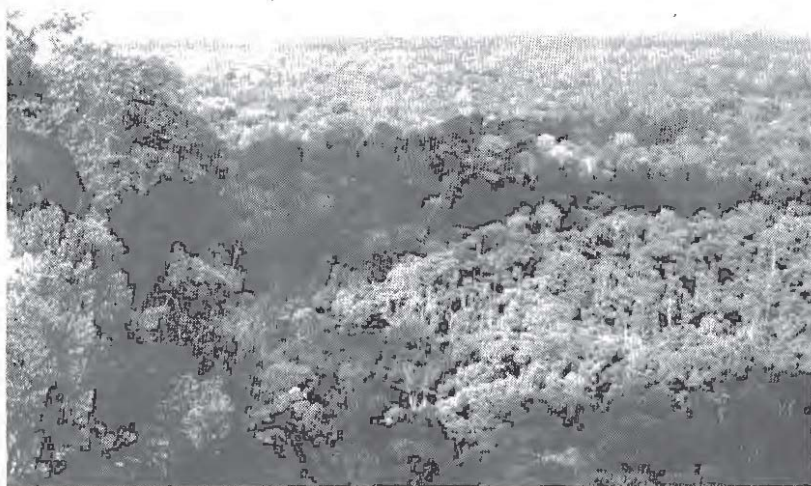
Figure 6 Scenic view looking south from the top of the Voltzberg, with part of the study area in the foreground. Note the other inselberg, the Van der Wijck top, at the horizon.

Figure 7 Understory and shrub layer of high forest in the Voltzberg study area, locally dominated by the "boegroemaka" palm (*Astrocaryum sciophilum*).

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shown by reaching a reproductive state. The composition of the fo-
rest shows distinct variations from place to place. Some species show
a wide ecological amplitude, others do not and are more local. Al-
so the method of dispersal probably plays an important role. For
example, seeds may be dispersed by wind, by water, endozoochori-
cally, exochorically by rodents or autochorically. Figure 8 shows the
distribution pattern of some species from high forest following diff-
ferent   dispersal strategies. It seems likely that species dispersed
by wind and those dispersed endozoochorically will show a random
distribution pattern (e.g., *Vataireopsis speciosa* and *Clarisia race-
mosa*, resp.) when it is considered that the entire seed shadow under
and nearby the parent plant will be destroyed by terrestrial seed
predators (e.g., bruchid weevils and rodents) which focus on these
concentrations of seeds (pers. obs.). On the other hand, species dis-
persed by scatter-hoarding rodents may show a clumped distribu-
tion pattern (e.g., *Eschweilera corrugata*) since these animals do not
carry seeds far away from the parent plant for storage. Seeds that
escape from predation in this way and manage to grow success -
fully will produce a non-random distribution pattern. This will also
be the case in species which produce relatively small fruits contai-
ning many seedlets, such as berries. The seeds are mostly dormant,
only germinating in a natural clearing caused by treefall. Germi-
nation is induced by strongly fluctuating soil temperature (as in *Ce-
cropia latiloba* (Holthuyzen and Boerbeem, 1982)

As demonstrated in figure 9, high forest has far more species
producing edible fruit for monkeys and man than any other forest
formation. Of a total of 486 species of fruit with an edible layer re-
corded for Surinam, 331 (68.1%) are found in high forest. Conse-
quently, high forest is the most important primate habitat in Surinam.
All eight primate species occur in high forest and several (e.g., *Ateles,
Cebus nigrivittatus* and *Chiropotes*) are largely restricted to this for-
mation.

The high forest of the Voltzberg region seems to offer a some-
what poorer appearance than the lowland rain forest in its optimal
form. In general, the lower part of the canopy and the undergrowth
are poorer in species, perhaps due to the abundance of *boegroe-
maka* palms (*Astrocaryum sciophilum*) that locally form a fairly con-
tinnuos layer at about 8 m height (fig. 7). The ground flora is very
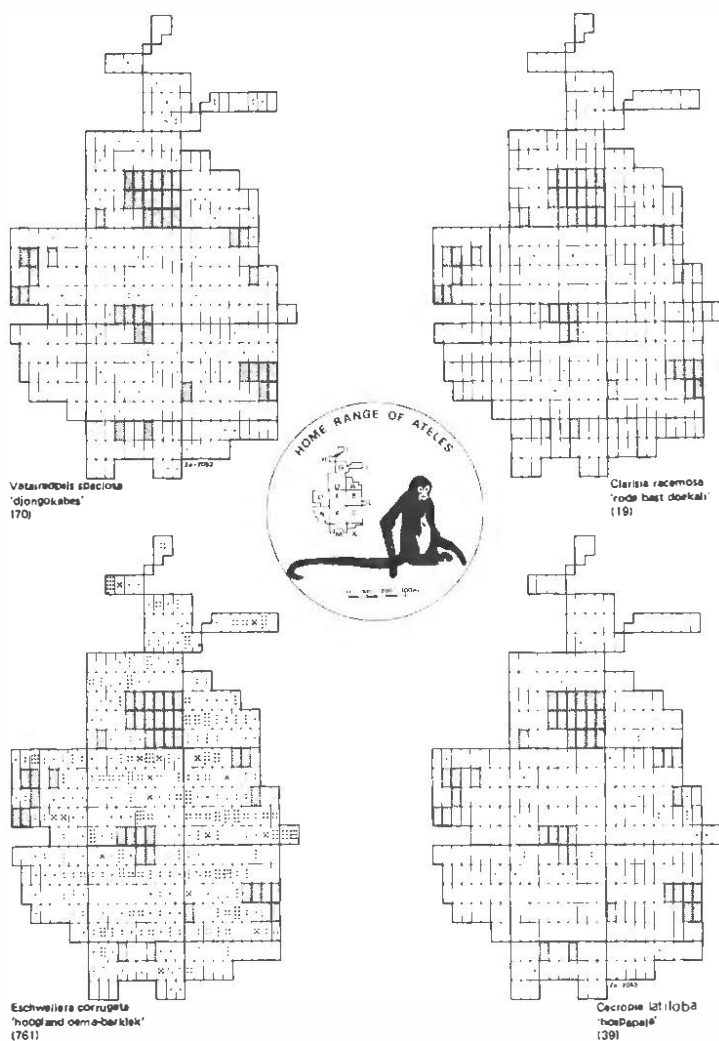
Figure 8 Distribution patterns of four tree species occurring in high forest in the Voltzberg region. The sampled area shown in the figure is part of the Voltzberg study area and is divided into ½ ha plots. The shaded areas indicate open granite and liane forest. *Vataireopsis speciosa*, an emergent tree, has wind-dispersed winged fruits; *Clarisia racemosa* has nutritious fruits containing one large seed, that is dispersed only by spider monkeys; *Eschweilera corrugata* has woody operculate fruits containing several large edible seeds that are mainly eaten and stored by agoutis and acouchis, and *Cecropia latiloba* is a pioneer plant, growing in edge habitats and treefall-clearings, dispersed via dormant seeds by a number of opportunistic fruit-eaters including many birds.

sparse. Young acaulescent *boegroemaka* palms locally dominate and, together with the old palms which have a well-developed trunk up to 5 m and sometimes even up to 12 m, they effectively intercept the light. High density of this palm seems to be possible because of its dispersal by scatter-hoarding rodents, its extremely slow growth, and its broad fishtrap-like, heavily spined crown that catches falling leaves and continually produces a circular heap of humus around the base of the trunk.

The observer, once experienced in correctly cutting leaves off the spiny young *boegroemaka* palms, could walk very easily thorough this type of high forest, an important factor in tracking fast moving monkeys as *Ateles*. In addition, it makes it easy to find one's way back or to trace a route of monkeys previously followed. The silvery underside of cut palm leaves clearly marks the trail through the forest.

Low rain forest. This term is used to designate a type of high forest that does not exceed 20 m in height. It is far richer in lianes than neighboring high forest and has far fewer *boegroemaka* palms. It usually forms a transition between high forest and liane forest, and sometimes between mountain savanna forest and liane forest. It isn't shown on the vegetation map (fig. 17) as it usually covers only small strips along the margins of other forest types.

Riverbank high forest. Riverbank high forest is absent from most of the coastal region, but it is common in the interior. In areas where river banks are high and not affected by seasonal flooding of river margins, riverbank high forest may grow right up to the river's edge. The structure of this type of forest is very similar to that of inland high forest, but the composition is clearly different. A continuum seems to exist; in the Raleighvallen area several indicator species for riverbank high forest could be determined, and these disappear about 700 m inland. The Voltzberg study area began almost two kilometers from the bank of the Coppename River and, therefore, this forest type was not present there.

Mountain Savanna Forest

Mountain savanna forest occurs on bauxite hills and low mountains where only a thin layer of soil covers the underlying rock. It is similar to white sand savanna forest in xeromorphy, thin-stemmed aspect, coriaceous structure of leaves and lack of clear differentia-
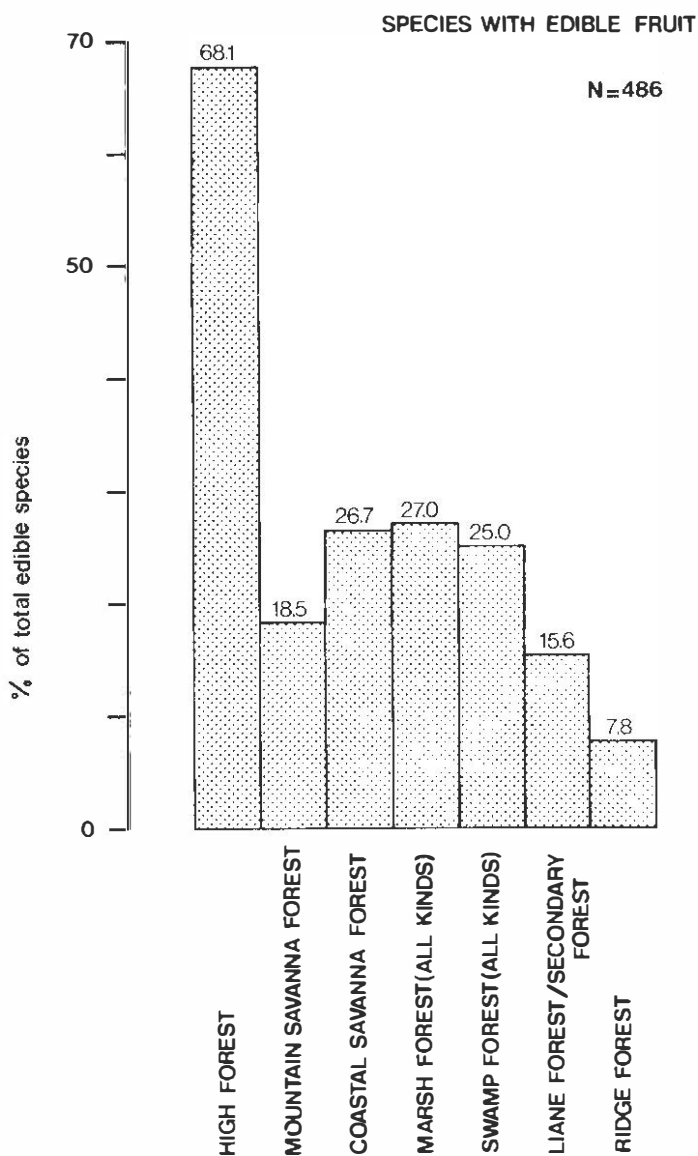
Figure 9 Woody plant species that produce fruit with an edible layer for monkeys and man and, exceed 2 m in height iin high forest and several other forest types in Surinam. Not included are the families Araceae and Palmae or those species that produce edible seeds. High forest has far more kinds of edible fruit than any other formation. Data on edibility are taken from Van Roosmalen's study on Surinam fruits (1977).

tion into storeys (it has a rather regular canopy of small crowns with few emergents), but it differs in floristic composition. Lianes are common, but not nearly as common as in formations such as liane forest. Understory palms such as *boegroemaka* are conspicuously absent. The undergrowth consists mainly of shrubs and treelets of the families Rubiaceae and Myrtaceae, and is easy to walk through. Visibility is much better than in high forest (fig. 10).

The dominant plant families in mountain savanna forest are Myrtaceae, Rubiaceae and Sapotaceae, which include several important fruit - producing trees for monkeys. In total, 90 species of tree and liane producing fruit with an edible layer have been recorded from mountain savanna forest (fig. 9).

A high mountain savanna forest formation, intermediate between typical mountain savanna forest and high rain forest, sometimes occurs on more favorable parts of the bauxite plateaus and in granite areas such as those surrounding the Voltzberg and the Van Stockumberg in the upper Coppename region. Some of the dominant species in this forest formation are *Ecclinusa guianensis*, *Guettarda acreana*, *Lafoensia pacari* and *Pteocarpus* vs. *santalinoides*. At edges high mountain savanna forest one frequently finds important food trees for monkeys such as *Ceiba pentandra*, *Hymenaea courbaril* and *Spondias mombin*.

During extremely dry seasons (e.g., 1976), which seem to occur irregularly at intervals of a few to many years, most of the trees from mountain savanna forest drop their leaves, giving the forest a dead appearance. In normal years only some of the trees seem to be deciduous.

Liane Forest

Liane forest is a formation in areas with stony lateritic soils providing bad rooting conditions and poor foothold for trees. It is noteworthy for the absence of storeys. Tall trees do occur, but they are so widely separated from one another that no true canopy exists. The space between the trees is filled with dense tangles of lianes, vines and twiners that grow in abundance because of unrestricted exposure to sunlight (fig. 11). Although occasional trees in liane forest may reach 30 m or more, the liane tangle itself rarely exceeds 10-15 m.

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Figure 10 Mountain savanna forest in the Voltzberg study area. Note the thin, staky appearance of most of the trees and the lack of understory palms.
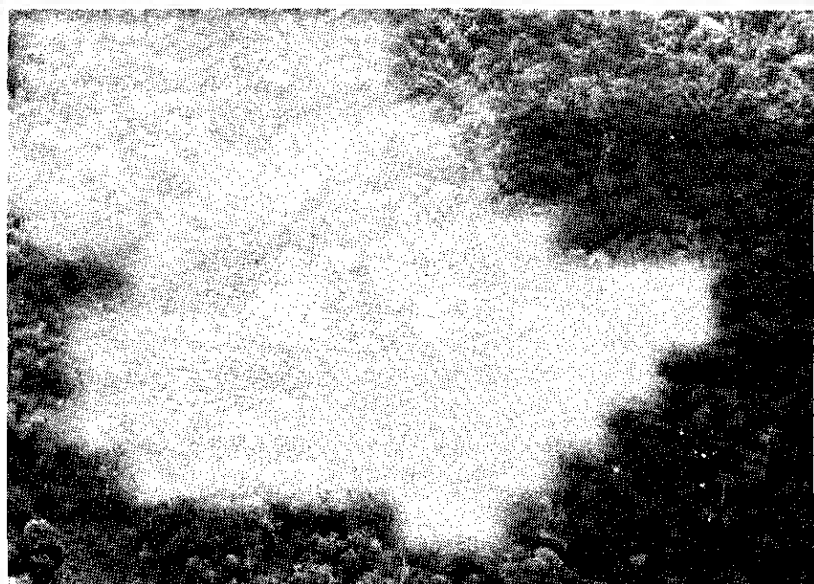
Figure 11 Aerial photograph of liane forest surrounded by high forest in the Raleighvallen - Voltzberg Nature Reserve. Note the isolated large-crowned emergents of the species *Vitex stahelii*.

Habitat...

A large number of species are represented in liane forest, but most of them are of very low frequency. A total of 76 species producing fruit with an edible layer have been recorded from liane forest in Surinam. The dense liane tangles provide many microhabitats for insects and other arthropods, making them a fertile foraging ground for partly insectivorous monkeys (e.g., *Saimiri* and *Cebus*).

1.8.2 WET FOREST TYPES

Swamp Forest

Following Beard (1955), the term swamp forest is used for forest on soil which stays wet to damp throughout the year and as a result aeration of this soil is permanently impeded. Swamp-forest soils are actually under water most of the year and, if not inundated, at least remain damp during the peak of the dry season. The soil is usually composed of heavy clays and litter. The litter decomposes poorly because of bad aeration and accumulates to form a peat layer.

In the Raleighvallen-Voltzberg region only a single type of swamp forest is present along the small creeks and streams that flow almost all year round. Because of dominance of the *pina* palm, *Euterpe oleracea*, which locally forms pure stands, it is called *pina swamp* (fig. 12). Pina swamp forest reaches at least 20 m in height and, because of scattered tall trees, it cannot be differentiated clearly into storeys. The irregular canopy ranges from 18-30 m and is characterized by trees such as the buttressed *Virola surinamensis* and *Pterocarpus officinalis*, the stilt-rooted *Symphonia globulifera*, and *Pachira insignis* and *Eperua falcata*, all of which are food plants of *Ateles*. The most common tree is *Euterpe oleracea* itself, reaching the canopy. Another palm tree, *Astrocaryum sciophilum*, is common, especially in drier places. Visibility is good. The undergrowth is open, since it is formed by relatively few saplings of the above mentioned species and *Euterpe oleracea* itself. Locally, a dense herb layer can be present, which can hinder progress.

A total of 122 tree and liane species producing fruit with an edible layer have been recorded from the various kinds of swamp forest, but pina swamp forest alone is rather poor in edible species (fig. 9).

Figure 12 Pina swamp forest along a creek flowing through the Voltzberg study area. Note the abundance of the *pina* palm (*Euterpe oleracea*).

Marsh Forest (Seasonal Swamp Forest)

Marsh forest or seasonal swamp forest in Beard's (1955) terminology is the term used for a number of two-storey forest types whose soils are periodically but not permanently inundated during the year. In drier parts of the year they lie above the ground-water table, making aeration possible.

Marsh forest is an important habitat for several monkey species.

The dense, liane-covered lower storeys along river margins provide excellent foraging grounds for the partly insectivorous species such as *Saimiri sciureus*. Marsh forest is rich in plant species, including many with seeds dispersed by wind or water. Of all tree and liane species producing fruit with an edible layer, 131 (27%) are found in marsh forest. However, the only type of marsh forest occurring in the Raleighvallen-Voltzberg region is riverbank marsh forest. *Riverbank marsh forest.* This type of marsh forest occurs along river margins and is seasonally flooded by rising waters. The *maripa* palm, *Attalea regia*, can be regarded as a good indicator species for all types of marsh vegetation. This palm and several *Bactris* spp. can dominate locally to create palm forests'.

1.8.3. XEROMORPHIC VEGETATION

Rocksavanna

Rocksavanna is a rare vegetation type found in the Voltzberg region only on granite where the rock is bare or covered by shallow soil. It consists of bushes, terrestrial epiphytes, cacti and grasses. No palms occur, but some thin lianes and twiners are present. Maximal height is 5 m. The vegetation is not closed. At edges of rocksavanna areas, an important edible-fruit producing tree, *Spondias mombin*, can be found (fig. 13)

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Figure 13 Transition from mountain savanna forest to rocksavanna. Important edible-fruit producing trees such as *Spondias mombin* and *Ecclinusa guianensis* can be found at edges of rocksavanna.

2. METHODS

2.1. The Study Area

The present study was conducted in the Raleighvallen-Voltzberg Nature Reserve, a protected area of 56,000 ha that was established in 1961 and is currently managed by STINASU; the Surinam Nature Conservation Foundation. It is located on the east bank of the Coppename River in central Surinam (fig. 5) and is bordered on the north by the Kwama Creek and on the south by the Tanjimama Creek (fig. 14). It includes Raleighvallen, the boulder-strewn rapids and falls (fig. 15) that mark the limit of navigability of the Coppename River, and several granitic 'inselbergs', most notably the 240 m dome-shaped Voltzberg (fig. 16) and the Van Stockumberg. The headquarters of the Raleighvallen-Voltzberg Nature Reserve are on Foengoe Island, which is situated at the lower end of the Raleigh-vallen rapids. The island can be reached by plane or by boat. A three-hour trip by car followed by a three to five-hour trip by motorized dugout-canoe brings a visitor to Foengoe, situated about six kilometers from the Voltzberg. It has restricted facilities for tourists and researchers and it served as a main base during the present study.

In March 1976, together with the primatologist R.A. Mittermeier, a detailed reconnaissance was carried out and the borders of the *Voltzberg Study Area* were established. With the help of several Surinam field assistants a grid of main trails was cut at 500 m intervals, for a total of 15.5 km of trail. In the 130 ha area surrounding the camp and at the edge of a large granite plate, an additional 11.2 km of side trails were cut at 100 m intervals, parallel to the long axis of the study area. The finer grid was necessary in this area because it was the most important part of the spider monkey group home range.

The study area consisted of 10 blocks of 25 ha each, two incomplete blocks limited by the Voltzberg and together covering about 44 ha, and a final section of about 12 ha extending the study area to the start of the main tourist trail ascending the Voltzberg (fig. 14). When the surface of the two large, open-granite clearings in the study area is subtracted, the total forested habitat was almost

exactly 300 ha. This study area was used during the first year for gathering synecological data on all eight Surinam primates. In the meantime, a group of spider monkeys was selected and the boundaries of its home range determined very roughly. It soon became
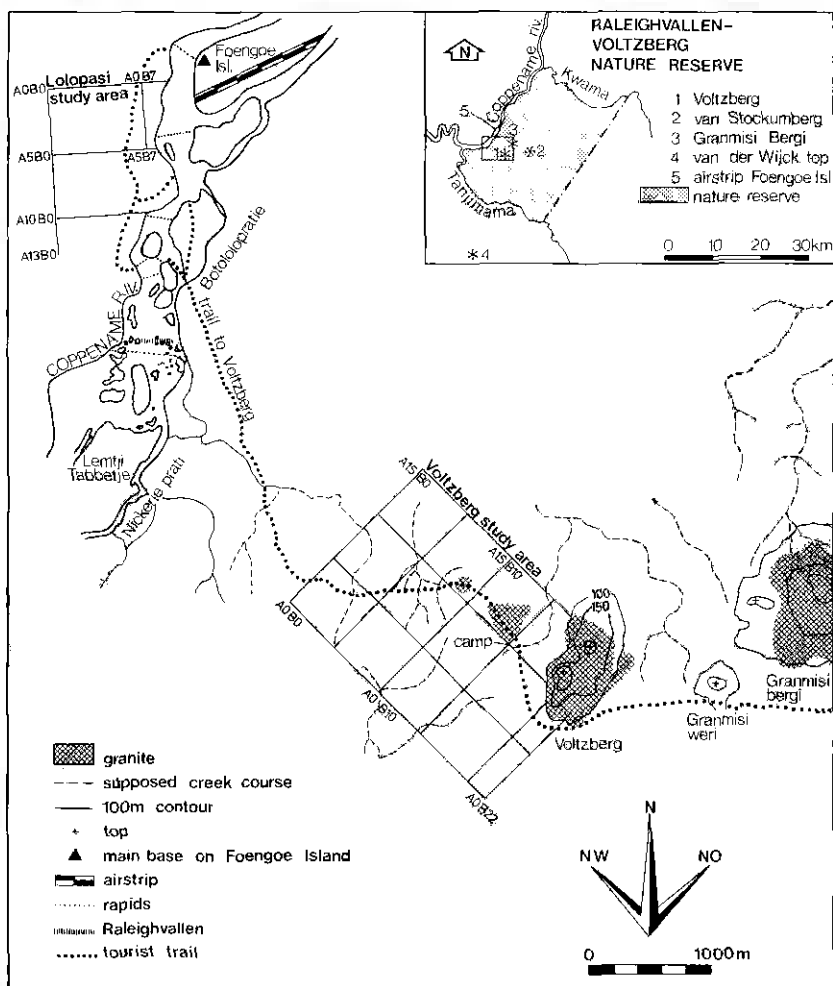
Figure 14 Map showing the location of both study areas in the Raleighvallen-Voltzberg Nature Reserve. The trail system of the Lolopasi study area was not completed since the group of spider monkeys living in the area was too difficult to follow. No progress was made in habituating them. This may have been due to light hunting pressure in the recent past. The main study area at the foot of the Voltzberg dome has only major trails at 500 m intervals indicated.

Figure 15 The 240 m Voltzberg (right in the background) and the 360 m Van Stockumberg (left in the background) seen from Raleighvallen rapids in the Coppename River about two kilometers upstream from Foengoe island.
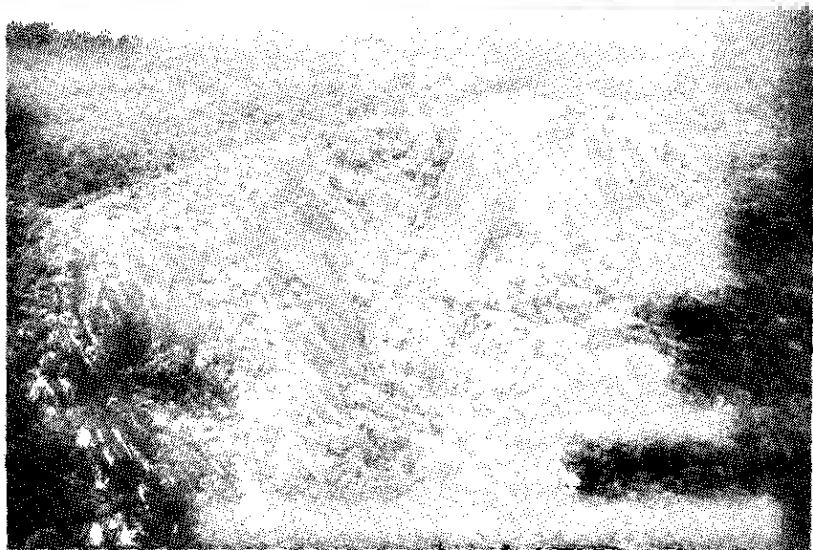
Figure 16 Aerial photograph of the Voltzberg. The forest in the foreground is part of the study area.

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evident that the original study area had to be extended approximately 15 ha to the northeast and 25 ha to the southwest in order to cover the entire range of the group (fig. 17).

All 100 m and 500 m trails were provided with red-painted sticks at 50 m intervals. Each of these had aluminium tags showing their coordinates in relation to an A-axis directed NE and a B-axis directed SE from a point of origin at the western corner of the study area. After trail-cutting, a vegetation map was made by first pacing off vegetation boundaries along all the trails and marking them on the map. Then, each vegetation boundary was traced by compass and mapped. Obviously, vegetation mapping is most accurate where the trail system is most extensive, namely in the main part of the spider monkey home range.

The forest in the study area can be divided into four major types (fig. 17). High forest predominates, followed by liane forest and mountain savanna forest. Pina swamp forest grows along the small creeks that flow through the area. Low forest is present as a transitional type but hasn't been mapped, as it usually occurs in narrow strips along the borders of liane forest. The Voltzberg study area has a greater diversity of forest types and edge habitats than would usually be expected in a tract of similar size in the interior. This is probably 'caused by the abundant granite outcroppings that do not provide sufficient support for most tall forest trees, but do permit the growth of comparatively rare formations such as mountain savanna forest and liane forest.

Since spider monkeys never enter low forest or liane forest, these formations, together with open granite and rocksavanna, act as natural boundaries. As shown in figure 17, large liane forest complexes and the Voltzberg itself form a considerable part of the boundaries of the spider monkey home range, giving it a peninsula-like appearance.

Other animals present. All eight primate species were well represented. Besides *Ateles paniscus*, one could regularly observe *Saguinus midas, Saimiri sciureus, Cebus apella, Cebus nigrivittatus, Chiropotes satanas, Pithecia pithecia* and *Alouatta seniculus.* In addition to these primate species, a number of other mammals, as well as birds and reptiles, inhabit the Voltzberg study area. Larger rodents such as the agouti (*Dasyprocta leporina*) and the acouchi (*Myo-*
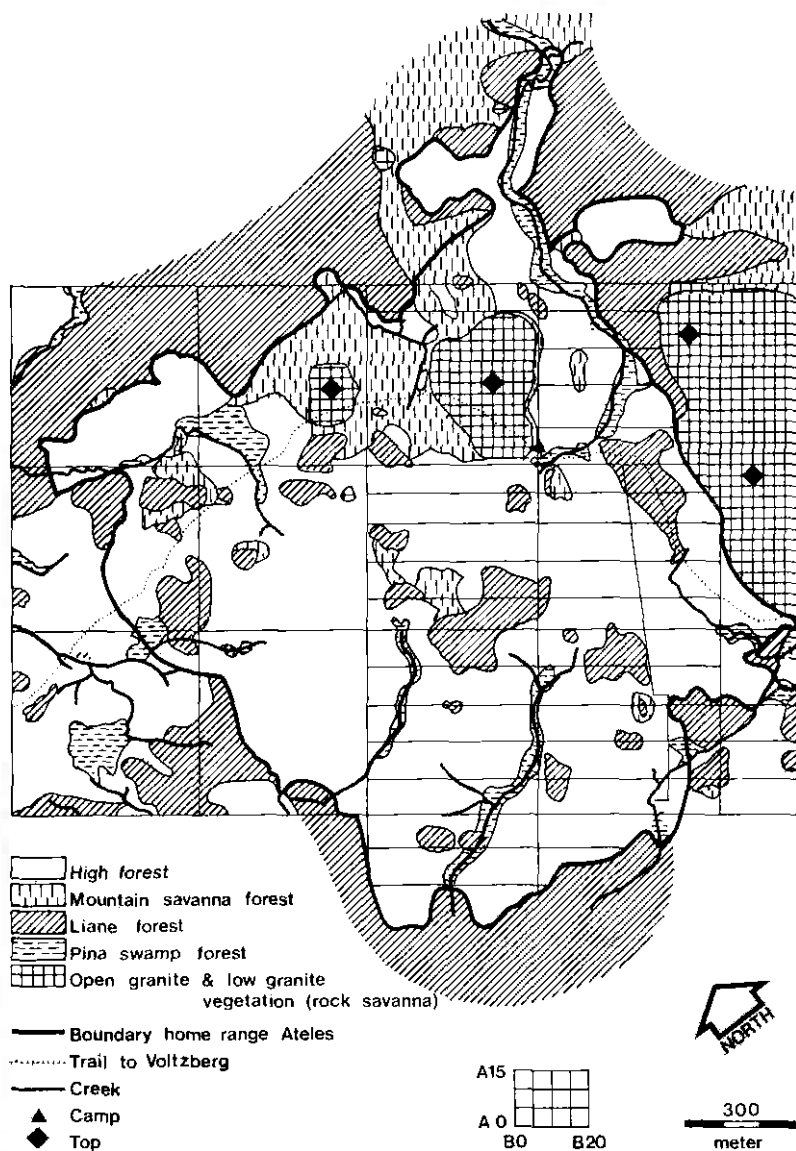
Figure 17 Map of the Voltzberg study area showing distribution of forest types and trail system. The areas of open granite, low granite vegetation ("rock savanna") and liane forest were not used by the spider monkeys. The large area of open granite at the right is the Voltzberg dome with its two tops. The camp is situated at the edge of the larger of the two granite plates. The perimeter of the spider monkey group range is marked by a heavy line.

procta exilis) are commom. Two kinds of squirreel (*Sciurillus pusillus, Sciurus aestuans)* and the prehensile-tailed porcupine *(Coendou prehensilis)* also occur, but are rarely seen. The carnivores are represented by one or two jaguars *(Panthera onca)*, several ocelots *(Felis pardalis)* and a number of tayras *(Eira barbara)*. Edentates include the giant armadillo, *(Priodontes giganteus)*, the nine-banded armadillo *(Dasypus novemcinctus)*, the tamandua *(Tamandua longicaudata)*, the giant anteater *(Myrmecophaga tridactyla)*, and two kinds of sloth (*Choloepus didactylus, Bradypus tridactylus)*. The common opossum *(Didelphis marsupialis)* and several smaller marsupials (e.g., *Marmosa* spp.) are present. Ungulates are represented by several collared peccaries *(Tayassu tajacu)* and at least one tapir *(Tapirus terrestris)*.

Many species of bird live in the study area and a comprehensive list is given in Mittermeier and Milton (1976) and in the field checklist of the Birds of the Guianas (Davis, 1966). The most conspicuous are large species such as the black curassow *(Crax alector)*, the marail guan *(Penelope marail)*, the gray-winged trumpeter *(Psophia crepitans)* and the tinamous *(Tinamus spp.)*. Cocks-of-the-rock *(Rupicola rupicola)* are surprisingly abundant. An important lek area and many nesting sites were found within and nearby the study area. In the canopy are scarlet macaws *(Ara macao)*, toucans *(Ramphastos* spp.), aracaris *(Pteroglossus* spp.) and a variety of parrots, especially red fan parrots (*(Deroptyus accipitrinus)*, orange-winged parrots *(Amazona amazonica)* and mealy parrots *(Amazona farinosa)*. A number of raptors, including the harpy eagle *(Harpia harpyja)*, occasionally visit the study area as well.

Frogs, lizards and snakes are common, and the turtles are represented by two abundant tortoises *(Geochelone carbonaria* and *G. denticulata)*.

Insect life is varied and abundant, but mosquitos are rare. Insect discomfort usually is caused by chiggers and a number of stinging and biting ants.

2.2. Data Collection

2.2.1. Habituation of spider monkeys. During the first year, when
the synecological part of the study took place, a group of spider monkeys was selected for the detailed autecological study that was

planned for the second year (May 1977 - May 1978). Since the area had been undisturbed for at least several decades, the animals were not particularly shy. From time to time, tourist groups walk along the main trail to the Voltzberg thorough part of the group's range. Therefore it is likely that each member of the *Ateles* group saw people before this study began. In any case, the animals in the groups, except for one old male, no longer responded to people with the screaming - branchshaking and dropping –defecating display typical of *Ateles* that have had no contact with humans. They also didn't flee at the first glimpse of humans as do spider monkeys where they are hunted.

While studyings synecology of the eight Surinam primate species during the first year, many census walks were made of the entire study area. Data were collected while looking for 'target' species or tracking them. During this period, many contacts were made with all members of the spider monkey study group and occasionally with members of two other groups that touched the study area. Every time spider monkeys were located, first sighting data were collected for synecological purposes and the animals were followed for as long as possible. When the animals were lost, the observer returned to the trail and again used the trail system to search for other monkeys. The cutting of palm leaves, saplings and lianes seemed to disturb the monkeys most, but after a while the observer got very experienced in zigzagging through the shrub layer with minimal cutting.

From February through April 1977, attemps were made to follow spider monkey subgroups as long as possible. After many attempts, and aided by the observer's growing experience in walking freely through the forest while keeping visual and especially auditory contact, it became possible by the beginning of April 1977 to track spider monkeys day after day without noticeably disturbing either their ranging behavior or activity patterns. Working alone seemed to be essential for this. When accompanied by one or more observers, it was hard to maintain contact and the monkeys' behavior seemed to be influenced significantly.

2.2.2. **The synecological part.** The synecological study in the Voltzberg study area was initiated in March, 1976. Synecological data were gathered on all eight primate species for 10-15 days each

month until April, 1977. A total of 132 field days were spent studying synecology only. During the first phase and later on, my colleague R.A. Mittermeier also collected data on synecology. We gathered data during 12 census walks of the entire study area, spread over a year, and while while looking for and tracking 'target' species selected for a given day. The following kinds of information were recorded every time a group was encountered: time, location in the study area, forest type, edge or non-edge habitat, activity (e.g., resting, traveling, feeding on plant food, foraging for or feeding on insects), height and level in the forest, how located (e.g., spontaneously seen, heard vocalizing, heard crashing, heard dropping fruit or faeces), path-animal distance and observer-animal distance (both for census purposes), group size and, if possible, group composition and direction of travel. All data on preferences for different forest types, vertical stratification, activity and location of the group were based on first sightings only, in order to avoid possible bias caused by the presence of the observer. When first sighted, the visible members of a subgroup were usually all engaged in the same activity, at the same level and in the same forest type, especially in the case of spider monkeys. In order to avoid confusion, first-sighting data were based on the first individual actually seen, which is essentially an instantaneous focal-animal sample.

A sighting was considered an edge when the first animal seen was within 20 m of a clearing or another forest type. Feeding on plant food was considered the activity when the first animal seen was eating fruits, leaves, flowers or vegetable matter. Foraging for or feeding on insects was considered the activity when the first animal seen was eating or actively searching for insects or other animal life.

For stratification, observations the forest was divided into six levels : shrub layer (0-3 m), understory (3—15 m), lower part of the canopy (15-20 m), middle part of the canopy (20-25 m), upper part of the canopy (25-30 m), and emergents (30-60 m). It was usually impossible to estimate the height of emergents accurately because of intervening vegetation and the limitations of the clinometer. However, it was usually quite easy to determine whether or not a tree was an emergent simply by its relationship to surrounding trees.

Location within the study area was determined by using the markers situated at 50 intervals along the trails. Measuring the dis-

tance from a particular tree to the nearest marker gave quite accurate coordinates for each sighting.

Synecological data continued to be gathered during the second part of the field study on spider monkey autecology. At this time *Ateles* became the 'target' species, and synecological data were only collected while searching for spider monkeys or when encountering other species while tracking spider monkeys.

2.2.3. **The autecological part.** The study on the autecology of spider monkeys in a strict sense was started in the Voltzberg study area at the end of April 1977, and lasted until the beginning of May 1978. For each month of attempt this full year an attemp was made to observe spider monkeys for seven full days, but in several months only five or six days were possible. A total of 135 days was spent in the field during this period, resulting in over 865 hours of observing only spider monkeys. Usually 10-14 days had to be spent each month in the study area, divided into two sessions of 5-7 days each. As a rule, the first and the third week of each month were spent in the study area, but sometimes the second and the fourth week were chosen.

In natural habitats, spider monkeys are usually observed in small subgroups of variable size and composition. The subgroups within a group interact peacefully with one another, but groups are separated from one another by agonistic interactions, particularly between the males who appeared to act territorially and to respect quite clearcut boundaries. In order to spot a 'target' subgroup at the start of a session, several methods could be used. On returning to the study area after an absence of 7-10 days the situation had always drastically changed. Changes in the fruit-producing plant species and also in individual plants usually resulted in completely different foraging routes for the monkeys. A fresh start had to be made every time. Therefore, at the start, part of trail system was covered until a subgroup was encountered. The searching could last for hours or sometimes for as much as a full day. A long call by a male spider monkey, which was somentimes performed in response to imitation calls, helped in saving time. The calling male or 'his" subgroup could then be found using a compass, or at least efforts could be concentrated on a more defined area. In case of prolonged lack of success, the Voltzberg could be climbed in the late afternoon in the

hope of seeing spider monkeys entering one of the huge, usually leafless or early flushing sleeping trees. If so, the tree was located before returning to camp and the next day an attempt was made to be present at the foot of this tree at 5.45 h. It was then necessary to remain continuously with the animals until evening, between 17.00 - 18.30 h, when they entered another sleeping tree. If contact with a subgroup was lost, it was necessary to return to the nearest trail and try to find this or another subgroup as soon as possible.

The following data were collected while tracking spider monkey subgroups. At five-minute intervals the composition of the subgroup was recorded, the activity of all members of the subgroup, and the stratum and forest type occupied. The coordinates of every trail crossing were recorded by pacing the distance to the nearest marker. When the animals were feeding complete samples (e.g., infructescences, inflorescences, leaves and/or bark) were collected whenever possible. Usually several visits to a particular food plant were needed, as spider monkeys generally show a very economic use of food resources. When the monkeys didn't drop a complete sample of the food plant, a collection was made as soon as possible by a native tree climber from the Surinam Forest Service. Each food plant actually used by the monkeys was marked with a numbered aluminium tag and a piece of red-fluorescent plastic flagging tape, nailed on just after the monkey(s) left the tree. Using a water-resistant pencil, date and monkey species were written on the plastic tape and, later, the coordinates of the food plant were determined. Food samples were collected in plastic bags sealed by a piece of plastic tape on which time and tag number were written. Back in the Voltzberg camp, a picture of all items eaten that day was taken with a Nikkormat EL camera, using a 52 mm macro lens. The samples were preserved by adding some formaldehyde (2% sulotion) and were then labelled. Upon returning to the base camp on Foengoe Island, all samples were identified if possible, using the book on the fruits of Surinam (Van Roosmalen, 1977) and monographs of certain plant families and genera (Berg, 1975; Wessels-Boer, 1965). After making a drawing of each new food item, including cross-sections and other details, all samples were put in jars, labelled and stored.

Faeces were also collected and preserved. Spider monkey faeces usually consisted mainly of undisgested and unharmed seeds

and stones (seeds protected by a hard endocarp), especially during the wet seasons. Consequently, the faeces were not compact and when they fell to the forest floor the seeds dispersed over quite a wide area. If this happened, as many of the seeds and/or stones as possible were collected.

Data on phenology of trees and lianes of many species, especially those used by monkeys, were gathered in the following manner. While searching for or tracking spider monkey subgroups, the observer visited almost every part of the groupu's range over the course of a few days. During these walks throughout the year, the presence of fresh flowers, fruits or fruit-parts on the forest floor was noted, and new species were collected and identified. In this way, timing and length of flowering and fruiting periods were determined for many plants, not only on a species but also on a individual level.

In September 1977, together with a native tree specialist and an assistant, a marking program was initiated, which lasted about seven months. By this time, almost all important food species of *Ateles* had been determined, and many of them had already been collected during the synecological part of the study. A list of 120 important species, including food trees, easily recognizable lianes and some sleeping trees, was compiled using vernacular names. When a species was not known to the tree specialist, samples from several individuals were shown to him so that he could learn its special properties such as type of habit, colour, taste and texture of bark and/or wood, presence of latex, type of leaves, etc. Each species was given a code number. The most important part of the spider monkey group range, approximately 205 ha, was inventoried. For this purpose, new transects were cut at 50 m intervals, perpendicular to the 100 m trails, resulting in about 370 rectangular blocks of half a hectare each (fig. 8). All individual trees and lianes belonging to the listed species were marked with an aluminium tag different from the kind used to mark trees which the spider monkeys were actually seen feeding. In this way, block after block was inventoried and the location of each numbered plant was approximately determined by its place in a certain half-hectare block. Trees below 12 m were not included, as this was determined to be the lower limit of the spider monkey vertical range. For the purpose of

this study, tagging and plotting was restricted to those individual plants that had obviously reached their own preferred stratum and this, in general, implies that they would flower and fruit. Plants which provided the monkeys with only edible leaves were plotted when they reached 12 m or more, regardless of whether they had reached their preferred stratum.

A total of about 10,000 trees and lianes were marked and plotted in special maps in order to determine their density and pattern of distribution (Appendix). In this way most of the trees and lianes, which had been marked when spider monkeys fed on them, were marked again, thus giving a double check of identification and location. Also, this provided an idea of the reliability of the tree specialist, which turned out to be high.

For measurement of dietary composition, the frequency with which different foods were chosen was used. If a subgroup or a solitary ranging animal was seen feeding on a single food plant, one observation was scored. If a subgroup or individual moved to another tree of the same species, another observation was scored. If a subgroup or individual moved to a different food plant species, one observation was scored for that species. If identifiable seeds or stones of a given species, which had not been seen being eaten that day, were found in the faeces of a monkey, one observation was scored for that species. This method may seem to be somewhat crude, but it a gave a good estimate of the relative importance of different food plant species and families in spider monkey diet. This method is preferred to determining the total feeding time for each species, because feeding rate can vary widely between foods. Some fruits are swallowed whole, others are woody and indehiscent and have to be opened first. Some fruits contain a lot of nutritions pulp and comparatively small seeds or stones; others produce very little pulp or are eaten only for a minuscule aril. Measurement of the proportion of feeding time spent on different foods has also the disadvantage that analysis of faecal samples cannot be taken into account. Faecal samples can give much information, particularly for spider monkeys, since the animals swallow and do not digest seeds and stones in 93.5% of all fruit-feeding observations. The method of quantification used in this study produces some bias towards foods that are eaten regularly but in small amounts, and towards plant species that

produce several edible items at the same time. Both features, however, are rare in the case of spider monkeys and consequently this bias is of little importance. A relatively more important bias may be that produced towards species that grow at high densities. For example, *Virola melinonii* (Myristicaceae) can be overestimated in this method because it is found locally in great abundance. When feeding on a particular tree of this species, the monkeys will also visit nearby trees, each of which provides only a small crop of fruit. If these trees were more widely dispersed, they would probably be ignored because of the small energy yield per tree.

2.3. The General Survey

Some other localities were investigated during the general survey, and these added data to the distribution map the habitat table for *Ateles*.

2.3.1. Lolopasi, west bank Coppename River, Raleighvallen-Voltzberg Nature Reserve.
Lolopasi is located directly across the Coppename River from Foengoe Island, site of the headquarters of Raleighvallen-Voltzberg Nature Reserve. A trail of 2.9 km has been cut through the forest to enable visitors to reach the Moedervallen, largest of the Raleighvallen rapids. During the first part of this study, additional trails at 500 m intervals were cut to the west, roughly perpendicular to the riverbank and 600-1,000 m inland (fig. 14). The trail system has not been finished, but a total of 7 km of trail were cut before the area was abandoned as a study site.

The Lolopasi area consists almost entirely of riverbank high forest and high forest, except for a narrow strip of marsh forest close to the riverbank. Pina swamp forest and some liane forest are present, but no mountain savanna forest occurs.

All eight Surinam monkey species were encountered in the area, but some of them, particularly *Ateles*, were very shy, probably because of recent hunting. It was impossible to keep track of spider monkeys for more than half an hour. No progress could be made in the habituation of the spider monkeys, but a rough idea of the population size and some dietary data were obtained.

2.3.2 Kayser Mountains.
The Kayser Mountains are located in the interior, in southwestern Surinam. The Surinam Geological Servi-

ce opened a large area for survey work by cutting transects. A two-week survey of monkeys was carried out there in September 1976, using a trail system of about 40 km. The area was undisturbed except for some hunting by the workers. Since certain preferred game species, such as black curassows (*Crax alector*) and peccaries (*Tayassu tajacu* and *Tayassu pecari)* occurred at high densities, these people did not hunt monkeys. The spider monkeys were not at all shy and reacted with typical first contact displays. The population density of *Ateles* and several other monkey species was determined to be somewhat higher than in the Voltzberg area. Less severe food scarcity in the long dry season seemed to be the main reason for this difference.

The vegetation is primarily high forest and mountain savanna forest, with some pina swmp forest in low-lying areas. Above 400 m, the boegroemaka palm (Astrocaryum sciophiloum) of the under-growth and shrub layer of high forest is replaced by the bergimaripa palm (Attalea speciosa), which reaches the canopy (15-18 m).

Additional data on diet, subgroup composition and habitat preferences of *Ateles* were collected, as were synecological data on all monkey species present.

2.3.3. **Other parts of Surinam.** Locality data for the distribution map (fig. 1) were taken from museum specimens of Surinam monkeys, from field observations by R.A. Mittermeier, and from reports by several other naturalists well-acquainted with the monkeys.

3. HABITAT PREFERENCES

3.1. Preferences for Different Forest Types

Where little or no hunting has taken place, *Ateles p. panis-cus* can be quite abundant in tracts of high forest. It also occurs in riverbank high forest but this habitat has often been subjected is severe hunting by Bushnegroes and/or Amerindians been subjected to. Even in uninhabited stretches of riverbank high forest, there has usually been at least some hunting by occasional field crews from the Meteorological, Geological and/or Mining Services. I never observed spider monkeys right at the river's edge. The reasons may be unpleasant hunting experience in the past, tendency of the monkeys to avoid edge hanitats, and/or lack of preferred food plant species at the river margins. Aside from the preferred habitats, *Ateles* was seen in Surinam only once in marsh forest, once in high savanna forest growing on the Coesewijne formation and three times in *Eperua falcata* savanna forest (Mittermeier, 1977).

Ateles also apparently prefer undisturbed high forest in other parts of South America (e.g., Janson, 1975; Bernstein, et al., 1976; Hernández-Camacho and Cooper, 1976). They are usually not found in areas where human activity has resulted in forest destruction. Their absence from most areas where there has been human activity may be a result of the hunting pressure that frequently accompanies partial habitat destruction, rather than the monkeys' inability to survive in isolated patches of habitat. *Ateles geoffroyi* from Central America is apparently more flexible in choice of habitat than most of its South-American relatives. Freese (1976) observed it in evergreen, semi-deciduous and sometimes even deciduous forest in Costa Rica, and Eisenberg and Kuehn (1966) and Alvarez del Toro (1977) report it even from mangrove forest in Chiapas, Mexico. The available evidence indicates that all *Ateles* species prefer undisturbed high forest. However, where such habitat is limited in extent, where hunting pressure is light or non-existent, and where other primate competitors are few in number, it appears to be able to live in several other forest types as well.

In the Voltzberg region, *Ateles* is predominantly seen in high rain forest (fig. 18A). Of all first sightings, 92.6% occurred in high
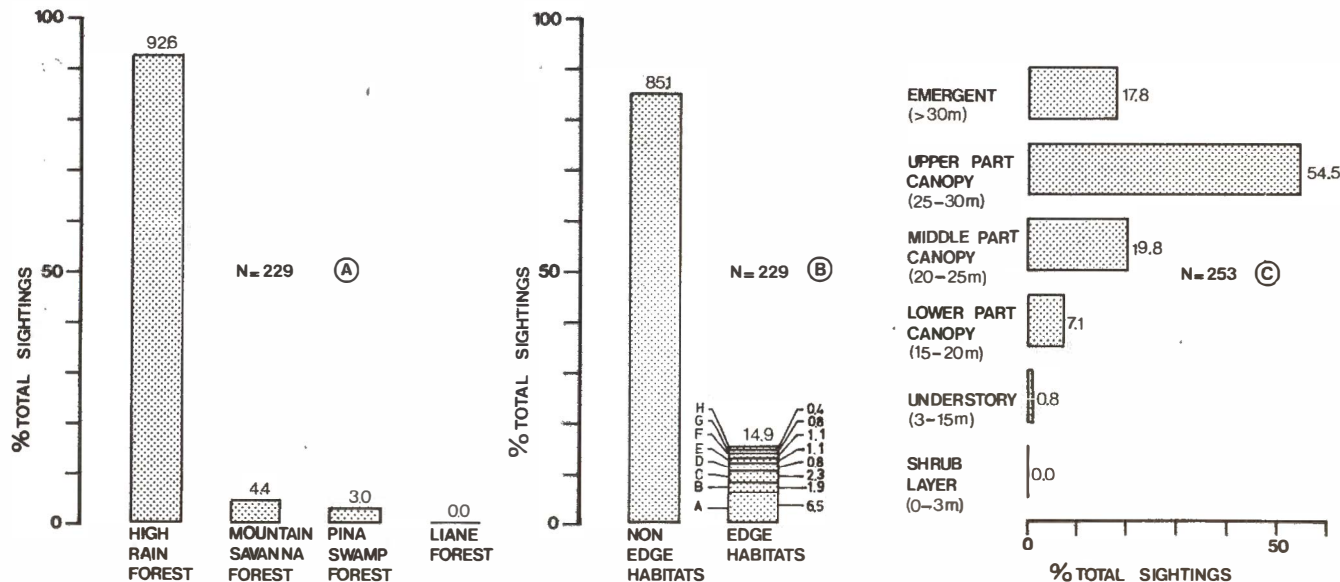
Figure 18 Habitat preferences of *Ateles p. paniscus* in the Voltzberg study area. Data are based on first sightings only.
   A. Forest type preferences - B Utilization of edge habitats (A = high forest, edge pina swamp forest· B = high forest, edge liane forest:
   C = high forest, edge clearing; D = high forest, edge mountain savanna forest; E = pina swamp forest, edge high forest; F = mountain savanna forest, edge clearing; G = mountain savanna forest, edge liane forest; H = mountain savanna forest, edge high forest) - C. Utilization of forest strata.

forest. It entered high mountain savanna forest only occasionally (4.4%), particularly when some food species typical of this formation was fruiting. During the long dry season, this vegetation type had almost nothing to offer for spider monkeys and consequently they were very rarely seen there at this time of year. The third forest type in which *Ateles* was occasionally seen was pina swamp forest (3.0%). Ateles did not avoid this type of forest while traveling; instead it used the flexible stems of the *pina* palms (*Euterpe oleracea*) as jumping-poles while hanging in the small crowns. Several tree species typical of pina swamp forest (e.g., *Carapa procera, Eperua falcata, Euterpe oleracea, Pterocarpus officinalis* and *Virola surinamensis*) provide seasonal sources of food for *Ateles*, and consequently the animals visit this formation more often during certain times of the year. I never observed *Ateles* in the other habitats available in the Voltzberg region (e.g., liane forest, low forest and 'rocksavanna'). In the Lolopasi area, *Ateles* was seen in riverbank high forest many times, but never within 150 m of the riverbank itself. However, its home range was situated with its long axis perpendicular to the riverbank and its center beyond the boundary-line between riverbank high forest and high forest, at about 700 m inland. Whether this was the original situation resulting from the habitat being relatively poor in nutritious fruits or whether it has been influenced by light hunting pressure was not clear.

Of all Surinam monkey species, *Ateles paniscus* is the most restricted in habitat (Mittermeier and Van Roosmalen, 1981). Only the bearded saki (*Chiropotes satanas*) shows a somewhat similar restriction in habitat choice. All other Surinam monkey species visit liane forest and/or low forest with some frequency.

3.2. **Edge Preferences**

At the Voltzberg study site, an area rich in edge habitats, *Ateles* did not show any preference for these situations (fig. 18B). In 85.1% of all first sightings, it was seen in non-edge habitats and only in 14.9% was it seen in edge habitats. Of these, only 6.1% were in edges with clearings or liane forest. Where hunting had not taken place in the recent past, spider monkeys did not appear to be afraid of exposing themselves at edges of open areas. Several of the sleeping trees, which were greatly prefered at a particular time of the year, were situated at the very edge of clearings and/or

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liane forest. The only reason for their apparent avoidance of edge habitats may be that these habitats do not offer them appropriate food resources. Fruits found at edges are mostly of the low-nutritious berry type or dry wind-dispersed, which are not of particular interest to a predominantly frugivorous species such as *Ateles* (Van Roosmalen, in prep.).

Of the eight Surinam monkey species, only *Saguinus midas* was seen more often in edge habitats than in non-edge habitats (Mittermeier and Van Roosmalen, 1981). *Saimiri sciureus* and *Cebus apeela* are also apparently partial to edge habitats. They tend to follow the edges of liane forest complexes in search of insects. *Alouatta seniculus* and *Pithecia pithecia* occurred somewhat more often in edge habitats than *Ateles* did and *Chiropotes satanas* and *Cebus nigrivittatus* less often.

3.3. **Vertical Stratification**

Ateles is primarily an animal of the upper levels of the forest with 17.8% of total first sightings in emergents and 54.5% in the upper part of the canopy. The middle levels of the forest were less frequently used, with 19.8% of total first sightings in the middle part of the canopy and only 7.1% in the lower part of the canopy. *Ateles* very rarely entered the understory and never descended below 12 m, and was seen in the understory in only 0.8% of total first sightings (fig. 18C).

Of the other Surinam monkey species, only *Chiropotes satanas* shows a vertical distribution very similar to that of *Ateles*, with 60.2% of total first sightings (n=93) in the two uppermost strata. All other Surinam monkey species prefer the middle and/or lower strata (Mittermeier and Van Roosmalen, 1981).

In summary, *Ateles* is the most restricted species in the Voltzberg area. It occurs almost exclusively in high forest, rarely enters edges and occurs primarily in the upper levels of the canopy and in emergents. Given the abundance of edges in the Voltzberg area (fig. 17), it actually seems to be avoiding these situations, which is probably due to low supply of preferred fruit.

4. DIET AND FEEDING BEHAVIOR

4.1. Food Categories

In this study, spider monkey food was divided into eight categories: (1) *fruits* — including young seeds, mature seeds, stones, plumula, aril, exocarp, mesocarp, endocarp, pericarp, perigonium, infructescence, compound fruit, fig., pseudofruit, juice and columella, (2) *flowers* — including floral buds, mature flowers and inflorescences, (3) *leaves* — including leaf buds, young or flush leaves, mature leaves, petioles and tender shoots, (4) *pseudobulbs*, (5) *aerial roots*, (6) *bark* and *decaying wood*, including fresh bark, decaying and decayed bark and wood, and rotten leaf bases, (7) *honey*, and (8) *insects*.

In table I, all food species and the part(s) eaten by spider monkeys are listed, ordered alphabetically first to family, then to genus and last to species. In total, 207 food plant species were identified of which 68.1% are trees, 25.6% lianes and stranglers, 1.0% herbaceous twiners and 5.3% epiphytes.

Of the 58 plant families providing the spider monkeys with food, Moraceae was the best represented with 29 species, followed by Mimosaceae (18 species), Bignoniaceae (12 species), Guttiferae (9 species) and Caesalpiniaceae (8 species). Ranked according to percentage of total feeding records, most important families were Moraceae (11.8%), Mimosaceae (11.6%), Myristicaceae (10.9%), Sapotaceae (8.6%), Meliaceae (5.8%) and Burseraceae (5.6%) (table II).

Among the genera, *Virola* comes first, followed by *Inga*, *Ecclinusa*, *Guarea*, *Tetragastris*, *Cecropia*, *Dimorphandra*, *Philodendron*, *Bagassa*, *Achrouteria* and *Laetia* (table III).

Of all food species recorded, *Virola melinonii* (Myristicaceae) is most important with 10.7% of total number of feeding records, followed by *Guarea grandifolia* (Meliaceae) with 4.0%, *Ecclinusa guianensis* (Sapotaceae) with 3.3%, *Cecropia sciadophylla* (Moraceae) with 3.2%, *Dimorphandra pullei* (Caesalpiniaceae) with 3.1%, *Bagassa guianensis* (Moraceae) with 2.8%, *Inga edulis* (Mimosaceae) and *Achrouteria pomifera* (Sapotaceae) with 2.6%, In-

ga alba (Mimosaceae) and *Tetragastris panamensis* (Burseraceae) with 2.5%. About 85 species were recorded only once or twice during the study period, and therefore account for less than 0.1% of total number of feeding records (table IV).

As shown in figure 19, *Ateles p. paniscus* is predominantly frugivorous in its overall diet, feeding on fruits in 82.9% of total feeding records (N=2,287). Flowers and leaves play a minor role, accounting for 6.4% and 7.9% respectively, but seasonally they can be important. Other foods are bark (1.7%), decaying wood (0.3%), pseudobulbs (0.1%), aerial roots (0.2%), honey (0.2%), termites (0.1%) and caterpillars (0.1%).
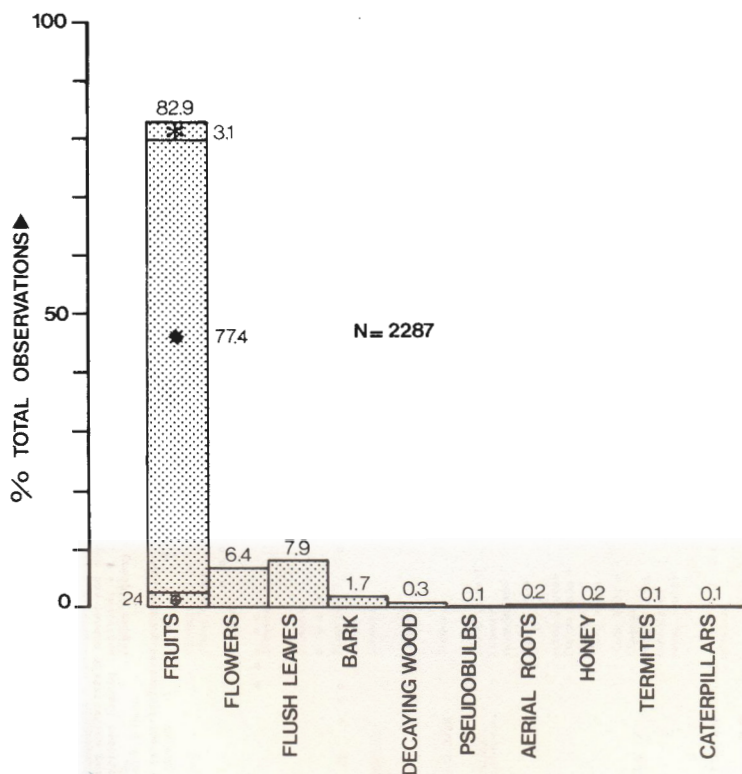
Figure 19 Annual utilization of different foods in *Ateles p. paniscus*, expressed as the percentage of the total number of feeding records for each food category (* = seeds predated, ∗ = seeds dispersed endochorically, ● = seeds dropped under the parent plant).

Table I. Food list of _Ateles p. paniscus_ in Surinam

List of signs and abbreviations:

- = not inventoried in Voltzberg study area, x = seed dispersion/predation, - = nil, — = maximum height in meters, () = not occurring in Voltzberg study area, ■ = number of food plants used by the study group, sp. = species, infruct. = infructescences, inflor. = inflorescences, h.riverb.f. = riverbank high forest, h.mount.sav.f. = high mountain savanna forest, rocksav. = rocksavanna, l.mount.sav.f. = low mountain savanna forest, sec.f. = secondary forest, pl. = places, loc. = locally, esp. = especially, o = mature fruit, y = young seeds, f = flowers, b = bark, m = miscellaneous, l = young leaves, DP = distribution pattern, + = non-random distribution pattern in high forest and/or high mountain savanna forest, — = random distribution pattern in high forest and/or high mountain savanna forest, ■ = individual plants restricted to high mountain savanna forest, pina swamp forest, edges and/or swampy places, and therefore not randomly distributed throughout the group's range.

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	DP	J	F	M	A	M	J	J	A	S	O	N	D
ANACARDIACEAE																				
Anacardium giganteum Hancock	pseudofruit (= pedicel)	-	-	tree — 30m	h.forest + h.riverb.f.	23	11	—		o	o	o								
Spondias mombin L.	mesocarp	x		tree — 30m	h.mount.sav.f. + creekf. on swampy places	28	13	□				o	o	o	o	o				
ANNONACEAE																				
Duguetia sp. (new species)	infruct.	x		tree — 15m	h.mount.sav.f.	14	7	□			o	o	o	o						
Ephedranthus guianensis R.E.Fries	mesocarp	x		tree — 15m	high forest	312	149	†		o	o				o	o	o			
Guattera chrysopetala (Steud.) Miq.	whole fruit	x		tree — 25m	high forest	1	0.5	—									o	o	o	o
Malmea obovata R.E.Fries	whole fruit	x		tree — 12m	high forest	-	-			o	o				o	o	o	o		
Unonopsis glaucopetala R.E.Fries	whole fruit	x		tree — 20m	high forest	63	30	†									o	o	o	o
APOCYNACEAE																				
Geissospermum sericeum (Sagot) Benth.	juice	-	-	tree — 30m	high forest	7	3	†			o	o	o							
Patahancornia fasciculata (Poir.) R.Ben.	mesocarp	x		tree — 40m	high forest + h.riverb.f.	-	-					o	o							
ARACEAE																				
Monstera adansonii (Schott) Madison	infruct.	x		epiphyte 'rootclimber'	high forest + h.mount.sav.f.	-	*	—						o	o					
Philodendron acutatum Schott	infruct. young leaves tips of aerial roots	x		epiphyte	high forest	common		—	o	o	1 1 / m m						o o / 1 1	o o / 1 1	o o / 1 1	o o / 1 i / m m
Philodendron scandens C.Koch et Sello	infruct. young leaves + base of petiole tips of aerial roots	x		lianalike epiphyte 'rootclimber'	high forest	common		—	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1	1 1 / o o	1 1	1 1	1 1 / m m
Heteropsis jenmani Oliver	infruct. young leaves	x		epiphyte	high forest	-	*											o o	o o / 1 1	o o

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	DP	J	F	M	A	M	J	J	A	S	O	N	D
BIGNONIACEAE																				
Stizophyllum inaequilaterum Bur.et K.Schum.	flowers	-	-	liana	high forest	-	-												f	f
Tanaecium nocturnum (Barb.Rodr.)Bur.et K.Schum.	young seeds	-	x	liana	high forest	-	-			y	y	y	y							
Tabebuia capitata (Bur.et K.Schum.) Sandw.	flowers	-	-	tree — 35m	h.mount.sav.f.	15	7	—											f	f
Tabebuia serratifolia (Vahl)Nicholson	flowers young leaves	-	-	tree — 35m	high forest + h.mount.sav.f. esp.swampy pl.	35	16	— ! !									f	f	f l	l l l
Species a.	flowers	-	-	liana	high forest	-	-						!							
Species b.	flowers	-	-	liana	high forest	-	-						!							
Adenocalymna sp.	flowers	-	-	liana	h.f.+h.m.s.f.+ h.r.h.f.	-	-										!	!		
Arrabidaea corallina (Jacq.) Sandw.	flowers	-	-	liana	h.m.r.f.edges + rocksav.	-	-										!	f	f	
Xylophragma seemannianum (O.Kuntze) Sandw.	flowers	-	-	liana	h.m.s.f. esp.at edges + h.r.b.f.	-	-												f	f !
Species c.	flowers	-	-	liana	high forest	-	-						!							
Distictella magnoliifolia (H.B.K.) Sandw.	flowers	-	-	liana	high forest	-	-													f
Anemopaegma granulosum (Bur.et K.Schum.) Sandw.	young leaves flowers young seeds	-	x	liana	h.mount.sav.f.	-	-												l !	l l l y y
BOMBACACEAE																				
Pachira aquatica Ulbrich	young leaves floral buds + flowers young seeds	-	x	tree — 35m	high forest + pinaswamp	51	24	□				!	f f	f f		f	f f	f	l l l	l l l l
Ceiba pentandra Gaertn.	floral buds + flowers young leaves exocarp of young fruits	-	-	tree — 50m	high forest + h.mount.sav.f. on swampy places	16	4	□											f l o	f l l o
BORAGINACEAE																				
Cordia lomatoloba J.M.Johnst.	mesocarp	x		tree — 25m	high forest	} 28	} 13	—		o	o o									
Cordia panicularis Rudge	whole fruit	x		tree — 20m	high forest	}	}	—						o	o					
Cordia sagotii J.M.Johnst.	whole fruit	x		tree — 20m	high forest, esp.at edges	}	}	□											o o	o

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	DP	J	F	M	A	M	J	J	A	S	O	N	D
BURSERACEAE																				
Protium neglectum Swart	mesocarp	x		tree — 20m	high forest	311	145	+									o	o	o	
Protium polybotryum (Turcz.) Engl.	mesocarp	x		tree — 25m	high forest	217	103	+									o	o	o	o
Tetragastris altissima (Aubl.) Swart	mesocarp	x		tree — 30m	high forest	1631	777	T				o	o	o	o	o	o	o		
Tetragastris panamensis (Engl.)O.Kuntze	mesocarp	x		tree — 25m	high forest	280	133	+				o	o	o	o	o	o	o		
CACTACEAE																				
Hylocereus sp. a	flowers / whole fruit	x		epiphyte	high forest + h.mount.sav.f. esp.at edges	–	–			f	f	f	l	f	f	f	l	f	f	f	f	f	f	f	f
Hylocereus sp. b	whole fruit / flowers	x		epiphyte	high forest + h.mount.sav.f. esp.at edges	–	–				o	o	o	o					f	f	f	f
Pereskia aculeata Mill.	flowers / whole fruit	x		liana	h.mount.sav.f. esp.at edges	–	–			•	o	o	o	o							f	f
CAPPARACEAE																				
Capparis maroniensis Ben.	mesocarp	x		tree — 30m	high forest	304	145	T		o	o	o	o	o	o	o	o				
CARICACEAE																				
Jacaratia spinosa (Aubl.) A.DC.	whole fruit / young leaves	x		tree — 20m	high forest + h.mount.sav.f. esp.at edges	7	3	□			l	l					o	o			
CELASTRACEAE																				
Cheiloclinium cognatum (Miers) A.C. Smith	(young)seeds		x	tree — 12m	high forest	20	10	□							y	y	y				
Cheiloclinium hippocrateoides (Peyr.) A.C. Smith	mesocarp	x		liana	h.riverb.f.	0	0				(o	o		o	o)					
Cheiloclinium podostemmum (Sandw.) A.C. Smith	mesocarp	x		liana	high forest + h.riverb.f.	–	–								o	o				
Cheiloclinium anomalum Miers	mesocarp	x		liana	high forest	1*	0.5*	—							o	o				
Amphizoma sp.	mesocarp	x		liana	high forest	2*	1*	—			o	o				o	o			
Maytenus sp.	aril	x		tree — 30m	high forest + h.mount.sav.f.	3	1	□				o	o			o	o			
CHRYSOBALANACEAE																				
Couepia caryophylloides R. Ben.	exocarp + mesocarp	–	–	tree — 25m	high forest	99	47	+										o	o	o
Licania densiflora Kleinh.	exocarp + mesocarp	–	–	tree — 30m	high forest	–	–					o	o							
Licania majuscula Sagot	exocarp + mesocarp + bark	–	–	tree — 30m	high forest + h.mount.sav.f.	67	32	+		o	o	o	o	o	o	o			o	o	o
Licania micrantha Miq.	young leaves + bark	–	–	tree — 30m	high forest	49	23	+		b	b	b	b					b		b b / l l	b b b b
Parinari campestris Aubl.	exocarp + mesocarp	–	–	tree — 25m	high forest + h.riverb.f.	12	6	+				o	o	o	o					
Parinari excelsa Sabine	exocarp + mesocarp	–	–	tree — 40m	high forest	22	10	+				o	o					o	o	o	

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km² DP	J	F	M	A	M	J	J	A	S	O	N	D
COMBRETACEAE																			
Combretum rotundifolium L.C. Rich.	young seed		x	liana	high forest	common	━	y	y										
CONVOLVULACEAE																			
Dicranostyles guianensis A. Mennega	mesocarp	x		liana	high forest	4*	2* ━									o	o	o	
Maripa glabra Choisy	young seed		x	liana	high forest	-	-							y	y				
Maripa scandens Aubl.	young seed		x	liana	high forest, esp. at edges	4	2 ━						y	y	y				
Operculina hamiltoni (G. Don) Austin et Staples	young seeds		x	liana	at edges of h.mount.sav.f.	-	-												y
CUCURBITACEAE																			
Cayaponia ophthalmica R.E. Schultes	mesocarp	x		liana	high forest, h.mount.sav.f. + h.riverb.f.	common	━			o	o	o	o	o	o				
Cayaponia rigida (Cogn.) Cogn.	whole fruit	x		liana	high forest	-	-				o	o	o						
DIOSCOREACEAE																			
Dioscorea cf. trifida	young leaves	-	-	twiner	l.mount.sav.f. + edge rocksav.	-	-									1			
EUPHORBIACEAE																			
Alchorneopsis floribunda (Benth.) Muell.Arg.	whole fruit		x	tree ━ 30m	high forest + pinaswamp	2	1 ▢					y	y	y					
Drypetes variabilis Uitt.	whole fruit	x		tree ━ 30m	high forest	35	17 ━ o	o	o	o	o	o	o						
Hyeronima laxiflora (Tul.) Muell.Arg.	whole fruit bark	x		tree ━ 30m	high forest	36	17 ▢	o	o		o	o				o	o	b	b
FLACOURTIACEAE																			
Laetia procera (Poepp.) Eichl.	aril	x		tree ━ 40m	high forest	30	14 ━	o	o	o	o	o	o	o					
GESNERIACEAE																			
not identified species	young leaves	-	-	twiner	edges of h.mount.sav.f.	-	-											1	
GNETACEAE																			
Gnetum urens (Aubl.) Blume	perigonium + seed(?)	x	x?	liana	high forest + h.riverb.f.	2	1 ━ o	o									o	o	o	o
GOUPIACEAE																			
Goupia glabra Aubl.	whole fruit	x		tree ━ 40m	high forest	8	4 ✝										o	o	
GUTTIFERAE/CLUSIACEAE																			
Clusia grandiflora Splitg.	aril	x		epiphytic liana(strangler)	high forest	-	- ━		o	o			o	o					
Clusia platystigma Eyma	♂ flowers, central body of staminodes	-	-	epiphytic liana	high forest	-	- ━								f	f			

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	DP	J	F	M	A	M	J	J	A	S	O	N	D
Clusia leprantha ,Mart.	aril	x		epiphytic liana	high forest	-	-	—										o	o	
Clusia scrobiculata R. Ben.	aril	x		epiphytic liana(strangler)	high forest	common		—		o o	o o	o o								
Clusia sp.	floral buds	-	-	epiphytic liana	high forest	-	-	—				f f								
GUTTIFERAE																				
Platonia insignis Mart.	aril	x		tree — 35m	h.riverb.f.	2	1	—		o o	u o									
Rheedia benthamiana Planch.et Triana	aril	x		tree — 15m	high forest	7	3	—										o o		
Rheedia macrophylla (Mart.) Planch.et Triana	aril	x		tree — 20m	high forest	n⁶	42	—				o	o o	o o						
Symphonia globulifera L.f.	flowers	-	-	tree — 25m	high forest + pinaswamp	2	1	▢										f	f f	
HUMIRIACEAE																				
Sacoglottis cydonioides Cuatr.	whole fruit bark	x		tree — 30m	high forest	21	10	▢	o o	o o	o o				o o				b	b
Vantanea parviflora Lam.	exo-mesocarp	-	-	tree — 40m	high forest	-	-													o
ICACINACEAE																				
Leretia cordata Vell.	whole fruit	x		liana	high forest	-	-									o o	o o			
LAURACEAE																				
Licaria canella (Meissn.) Kosterm.	young leaves	-	-	tree — 25m	h.mount.sav.f.	2	1	▢												l l
Nectandra kunthiana (Nees) Kosterm.	bark	-	-	tree — 30m	h.mount.sav.f.	24	11	▢												b
Ocotea wachenheimii R. Ben.	whole fruit	x		tree — 28m	high forest	2	1	—				o o								
LECYTHIDACEAE																				
Couratari guianensis Aubl.	young seeds		x	tree — 50m	high forest + h.riverb.f.	17	o	—				y y								
Couratari stellata A.C. Smith	young seeds bark		x	tree — 45m	high forest	403	29	—						y y	y y					b
Eschweilera congestiflora (R.Ben.) Eyma	young seeds + aril		x	tree — 25m	high forest	2	1		y y y											y y
Eschweilera corrugata (Poit.) Miers	young seeds + aril		x	tree — 25m	high forest + pinaswamp	761	362	†		y y	y y	y y	y y	y y					
Eschweilera poiteaui (Berg) Ndz.	young seeds + aril		x	tree — 35m	high forest	336	160	†					y y	y					
Gustavia hexapetala (Aubl.) J.E. Smith	mesocarp + funicle	x		tree — 15m	high forest + h.mount.sav.f.	-	-											o o	o	
Lecythis davisii Sandw.	mesocarp	-	-	tree — 30m	high forest + h.riverb.f.	0	0	▢									(o o)			

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km² DP	fruiting/flowering period(s)/time(s) of availability (J F M A M J J A S O N D)
LEGUMINOSAE/CAESALPINIACEAE								
Copaifera epunctata Amsh.	aril	x		tree — 40m	high forest	0	0	(o o o)
Copaifera guianensis Desf.	aril	x		tree — 40m	high forest + h.riverb.f.	14	7 — o o	
Cynometra marginata Benth.	young leaves	-	-	tree — 20m	high forest, esp.on swampy places	-	-	1 1
Dialium guianense (Aubl.) Steud.	aril	x		tree — 30m	h.mount.sav.f.	13	6 □	o o o o o o o o o
Dimorphandra pullei Amsh.	mesocarp bark	x		tree — 45m	high forest	35	17 □	o o o o o o o o o o o; b b
Eperua falcata Aubl.	plumula flowers young leaves		x	tree — 30m	high forest + pina swamp	102	49 □	f f ; y y y ; 1 1 ; f f f
Eperua rubiginosa Miq.	plumula		x	tree — 30m	h.riverb.f. + creekforest	1	0.5 (y y)	
Peltogyne venosa (Vahl) Benth.	aril	x		tree — 35m	high forest, esp.along creeks	0	0	(o o)
LEGUMINOSAE/MIMOSACEAE								
Cedrelinga cateniformis (Ducke)Ducke	young seeds		x	tree — 60m	high forest	34	16 — v v ; y	
Enterolobium schomburgkii Benth.	inflor.	-	-	tree — 40m	high forest	12	6 — f ?	
Inga acrocephala Steud.	mesocarp	x		tree — 25m	high forest	96	46 — o o o o o	
Inga cinnamomea Spruce ex Benth.	mesocarp	x		tree — 20m	high forest, esp.at edges	4*	2* — o o o o o	
Inga alba (Sw.) Willd.	mesocarp bark	x		tree — 35m	high forest	224	107 — o o o o o o ; b b b b b b b b ; o ; b b	
Inga bourgoni DC.	mesocarp	x		tree — 20m	high forest, esp.at edges	11*	5*+ o o o o	
Inga cf. capitata Desv.	mesocarp	x		tree — 20m	high forest	41	20 — o o o o o	
Inga coriacea (Pers.) Desv.	mesocarp	x		tree — 25m	high forest	-	-	o o
Inga edulis Mart.	mesocarp	x		tree — 30m	high forest, esp.at edges + sec.f.	20±	10*+ o o o' o o	
Inga leiocalycina Benth.	mesocarp bark	x		tree — 25m	high forest, esp.along creeks	6±	3* — o o o ; b b	
Inga pezizifera Benth.	mesocarp	x		tree — 25m	high forest	-	-	o o
Inga rubiginosa (L.C.Rich.) DC.	mesocarp	x		tree — 25m	high forest	-	-	o o
Inga stipularis DC.	mesocarp	x		tree — 25m	high forest + pina swamp	-	-	o o
Inga thibaudiana DC.	mesocarp	x		tree — 25m	high forest esp.at edges	-	-	o o

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km² DP	J	F	M	A	M	J	J	A	S	O	N	D
Piptadenia suaveolens Miq.	inflor. (young buds)	-	-	tree — 50m	high forest	45	11 —		f	f									
Parkia nitida Miq.	inflor. mesocarp	x		tree — 50m	high forest	11	5 —				f	f	f	f				o	o
Parkia pendula (Willd.) Benth.	inflor.	-	-	tree — 45m	high forest	15	7 —									f	f		
Pithecellobium jupunba (Willd.) Urb.	young leaves bark	-	-	tree — 35m	high forest	36	17 —									l			b
LEGUMINOSAE/PAPILIONACEAE																			
Dioclea macrocarpa Huber	young seeds		x	liana	high forest	-	-		y										
Dipteryx odorata (Aubl.) Willd.	young leaves	-	-	tree — 30m	high forest	11	5 —	l									l		
Hymenolobium petraeum Ducke	young leaves	-	-	tree — 50m	high forest	8	4 —	l	l										
Ormosia paraensis Ducke	young seeds		x	tree — 30m	high forest, esp. along creeks	0	0									(y)			
Platymiscium ulei Harms	flowers	-	-	tree — 30m	high forest	22	10 —									f	f		
Pterocarpus officinalis Jacq. (.P.vs.santalinoides)	young leaves	-	-	tree — 30m	pinaswamp + h.mount.sav.f.	110	52 □									l	l	l l	l
Vataireopsis speciosa Ducke	young leaves	-	-	tree — 45m	high forest	70	33 —	l	l	l							l	l l	l l
LOGANIACEAE																			
Strychnos tomentosa Benth.	mesocarp	x		liana	high forest	3	1 —	o	o	o	o	o	o	o	o	o	o	o o	o o
LORANTHACEAE																			
not identified species	young fleshy leaves	-	-	epiphyte/ parasite	high forest	*	-										l	l	
MARCGRAVIACEAE																			
Norantea guianensis Aubl.	flowers	-	-	liana	high forest, h.mount.sav.f., h.riverb.f.	8	4 —	f	f	f	f							f	f
MELASTOMATACEAE																			
Bellucia grossularioides (L.) Triana	whole fruit	x		tree — 20m	h.mount.sav.f. on granite	2*	1* —o	o		o	o						o	o o	o
MELIACEAE																			
Carapa procera DC.	flowers	x		tree — 30m	high forest on swampy places + pinaswamp	417	199 +	f	f								f	f f	f
	young seeds										y	y		y	y				
	young leaves										l					l	l l	l l l	l l
Cedrela odorata L.	young seeds + columella	x		tree — 40m	high forest	9	4 —	y	y										y y
Guarea grandifolia DC.	flowers			tree — 30m	high forest	449	214 +		f	f						f	f	f f	f
	aril	x								o	o	o	o	o	o		o	o	
Guarea kunthiana A. Juss.	aril	x		tree — 30m	high forest + h.riverb.f.	88	42 +									o	o	o	

fruiting/flowering period(s)/time(s) of availability

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km² DP	J	F	M	A	M	J	J	A	S	O	N	D
Trichilia martiana C.DC.	aril	x		tree — 25m	h.mount.sav.f.+ h.riverb.f.	1*	0.5* —				o	o							
Trichilia quadrijuga H.B.K.	aril	x		tree — 25m	high forest	} 102	49 —		o	o	o	o							
Trichilia surinamensis (Miq.) C.DC.	whole fruit	x		tree — 40?	high forest, esp.on swampy places				o	o								o	o
MENISPERMACEAE																			
Abuta grandifolia (Mart.) Sandw.	mesocarp	x		liana	high forest, esp.at edges	4*	2* —				o	o					o	o	
MORACEAE																			
Bagassa guianensis Aubl.	unripe + ripe infruct.	x		tree — 45m	high forest	36	17 — o o o							o	o	o	o o	o o y y y	o o y y
Brosimum lactescens (S. Moore) C.C. Berg	infruct.	x		tree — 35m	high forest + h.mount.sav.f.	32	15 □ o o.										o	o o	o o
Brosimum parinarioides Ducke	infruct.	x		tree — 40m	high forest	12	6 —										o	o	o
Cecropia sciadophylla Mart.	infruct. young leaves	x		tree — 30m	high forest (old treefall clearings)	40	19 — o o o o o o o o			1 1							o o	o o o	o o o o
Cecropia latiloba Miq.	infruct.	x		tree — 25m	sec.f., at edges of high forest + h.mount.sav.f.	39	19 □ o o o o								o	o		o o	o o
Clarisia racemosa R.et P.	whole fruit	x		tree — 40m	high forest	19	9 —						o	o			o	o	o
Coussapoa angustifolia Aubl.	infruct.	x		epiphytic tree/liana	high forest	15	7 —									o	o o	o o	o
Coussapoa asperifolia Tréc.	infruct. pistillate inflorescences	x		epiphytic tree/liana	high forest	5	2 —						f	f			o	o o	
Coussapoa latifolia Aubl.	infruct.	x		epiphytic tree/liana	high forest	47	41 —											o o	o o
Ficus guianensis Desv.exHam.	figs	x		epiphytic tree/liana	high forest, on swampy places	1*	0.5*												o
Ficus broadwayi Urb.	figs	x		epiphytic tree/liana	high forest	1*	0.5*											o	
Ficus citrifolia Mill	figs	x		treelet/ liana	l.mount.sav.f. on granite	1*	0.5*												o
Ficus gardneriana (Miq.) Miq.	figs	x		liana	high forest (old treefall clearings)	1*	0.5*												o
Ficus gomelleira Kunth et Bouché	figs	x		strangler	high forest	2*	1*				o	o							
Ficus insipida Willd.	figs	x		tree — 30m	high forest + pinaswamp	1*	0.5*									o	o		
Ficus malacocarpa Standl.	figs	x		epiph.tree/ strangler	high forest	1*	0.5*											o	

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	DP	J	F	M	A	M	J	J	A	S	O	N	D
Ficus nymphaeifolia Mill.	figs	x		tree — 35m	high forest	2*	1*		o										o	
Ficus pertusa L.f.	figs	x		epiphytic tree — 35m	high forest + pinaswamp	1*	0.5*					o								
Ficus trigona L.f.	figs	x		epiph.tree/ strangler	high forest	1*	0.5*												o	
Ficus gomelleira L.	figs	x		tree — 35m	high forest + h.mount.sav.f.	2*	1*							o	o			o	
Helicostylis pedunculata R. Ben.	infruct.	x		tree — 25m	high forest	1	0.5	—										o	o	
Helicostylis tomentosa (P. et E.) Rusby	infruct.	x		tree — 30m	high forest	31	15	—				o	o	o						
Maquira guianensis Aubl.	young leaves	-	-	tree — 20m	high forest	12	6	—								1		1		1
Perebea mollis (P. et E.) Hub.	infruct.	x		tree — 30m	high forest	1*	0.5*	—				o								
Pourouma minor R. Ben.	whole fruit	x		tree — 25m	high forest	64	31	—		o	o									
Pourouma mollis Tréc.	whole fruit	x		tree — 25m	high forest + pinaswamp	33	16	—		o	o	o								
Pourouma sp.	whole fruit	x		tree — 25m	high forest	-	-				o									
Trymatococcus oligandrus (R.Ben.) Lanj.	whole fruit	x		tree — 20m	high forest	1*	0.5*	—											o	
Trymatococcus paraensis Ducke	whole fruit	x		tree — 30m	high forest	1*	0.5*	—								o				
MYRISTICACEAE																				
Virola melinonii (R.Ben.) A.C. Smith	aril young leaves	x		tree — 30m	high forest	313	66	↑	o o	o o	o o						1		o o	o o
Virola surinamensis (Rol.) Warb.	aril	x		tree — 35m	pinaswamp	32	15	□						o	o					
MYRTACEAE																				
Campomanesia aromatica (Aubl.) Griseb.	whole fruit	x		tree — 13m	h.mount.sav.f. esp.at edges (granite)	-	-			o	o									
Eugenia feijoi Berg	whole fruit	x		tree — 15m	h.riverb.f.	0	0		(o)											(o)
OLACACEAE																				
Minquartia guianensis Aubl.	whole fruit	x		tree — 25m	high forest	30	14	—									o	o		
ORCHIDACEAE																				
Two species	pseudobulbs	-	-	epiphytes	high forest	-	-										m			m
PALMAE																				
Attalea maripa (Corr.Serr.)Mart.	decaying leaf-bases	-	-	tree — 18m	edges of liane forest, in poor-ly drained pla-ces	-	-		-	m m	m m	m m							m m	m

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	DP	J	F	M	A	M	J	J	A	S	O	N	D
Euterpe oleracea Mart.	whole fruit	x		tree — 20m	pinaswamp, along creeks	loc. abundant		□					o	o	o	o				
Euterpe precatoria Mart.	whole fruit	x		tree — 27m	high forest	-	-										o	o	o	o
Oenocarpus bacaba Mart.	whole fruit	x		tree — 22m	high forest + at edges of it	67	32	—			o	o	o	o					
Iriartea exorrhiza Mart.	whole fruit	x		tree — 30m	pinaswamp	2*	1*	□			o		o						
PASSIFLORACEAE																			
Passiflora glandulosa Cav.	whole fruit	x		liana	high forest, esp. at edges	-	-										o		
PIPERACEAE																			
Peperomia glabella (Sw.) A. Dietr.	young leaves	-	-	epiphyte	high forest, esp. on boughs of emergent trees	abundant				1	1						1	1 1	1 1	1 1 1
POLYGALACEAE																			
Moutabea guianensis Aubl.	mesocarp	x		liana	high forest	5	2	—	o	o		o	o	o	o		o	o		
RUBIACEAE																			
Coussarea paniculata (Vahl) Standl.	whole fruit	x		tree — 12m	high forest	common		+					o	o					
Guettarda acreana Krause	whole fruit	x		tree — 15m	h.mount.sav.f. on granite	106	50	□			o	o	o	o					
Hillia illustris (Vell.) Schum.	flowers	-	-	epiphytic scrub in tree crowns	high forest	-	-												f
RUTACEAE																			
Zanthoxylum rhoifolium Lam.	young leaves	-	-	tree — 15m	high forest	1*	0.3*												1	1 1
SAPINDACEAE																			
Paullinia sp.	whole fruit / young leaves	x		liana	high forest	-	-										o o / 1 1			
Paullinia acuminata Uitt.	aril	x		liana	high forest	-	-				o	o								
Paullinia sphaerocarpa L.C. Rich. ex. Juss.	young seeds / aril	x	x	liana	high forest, h.riverb.f.	-	-		y	y	y	o	o	o						y y
Paullinia spicata Benth.	aril	x		liana	high forest, esp. in pina-swamp	3*	1*	—			o					o			
Paullinia tricornis Radlk.	aril	x		liana	high forest	2*	1*	—									o	o o	
Talisia squarrosa Radlk.	mesocarp	x		tree — .m	high forest	-	-											o	

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	DP	J	F	M	A	M	J	J	A	S	O	N	D
SAPOTACEAE																				
Achrouteria pomifera Eyma	mesocarp	x		tree — 30m	h.mount.sav.f., high forest	19	9	—									o	o	o	o
Chrysophyllum auratum Miq.	mesocarp	x		tree — 25m	h.mount.sav.f.	1*	0.5*	□			o									
Ecclinusa guianensis Eyma	mesocarp	x		tree — 25m	h.mount.sav.f. on granite + h.riverb.f.	363	173	□ o									o	o		o
Prieurrella sp.	young seeds / mesocarp	x (predation) / x (dispersal)	x	tree — 30m	high forest	138	66	—		y	y	o	o	o	o					
Microholis guyanensis (A.DC.) Pierre	mesocarp	x		tree — 40m	high forest	0	0									(o	o)			
Pouteria guianensis Eyma	mesocarp	x		tree — 30m	high forest	9	4	—				o	o	o						
Pouteria sp.	young seeds / mesocarp	x (predation) / x (dispersal)	x	tree — 30m	high forest	15	7	—			o	o	o	o					y	y
SIMAROUBACEAE																				
Quassia simarouba L.f.	mesocarp / bark	x		tree — 30m	high forest	53	25	—			o	o							b	
STERCULIACEAE																				
Guazuma uimifolia Lam.	whole fruit / mesocarp	x		tree — 25m	high forest	-	-										o			
Sterculia excelsa Mart.	flowers	-	-	tree — 33m	high forest	155	74	—									f			
STYRACACEAE																				
Styrax aff. fanshawei Sandw. et micrasterus Perkins	whole fruit / mesocarp	x		tree — 40m	high forest	4*	2*	—			o	o	o	o						
MENDONCIACEAE																				
Mendoncia hoffmannseggiana Nees	mesocarp	x		liana	high forest, esp. at edges of clearings	-	-							o	o	o	o	o		
TILIACEAE																				
Apeiba echinata Gaertn.	flowers / mesocarp	x		tree — 35m	high forest	145	70	—									o	o	f	f f
Apeiba glabra Aubl.	mesocarp	x		tree — 30m	high forest	54	26	—						o	o	o	o	o	o	o
Apeiba schomburgkii Szyszyl.	mesocarp	x		tree — 20m	h.mount.sav.f.	4	2	—				o					o			
Apeiba tibourbou Aubl.	mesocarp	x		tree — 25m	h.mount.sav.f.	8	4	—									o	o		

FAMILY / Species	parts eaten	seed dispersal	seed predation	habit of plant	forest type	no. of food plants	no./km²	J	F	M	A	M	J	J	A	S	O	N	D
ULMACEAE																			
Ampelocera edentula Kuhlmann	young leaves flowers																1	1	l
	mesocarp	x		tree — 20m	high forest	19	9 —	o											f
VERBENACEAE																			
Vitex stahelii Moldenke	whole fruit/ mesocarp	x		tree — 45m	high forest, h.mount.sav.f., esp. edges of liana forest	72	34 —			o	o		o	o	o	o	o	o	o
VIOLACEAE																			
Leonia glycycarpa R. et P.	mesocarp	x		tree — 20m	high forest, esp. in swampy places	1*	0.5* —						o	o					
VOCHYSIACEAE																			
Qualea dinizii Ducke	flowers	-	-	tree — 40m	high forest	50	24 —										f	f	f
HONEY															m	m		m	
INSECTA																			
Lepidoptera	caterpillars			in high trees	high forest							m	m					m	
Isoptera	termites			on trunks of emergent trees	high forest				m		m	m	m						
Hymenoptera Larvae of pollinating and parasitic wasps in figs of different species (fam. Agaonidae)				in figs					m			m	r	n		m	m	m	m

Table II. The 58 plant families providing spider monkeys with food during the present study are ranked according to the number of species eaten. For each family the percentage of the total number of feeding records is also given. The three subfamilies of the Leguminosae are counted as families, and the family Guttiferae is taken *sensu lato*.

Plant family	N.° of food species	% Total feeding records (N=2,279)	Plant family	N.° of food species	% Total feeding records (N=2,279)
Moraceae	29	11.8	Orchidaceae	2	0.1
Mimosaceae (Leg.)	18	11.6	Sterculiaceae	2	0.2
Bignoniaceae	12	2.3	Capparaceae	1	1.0
Guttiferae	9	2.1	Caricaceae	1	0.1
Caesalpiniaceae (Leg.)	8	3.9	Combretaceae	1	0.05
Lecythidaceae	7	1.8	Dioscoreaceae	1	0.05
Meliaceae	7	5.8	Flacourtiaceae	1	2.2
Papilionaceae	7	2.4	Gesneriaceae	1	0.05
Sapotaceae	7	8.6	Gnetaceae	1	0.2
Celastraceae	6	1.1	Goupiaceae	1	0.05
Chrysobalanaceae	6	1.7	Humiriaceae	1	0.9
Sapindaceae	6	0.9	Loganiaceae	1	0.5
Annonaceae	5	3.6	Loranthaceae	1	0.05
Araceae	4	3.1	Marcgraviaceae	1	0.7
Burseraceae	4	5.6	Melastomataceae	1	0.6
Convolvulaceae	4	1.1	Menispermaceae	1	0.6
Palmae	4	0.9	Olacaceae	1	0.3
Tiliaceae	4	1.1	Passifloraceae	1	0.05
Boraginaceae	3	1.7	Piperaceae	1	0.4
Cactaceae	3	1.0	Polygalaceae	1	0.5
Euphorbiaceae	3	0.9	Rutaceae	1	0.1
Lauraceae	3	0.4	Simaroubaceae	1	0.2
Rubiaceae	3	0.5	Styracaceae	1	0.3
Anacardiaceae	2	0.8	Thunbergiaceae	1	0.1
Apocynaceae	2	0.7	Ulmaceae	1	0.7
Bombacaceae	2	1.8	Verbenaceae	1	0.6
Cucurbitaceae	2	1.2	Violaceae	1	0.05
Icacinaceae	2	0.3	Vochysiaceae	1	0.05
Myristicaceae	2	10.9	Unidentified	1	0.1
Myrtaceae	2	0.1			

4.1.1. **Fruits.** In total, spider monkeys were feeding on 171 kinds of fruit. In addition to berries, drupes, pods and capsules, infructescences with the fruits adnate to the enlarged receptacle or to the fleshy perianth (as in several Moraceae) forming the major edible part, figs and compound fruits are also referred to as fruits. Fruits can be dehiscent or indehiscent, dry or pulpy; the outer layer can be thin, leathery or woody. Fruits consumed by spider monkeys ranged in size from the tiny globose drupes of *Hyeronima laxiflora*, 0.3-0.5 cm in diameter, to the woody, thick-walled, operculate fruits

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of *Lecythis davisii* tath grow to about 20 cm in diameter, or to the leathery elongate pods of *Cedrelinga cateniformis* that measure up to 80 cm in length. As a rule, spider monkeys didn't waste energy and time by selectively feeding on particular parts of fruits, but instead swallowed whole fruits or, in the case of a thick or tough outer layer, bit open the fruit and swallowed the contents (pulp including seeds, or seed(s)/stone(s) surrounded by an edible layer of mesocarp, or with an edible aril attached).In many kinds of fruit the layer of mesocarp or the aril is strongly attached to the seed or stone (e.g., in all Burseraceae and *Inga*) and is therefore hard to separate. This may be an adaptation of the plant species to dispersal by specialized frugivorous birds and mammals such as *Ateles*. Most other Surinam monkey species, when feeding on fruits of this kind, spit out the seed(s) or stone(s) after chewing or sucking off the edible part. In many cases they damage the seeds, spoiling them for germination. Spider monkeys swallowed whole fruits in 25.2% of total fruit-feeding records (39.3% of total fruit species eaten). They dropped the outer layer and swallowed the mesocarp or aril (mostly including seeds or stones) in 68.2% of total fruit-feeding records (44.7% of total fruit species eaten) (table V). Young seeds or parts of them (e.g., the plumula in *Eperua*) were consumed in 3.7% of total fruit-feeding records (13.7% of total fruit species eaten). Fruits of some genera, such as *Licania, Couepia* and *Gnetum*, were eaten by scraping off the exo-and mesocarp c.q. perigonium, and dropping the seed/stone (1.5% of total fruit-feeding records; 4.2% of total fruit species eaten). Furthermore, spider monkeys fed exclusively on the exocarp in young fruits of *Ceiba pentandra* (0.3%; 0.6%), on the young columella of *Cedrela odorata* (0.2%; 0.6%), the pseudofruit (= fleshy pedicel) of *Anacardium giganteum* (0.1%; 0.6%) and the juice of *Geissospermum sericeum* (0.9%; 0.6%), dropping the rest of the fruit.

It is important to distinguish between ingestion of seeds and digestion of seeds. Spider monkeys mostly swallow seeds intact with out mastication and the seeds pass through the digestive tract without losing their ability to germinate. In addition, seeds are sometimes dropped after the softer edible parts have been removed from them with the hands or mouth. On the other hand, seeds of certain families (e.g., Lecythidaceae) are eaten in an

Table III. The most important plant genera providing the spider monkeys with food, ranked accoording to the percentages of the total number of feeding records.

Genus (Family)	N.º of species	% Total feeding records (N=2,287)
Virola (Myristicaceae)	2	10.9
Inga (Mimosaceae)	12	9.5
Ecclinusa (Sapotaceae)	2	5.5
Guarea (Meliaceae)	2	4.3
Tetragastris (Burseraceae)	2	3.7
Cecropia (Moraceae)	2	3.2
Dimorphandra (Caesalpiniaceae)	1	3.1
Philodendron (Araceae)	3	3.0
Bagassa (Moraceae)	1	2.8
Achrouteria (Sapotaceae)	1	2.6
Laetia (Flacourtiaceae)	1	2.2

unripe stage. After extracting these young seeds from the fruit, they are chewed into a mealy pulp and digested. Such behavior is referred to as seed predation because the seeds obviously are destroyed. Swallowing seeds and excreting them intact results in seed dispersal (endozoochory). When seeds are removed from the fruit and dropped, this behavior is referred to as seed droping. When the monkeys drop seeds from the fruiting tree, these seeds are not dispersed any more than would be the case if they fell by themselves. However, in some cases the monkeys may carry fruits for considerable distances away from the source tree before eating them and dropping the seeds intact. This is a definite case of dispersal (exozoochory), but for the sake of convenience I include these rare cases under seed dropping.

Spider monkeys consumed fruits in a ripe stage in 96.0% of total fruit-feeding records (150 species; N=1,902). Seed dispersal took place in 93.5% of total fruit-feeding records (138 species), and seed dropping in 2.7% of total fruit-feeding records (10 species).Parts of young fruits were eaten only in 4.0% of total fruit-feeding records (24 species), whereas seed predation was recorded in 3.7% (23 species) (table VI). As shown in figure .19, seed predation was recorded in 3.1%, seed dispersal in 77.4% and seed dropping in 2.4% of all feeding records (N=2,287).

Seeds dispersed by spider monkeys ranged from the tiny seedlets of many Moraceae (e.g. Bagassa, Cecropia, Coussapoa, Ficus) to the large ellipsoid seeds of Platonia insignis (Guttiferae), which measure up to 4 x 2 cm.

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Table IV. Food species used by spider monkeys, ranked according to the number of feeding records:
(A) - in the study period March 1976 - May 1978, and (B) - in the period of intensive autecological study (May 1977 - May 1978). Column C gives the percentages of the total number of feeding records over the entire study period (N = 2287).

Rank	Species	A	B	C	Rank	Species	A	B	C
1	Virola melinonii	243	233	10,7	30	Carapa procera	20	19	0.9
2	Guarea grandifolia	91	72	4.0	31	Ampelocera edentula	19	19	0.8
3	Ecclinusa guianensis	76	76	3.3	32	Pachira msignis	19	18	0.8
4	Cecropia sciadophylla	72	71	3.2	33	Apeiba echinata	18	13	0.8
5	Dimorphandra sullei	70	64	3.1	34	Clusia scrobiculata	17	15	0.7
6	Bagassa guianensis	63	59	2.8	35	Spondias mombin	17	14	0.7
7	Inga edulis	60	60	2.6	36	Norantea guianensis	17	13	0.7
8	Achrouteria pomifera	59	59	2.6	37	Geissospermum sericeum	16	16	0.7
9	Inga alba	57	37	2.5	38	Licania micrantha	16	15	0.7
10	Tetragastris panamensis	56	48	2.5	39	Brosimum parinarioides	16	13	0.7
11	Laetia procera	50	50	2.2	40	Brosimum lactescens	16	12	0.7
12	prieurella sp.	50	49	2.2	41	Protium neglectum	16	8	0.7
13	Philodendron scandens	39	34	1.7	42	Dicranostyles guianensis	15	9	0.6
14	Vataireopsis speciosa	36	36	1.6	43	Hylocereus sp. a	14	14	0.6
15	Ephedranthus guianensis	34	33	1.4	44	Vitex stahelii	14	14	0.6
16	Guatteria chrysopetala	32	32	1.4	45	Abuta grandifolia	14	13	0.6
17	Cordia lomatoloba	29	29	1.2	46	Bellucia grossularioides	14	13	0.6
18	Tetragastris altissima	29	24	1.2	47	Inga cf. capitata	14	12	0.6
19	Inga bourgoni	27	27	1.1	48	Inga a acroceyhola	14	11	0.6
20	Philodendron acutatum	26	25	1.1	49	Adenocalymna sp.	13	13	0.6
21	Protium polybotryum	26	19	1.1	50	Licania majuscula	13	13	0.6
22	Clarisia racemosa	24	24	1.0	51	Maytenus sp.	13	13	0.6
23	Couratari stellata	23	21	1.0	52	Coussapoa latifolia	13	9	0.6
24	Ceiba pentandra	22	22	1.0	53	Inga cinnamomea	12	12	0.5
25	Rheedia macrophylla	22	20	1.0	54	Moutabea guianensis	12	11	0.5
26	Inga leiocalycina	22	13	1.0	56	Pouroma mollis	11	2	0.5
27	Capparis maroniensis	22	6	1.0	57	Arrabidaea corallina	10	10	0.4
28	Cayaponia ophthalmica	21	20	0.9	58	Hyeronima laxiflora	10	10	0.4
29	Sacoglottis cydonioides	21	13	0.9	59	Eperua falcata	10	9	0.4

Table IV. (Continued)

60	Trichilia quadrijuga/surinamensis	10	9	0.4	92	Paullinia spicata	5	4	0.2
61	Maripa scandens	9	9	0.4	93	Tabebuia serratifolia	5	4	0.2
62	Pterocarpus officinalis	9	7	0.4	94	Honey	5	2	0.2
63	Helicostylis tomentosa	9	4	0.4	95	Quassia simarouba	5	1	0.2
64	Anomocteriun granulosum	8	8	0.3	96	Apeiba glabra	4	4	0.2
65	Ficus gardneriana	8	8	0.3	97	Gustavia hexapetala	4	4	0.2
66	Guettarda acreana	8	8	0.3	98	Hylocereus sp. b	4	4	0.2
67	Peperomia glabella	8	8	0.3	99	Inga pezizifera	4	4	0.2
68	Attalea maripa	7	7	0.3	100	Inga rubiginosa	4	4	0.2
69	Cordia sagotii	7	7	0.3	101	Oenocarpus bacaba	4	4	0.2
70	Guarea kunthiana	7	7	0.3	102	Gnetum urens	4	3	0.2
71	Unonopsis glaucopetala	7	7	0.3	103	Paullinia sphaerocarpa	4	3	0.2
72	Euterpe oleracea	7	6	0.3	104	Dialium guianense	4	2	0.2
73	Cayaponia rigida	7	5	0.3	105	Eschweilera carrugata	4	2	0.2
74	Duguetia sp.	7	5	0.3	106	Couepia caryophylloides	4	0	0.2
75	Minquartia guianensis	7	2	0.3	107	Alchorneopsis floribunda	3	3	0.1
76	Piptadenia suaveolens	6	6	0.3	108	Caterpillars (2 species)	3	3	0.1
77	Parinari excelsa	6	6	0.3	109	Cedrela odorata	3	3	0.1
78	Pereskia aculeata	6	6	0.3	110	Cheioclinium podostemmum	3	3	0.1
79	Styrax aff fanshawei et micrasterus	6	6	0.3	111	Clusia grandiflora	3	3	0.1
80	Eschweilera poiteaui	6	5	0.3	112	Maquira guianensis	3	3	0.1
81	Leretia cordata	6	5	0.3	113	Perebea mollis	3	3	0.1
82	Xylophragma seemannianum	5	5	0.2	114	Heterópsis jenmani	3	3	0.1
83	Amplizoma sp.	5	5	0.2	115	Pouteria guianensis	3	3	0.1
84	Drypetes variabilis	5	5	0.2	116	Termites	3	3	0.1
85	Helicostylis pedunculata	5	5	0.2	117	Dipteryx odorata	3	2	0.1
86	Ocotea wachenheimii	5	5	0.2	118	Stizophyllum inaequilaterum	3	2	0.1
87	Parkia nitida	5	5	0.2	119	Hymenolobium petraeum	3	2	0.1
88	Parkia pendula	5	5	0.2	120	Mendoncia hoffmannseggiana	3	2	0.1
89	Paullinia acuminata	5	5	0.2	121	Pithecellobium jupunba	3	2	0.1
90	Pouteria sp. n.º 400	5	5	0.2	122	Paullinia tricornis	3	1	0.1
91	Virola surinamensis	5	5	0.2	123	Pourouma minor	3	0	0.1

Table IV.

124	Coussapoa angustifolia	2	2	0.1		156	Dioclea macrocarpa	1	1	0.05
125	Coussapoa asperifolia	2	2	0.1		157	Dioscorea trifida	1	1	0.05
126	Coussarea paniculata	2	2	0.1		158	Enterolobium schomburgkii	1	1	0.05
127	Zonthorylum nhoifolium	2	2	0.1		159	Eschweilera congestiflora	1	1	0.05
128	Ficus broadwayi	2	2	0.1		160	Euterpe precatoria	1	1	0.05
129	Ficus gomelleira	2	2	0.1		161	Ficus guianensis	1	1	0.05
130	Ficus trigonata	2	2	0.1		162	Ficus citrifolia	1	1	0.05
131	Guazuma ulmifolia	2	2	0.1		163	Ficus malacocarpa	1	1	0.05
132	Jacaratia spinosa	2	2	0.1		164	Ficus nymphaeifolia	1	1	0.05
133	Licaria canella	2	2	0.1		165	Ficus pertusa	1	1	0.05
134	Malmea obovata	2	2	0.1		166	Ficus trigona	1	1	0.05
135	Monstera adansonii	2	2	0.1		167	Gesneriaceae (1 species)	1	1	0.05
136	Platymiscium ulei	2	2	0.1		168	Hillia illustris	1	1	0.05
137	Sterculia excelsa	2	2	0.1		169	Inga stipularis	1	1	0.05
138	Talisia squarrosu	2	2	0.1		170	Leonia glycycarpa	1	1	0.05
139	Trichilia martiana	2	2	0.1		171	Vantarria parvifloro	1	1	0.05
140	Iriactea exorrhizo	2	2	0.1		172	Licania densiflora	1	1	0.05
141	Cheiloclinium cognatum	2	1	0.1		173	Loranthaceae (1 species)	1	1	0.05
142	Orchidaceae (2 species)	2	1	0.1		174	Maripa glabra	1	1	0.05
143	Pourouma sp.	2	0	0.1		175	Tanaecium nocturnum	1	1	0.05
144	Bignoniaceae sp. b	1	1	0.05		176	Nectandra kunthiana	1	1	0.05
145	Bignoniaceae sp. c	1	1	0.05		177	Operculina hamiltoni	1	1	0.05
146	Campomanesia aromatica	1	1	0.05		178	Parabancornia fiscianlata	1	1	0.05
147	Cecropia latiloba	1	1	0.05		179	Parinari campestris	1	1	0.05
148	Cedrelinga cateniformis	1	1	0.05		180	Platonia insignis	1	1	0.05
149	Cheiloclinium anomalum	1	1	0.05		181	Qualea dinizii	1	1	0.05
150	Clusia sp.	1	1	0.05		182	Symphonia globulifera	1	1	0.05
151	Combretum rotundifolium	1	1	0.05		183	Trymatococcus oligandrus	1	1	0.05
152	Cordia panicularis	1	1	0.05		184	Trymatococcus paraensis	1	1	0.05
153	Couratari guianensis	1	1	0.05		185	Anacardium giganteum	1	0	0.05
154	Paulinia sp.	1	1	0.05		186	Apeiba schomburgkii	1	0	0.05
155	Cynometra marginata	1	1	0.05		187	Apeiba tibourbou	1	0	0.05

Table IV.

188	Bignoniaceae sp.a	1	0	0.05	198	Goupia glabra	1	0	0.05
189	Cheiloclinium hippocrateoides	1	0	0.05	199	Inga coriacea	1	0	0.05
190	Chrysophyllum auratum	1	0	0.05	200	Inga thibaudiana	1	0	0.05
191	Clusia platystigma	1	0	0.05	201	Lecythis davisii	1	0	0.05
192	Clusia purpurea	1	0	0.05	202	Micropholis guyanensis	1	0	0.05
193	Copaifera epunctata	1	0	0.05	203	Ormosia paraensis	1	0	0.05
194	Copaifera guianensis	1	0	0.05	204	Passiflora glandulosa	1	0	0.05
195	Eperua rubiginosa	1	0	0.05	205	Peltogyne venosa	1	0	0.05
196	Eugenia feÿoi	1	0	0.05	206	Rheedia benthamiana	1	0	0.05
197	Ficus insipida	1	0	0.05	207	Tabebuia capitata	1	0	0.05

Table V. Different food items eaten by *Ateles p. paniscus*, , expressed as: (A) — percentage of total number of fruit species eaten for any part of fruit, (B) — percentage of total number of food species eaten for any part of food plant, (C) — percentage of total number of fruit-feeding records for any part of fruit, and (D) — percentage of total number of feeding records for any part of food plant and other food.

Parts eaten	N.° of species used	A % Total fruit species (N=171)	B %Total food species (N=207)	C % Total fruit feeding records (N=1,895)	D % Total feeding records (N=2,287)
Whole fruit/infruct./fig swallowed	66	39.3	31.9	25.2	20.9
Mesocarp (exocarp dropped, seed(s) ingested)	50	29.8	24.1	43.8	36.3
Aril (exocarp dropped, seed(s) ingested)	25	14.9	12.0	24.4	20.2
Young seed(s)/plumula ± young aril	23	13.7	11.1	3.7	3.1
Exo-and mesocarp/pericarp/perigonium (seeds dropped)	7	4.2	3.3	1.5	1.3
Exocarp (rest of fruit dropped)	1	0.6	0.5	0.3	0.2
Juice (chewed fruit dropped)	1	0.6	0.5	0.9	0.7
Columella + young seeds . Pseudofruit (fleshy pedicel) (fruit dropped)	1	0.6	05.	0.1	0.05
Flowers/inflorescences/floral buds	.33.		16.0		6.4
Young leaves/shoots/petioles	28.		13.5		7.9
Pseudobulbs (fleshy thickened stems of certain orchids)	2		1.0		0.1
Aerial roots	2		1.0		0.2
Bark	11		5.3		1.7
Decaying wood/rotten sheaths of *Attalea regia*	1		0.5		0.3
Honey	—		—		0.2
Caterpillars	2		—		0.1
Termites	1		—		0.1

Table VI. Seed dispersal, seed predation and seed dropping in *Ateles p. paniscus* expressed as the percentage of total number of fruit species and as the percentage of total number of fruit-feeding records.

Category	No. of fruit species	% Total fruit species (N=171)	% Total fruit-feeding records (N=1,902)
Seed dispersal	138	80.7	93.5
Seed predation	23	13.5	3.7
Seed dropping	10	5.8	2.7

Generally, the faeces of spider monkeys which are dropped out of a tree, contain a number of differents kinds of seed and fall apart because of a lack of binding substance. The seeds and stones are widely spread over the forest floor. Within a few minutes, all kinds of dung beetles arrive, attracted by the smell, and bury both faeces and seeds under the soil surface. Seeds and stones dispersed in·this way by spider monkeys usually do not attract terrestrial seed predators and therefore have a fair chance of germinating successfully. In contrast, many fruiting trees used by the monkeys attract

terrestrial seed predators such as agoutis, acouchis, pacas, deer and peccaries when their fruits fall in quantity.

Also, other animals such as bruchid weevils (Bruchidae), several terrestrial birds, and tortoises are attracted by the fruits dropped from these trees. In particular curassows (*Crax alector*) and trumpeters (*Psophia crepitans*) appear to be attracted by crashing sounds and vocalizations of *Ateles*, and frequently feed on the soft parts of fruits accidently dropped by the monkeys. By analyzing stomach contents of many curassows and trumpeters, it appeared that all seeds and stones ingested had been more or less damaged by either the bill or by grinding (Van Roosmalen and Mittermeier, in prep.). Consequently, these birds do not act as dispersers of larger seeds. Analysis of many dung samples of tortoises (*Geochelone* spp.) living in the area showed that these animals can act as seed disperser at least for several plant species (e.g., *Anacardium giganteum*, *Tetragastris* spp., *Protium* spp., *Spondias mombin*, *Cayaponia* spp., *Ecclinusa guianensis*). However, in contrast to *Ateles*, these animals swallow only small amounts of fruits and their daily travel distance is small.

Ateles p. paniscus* appeared to be an important seed disperser for many plant species and it seemed to be the only dispersal agent for several species that were not eaten by specialized frugivorous birds (e.g., cotingids, trogons, toucans and guans), *Alouatta* or *Geochelone*. In cases where seed predation by other monkeys, tree porcupines, insects, birds and terrestrial animals is strong, the plant's dispersal may be completely dependent on *Ateles*. Most obviously, this was the case for the following species: *Capparis maroniensis, Sacoglottis cydonioides, Gustavia hexapetala, Dimorphandra pullei, Guarea grandifolia, Guarea kunthiana, Trichilia* spp., *Brosimum parinarioides, Clarisia racemosa, Minquartia guianensis*, and *Ecclinusa* spp. This phenomenon is demonstrated nicely by fruiting *Brosimum parinarioides* (Moraceae), a widely dispersed tree that is not common in the Voltzberg study area (table I). First of all, *Chiropotes satanas*, an important seed predator (Van Roosmalen, Mittermeier and Milton, 1981), visited a particular tree regularly over several months, feeding on the young seeds. Macaws (*Ara* spp.) and squirrels (*Sciurus, Sciurillus*) also occasionally fed on the young seeds. Many maturing fruits were seen still hanging in the tree. Except for

Ateles, which swallowed the fruits whole, other monkeys such as *Saimiri sciureus*, *Cebus apella* and *Cebus nigrivittatus* were seen feeding on the pulp and dropping the mature seeds. Fruiting was abundant and many fruits fell down spontaneously, especially when monkeys moved through the crown. When *Ateles* or other monkeys fed on the ripe fruits, several terrestrial seed predators (e.g., agoutis (*Dasyprocta*), acouchis (*Myoprocta*), deer (*Mazama*) and sometimes peccaries (*Tayassu*))could be seen coming into the area to feed on the falling seeds. Curassows (*Crax*) and trumpeters (*Psophia*) were also seen feeding on the pulp of fallen fruits and swallowing the seeds. At this time, hundreds of seeds could be seen still lying on the forest floor under the tree. However, the next day all the seeds were gone. All the mature seeds that were dropped on the forest floor were either eaten or buried by scatter-hoarding rodents (e.g., agoutis), which protect the seeds in this way against predation by bruchid weevils. In this particular case, the tree may depend completely on *Ateles* for its dispersal, especially since a single seed that germinates far from the parent plant will have much greater chances for survival. Seeds from forgotten stocks or ones opened too late by scatter-hoarders may all germinate, but these monospecific beds of seedlings may well be discovered by herbivores (e.g., *Mazama*, *Tapirus*) which also forage for such edible seedling beds.

4.1.2. **Flowers.** Flowers contribute only a small portion to the spider monkey diet. In total, *Ateles* fed on 33 species of flower (16% of total food plant species recorded) in 6.4% of total feeding records (table V; fig. 19). Of the 33 plant species producing edible flowers, 17 are trees, 13 lianes and three epiphytes. Ranked according to the percentage of total flower-feeding records, the most important family was Bignoniaceae (25.9%; 11 species), followed by Meliaceae (17.7%; two species), Marcgraviaceae (11.6%; one species), Cactaceae (10.9%; three species), Bombacaceae (9.5%; two species), Mimosaceae (6.8%; four species), Ulmaceae (4.8%; one species), Tiliaceae (2.7%; one species), Caesalpiniaceae (2.0%; one species), Guttiferae (1.4%; two species), Papilionaceae (1.4%; one species), and Moraceae, Rubiaceae, Sterculiaceae and Vochysiaceae (0.7%; one species each).

Most of the flowers were consumed when at the mature stage or at a stage just before opening. When small, the entire flower or

inflorescence was swallowed. (e.g., *Ampelocera edentula, Carapa procera, Enterolobium schomburgkii* and *Piptadenia* suaveolens),but most flowers were only partly eaten. In particular corolla and/or tips of petals were preferred in many species (especially in Bignoniaceae), so that the calyx was dropped or the rest of the flower was not picked off the peduncle, stem or twig. Several species were used only for the tips of stamens, style and/or for the stigma (e.g., *Pachira insignis, Hylocereus* spp., *Pereskia aculeata* and *Parkia* spp.), some for the sticky central body of staminodes (*Clusia* spp.), for the bracts transformed in honeycups (*Norantea guianensis*) or for the thickened perianth (as in pistillate inflorescences of *Coussapoa* spp.).

Ranked according to the percentage of total flower-feeding records, most important species were *Guarea grandifolia* (13.6%), *Norantea guianensis* (11.6%), *Hylocereus* sp. a. and *Adenocalymna* sp. (8.8%), *Pachira insignis* (7.5%), *Arrabidaea corallina* (6.8%), *Ampelocera edentula* (4.8%),*Piptademia suaveolens* (4.1%), *Carapa procera* (4.1%) and *Xylophragma seemannianum* (3.4%). The other 23 species contributed less than 3.0% of total flower-feeding records.

4.1.3. **Leaves.** As flowers, leaves only contributed a small portion to the spider monkey diet. In total, *Ateles* fed on 28 species of leaf (13.5%) of total food plant species recorded) in 7.9% of all feeding records (table V; fig. 19). Of the 28 plant species producing edible leaves, 19 are trees, four lianes, one twiner and four epiphytes. Ranked according to the percentage of total leaf-feeding records, the most important family was Papilionaceae (29.7%; four species), followed by Araceae (25.0%; three species), Bombacaceae (12.2%; two species), Meliaceae (5.8%; one species), Bignoniaceae and Moraceae (4.7%; two species), Piperaceae (4.7%; one species), Caesalpiniaceae (3.5%; two species), Ulmaceae (2,3%; one species), Mimosaceae (1.2%; one species), Lauraceae (1.2%; one species), and Myristicaceae, Chrysobalanaceae, Rutaceae, Caricaceae, Sapindaceae, Dioscoreaceae, Gesneriaceae and Loranthaceae (0.6%; one species each).

It has to be emphasized that spider monkeys fed exclusively on young or flush leaves during the present study. They were never seen eating a single mature leaf. In many cases only the apex of flush leaves was eaten (e.g., *Pachira insignis,* , *Ceiba pentandra,*

Van Roosmalen

Jacaratia spinosa, Tabebuia serratifolia and *Cecropia sciadophylla*) or parts of the lamina were ripped off the costa with the mouth (e.g., *Ceiba pentandra, Pachira insignis*). In addition to flush leaves, young shoots and young leaves still rolled up in the sheath were also eaten (e.g., in *Philodendron scandens* and *P. acutatum*), and so was the base of the petiole (e.g., in *Philodendron scandens* and *Carapa procera*).

Ranked according to the percentage of total leaf-feeding records, the most important species were *Vataireopsis speciosa* and *Philodendron scandens* (both 20.9%), followed by *Ceiba pentandra* (8.1%), *Carapa procera* (5.8%), *Pterocarpus officinalis* and *P. vs. santalinoides* (5.2%), *Peperomia glabella* (4.7%), *Pachira insignis* (4.1%) and *Philodendron acutatum* (3.5%). The other 20 species contributed less than 3.0% in total leaf-feeding records.

4.1.4. **Pseudobulbs.** Pseudobulbs are the thickened, fleshy stems of certain Orchidaceae, mostly epiphytes, that function as a food and water reservoir. Spider monkeys fed on parts of pseudobulbs, while dropping the leaves or part of the entire plant, of two epiphytic orchid species which were growing on boughs high up in tall trees. They contributed only 1.0% to the total food plant species recorded and only 0.1% to total feeding records (table V; fig. 19). Neither species could be identified from the collected sterile samples, but both seemed to be quite abundant in the study area.

4.1.5. **Aerial roots.** Aerial roots are the roots growing out of stems of certain plants that hang in the air. On reaching the ground, they may take hold in the forest soil and start to act as normal roots. Many tropical epiphytes produce aerial roots. Spider monkeys fed on the tips of aerial roots of two species of Araceae. To reach the tip of these pendent aerial roots, the monkeys had to pull up several meters of them. The two species of *Philodendron* contributed only 1.0% in total food plant species recorded and 0.2% in total feeding records (table V; fig. 19).

4.1.6. **Bark and decaying wood.** In total, *Ateles p. paniscus* was seen feeding on the bark of 11 species (5.3% of total food plant species recorded), in 1.7% of all feeding records (table V; fig. 19). All species were trees. Ranked according to the percentage of total bark-feeding records, the most important species was *Licania micrantha* (37.5%), followed by *Inga alba* (30.0%), *Sacoglottis cydo-*

nioides (10.0%) and *Inga leiocalycina* (5.0%), with seven other species contributing 2.5% each.

Spider monkeys seemed to prefer decaying bark. Since almost all trees used were healthy, the edges of scars, waterholes and certain patches along the underside of boughs were particularly selected. These patches, though not always easily reached, had a softer, more or less decaying texture resulting from rain water flowing out of holes in the bough or trunk.

Occasionally, and apparently only in some adults, spider monkeys were seen feeding on the rotten sheaths of previously shed leaves of the palm *Attalea maripa*, which were found under the crown just above the smooth trunk. In particular an old female several times entered low forest at the very edge of liane forest or "rock savanna", where this palm frequently occurs, to feed on this rotten palm wood. The material, which looked from a distance like peat, was consumed as if palatable and by the handful. This food was taken in only 0.3% of all feeding records (table V; fig. 19).

4.1.7. Honey. Occasionally, spider monkeys fed on honey from bees nests in tree holes. This occurred in only 0.2% of all feeding records (table V; fig. 19). The monkeys obtained honey by reaching with one hand into the hole and licking the honey off the fingertips. The holes were difficult to reach and the monkeys often had to climb down big trunks.

4.1.8. Insects. Spider monkeys were definitely seen feeding on insects in a few cases. At least two species of small caterpillars were eaten, and accounted for 0.1% of all feeding records. Both species were collected but were not identifiable. The caterpillars were found in clumps of several hundred, attached by silk to the leaf. Spider monkeys were also seen eating one species of termite in 0.1% of all feeding records (table V; fig. 19). They usually opened the tunnels of termites that ran up the huge bole of an emergent tree, especially of the species *Hymenolobium flavum,* and waited until a number of termites walked into the open. They picked up the termites with their tongues and seemed to select only certain types of termites. Whether they selected workers or soldiers was not clear. Spider monkeys were never seen opening the termite nests that sometimes high occurred up in tree crowns.

In addition to actively feeding on insects, spider monkeys accidently ingest minute insects such as the stages of pollinating and parasitic wasps that are present in all kinds of figs. However, *Ficus* species were rare and widely dispersed in the Voltzberg study area. In total, 11 species of fig were eaten, contributing only 1.0% in the total number of feeding records.

The animal-protein intake of *Ateles p. paniscus* is probably restricted to the above mentioned cases. It never fed on rotten fruits which usually contain animal life, and wormy fruits were dropped as well.

4.2. Feeding Behavior

This section deals with spider monkey daily activities, with special emphasis on feeding behavior. A typical day for the long wet season is compared with a typical day for the long dry season, since feeding behavior appears to be strikingly influenced by the seasons.

A typical spider monkey day during the long wet season. In Surinam, day dawns at 5.45 h local time. At first light, when it is still dark on the forest floor, a subgroup of spider monkeys moves out of its sleeping site for the past night, the huge, isolated crown of a 50 m tall *Hymenolobium flavum* at the foot of the Voltzberg. Just before they depart, the area beneath the crown is bombed by enormous amounts of excreta as the members of the subgroup urinate and defecate almost simultaneously. The old female with her son, a juvenile-3, is the first to move. The others, a female with her daughter, a juvenile-2, and an old male follow in a row. Soon, they all reach a group of food trees not far from the sleeping tree. Apparently, the proximity of these trees was one of the reasons for choosing the *Hymenolobium* as the past night's sleeping site. After feeding on four trees from 6.00 - 7.00 h, without once feeding together at the same time on the same food tree, they leave and travel over one kilometer within 20 minutes. Throughout this travel, the old female determines the route taken and the activity patterns of the subgroup as a whole. Suddenly, the female with the juvenile-2 splits off. Apparently, she has in mind a different foraging route and other food sources than the old female. Within a short time, they are out of sight and we continue to follow the old female, her son and the old male. Before 8.00 h, they feed together on two other trees. At 8.00 h, the

female starts to bark and is immediately followed by the male, resulting in a siamang-like barking duet. This call seems to act as a long distance contact call advertising the presence of this subgroup to other spider monkeys in the area. It differs considerably from the long call that only adult males give. After feeding on another tree, the monkeys rest for half an hour. After another feeding bout of 15 minutes in the same tree, they leave and move quickly over 500 m. After feeding for a short time, they start another barking duet in which the juvenile tries to take part. They then feed again for 20 minutes in the same tree. Between 10.15 - 12.15 h, the monkeys feed on ten different trees over a 500 m route that is still fully determined by the old female. After that, they rest for 40 minutes in the upper part of the canopy. The old female lies on her back with the eyes closed in a branches fork. After feeding another 15 minutes in a nearby tree, they rest again for half an hour. At 14.00 h, they move away and soon join another subgroup. This subgroup usually ranges in another "core area" within the home range inhabited by the group. It contains four animals: two females, a male juvenile-2 and a dependent infant-1(-2). A greeting ceremony follows. This is usually performed only by the males on such occasions but this time also involve the females who briefly embrace one another. The greeting completed, the juveniles start to play, whereas the adults rest for 45 minutes in an emergent tree. At the beginning of the rest period, the old male gives a long call, answering another male about 500 m away. At 14.45 h, all seven animals move and the adults feed for 20 minutes on two nearby trees. The juveniles keep on playing. They then all travel in roughly the same direction from which the old female's subgroup came prior to uniting with the second subgroup. After briefly traveling and feeding, the other subgroup splits off at 16.00 h, and moves away very rapidly in the direction of the long call heard just before, the one given by the third male of the spider monkey study group. The old female's subgroup follows them for a short time but soon returns to its own route. At this point, they are in the same area as they were at 8.00 h. After feeding on two trees, the old female's subgroup moves back the way it just came, but then turns more to the north. Now, they seem to be in a hurry, traveling very fast for over 600 m. I have a lot of trouble tracking them now. Another male is calling nearby and some minutes later a young male meets and joins

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the subgroup after a short greeting ceremony with the two males of the subgroup. Immediately after this, the two adult males start a barking duet. The newcomer then moves away and is followed by the other males. The old female, who has so far led the subgroup, stays back. She searches for new food sources, entering the lower part of the canopy here or the top of a tall tree there, and she checks several fruiting trees for stage of maturity. In the meantime, the males are rushing forward in the direction of the coming night's sleeping tree some 500 m away. Somewhat later, the old female follows at a distance of about 50 m. After feeding together on one tree at 17.15 h, all four travel toward the sleeping tree, the female in front. They feed on another four trees in the direct neighbourhood of the sleeping tree until 18.00 h. For part of the time, the juvenile and the young male playfight and chase each other. From 18.00 - 18.30 h, they feed on another three trees next to the large buttressed sleeping tree, a *Piptademia suaveolens*. At 18.30 h, the young male moves away to another sleeping tree. Ten minutes later, the old male and the juvenile enter the sleeping tree by crossing a gap between two crowns, swaying back and forth, grasping the extreme twigs of a crownlet of the sleeping tree, and sweeping across. Some minutes later, the female enters the tree in the same way and all three feed for a while on the inflorescences of the sleeping tree itself and on the young leaves of two epiphytes (Araceae) hanging down along the huge bole of the tree. At 18.40 h, when it is almost dark on the forest floor, the monkeys prepare for the night, each in its own site. The juvenile rests against his mothers belly for a while, then moves to his own site some 6 m away from her. When I finally reach the camp, it is completely dark.

Today, the three animals observed continuously have fed on a total of 38 different food plants belonging to 13 species, of which two were very important: *Virola melinonii,* of which 17 different trees were used, and *Laetia procera*, of which six different trees were used. A total of 32 feeding records was made for fruits (not including the data from faeces), four for flowers and two for young leaves. Total feeding time was 5½ hours, total resting time between 6.00 - 18.45 h was three hours, and total travel distance was 4,500 m.

A typical spider monkey day during the long dry season. When I reach the night's sleeping tree at 6.00 h, the sky is clear. The spi-

der monkeys are still resting high up in the crown of a 50 m tall *Vochysia tomentosa*. The crown is completely isolated from the canopy beneath and difficult to enter. This subgroup consists of an old female and her juvenile son about three years old, two of the same animals as followed in the previous example, and a second adult female. At about 6.30 h, all animals defecate. The faeces are compact, containing mainly vegetable matter and a few seeds of only one species. Sitting side by side, the mother leans over her son and nurses him for two minutes. Although over three years old, he is still nursed from time to time. Within one or two months he will be weaned, and shortly after this his mother will come into estrus for the first time in about four years. At 6.45 h, the second female descends to the canopy by leaping across a gap. Mother and son keep on resting. Twenty minutes later, they also move out of the sleeping tree and join the other female some 120 m away, where she was waiting for them and uttering soft contact calls. Together, they travel about 100 m toward a fruiting tree of the most important food species of the moment, *Dimorphandra pullei*, which offers edible pods for four to seven months. For the next 40 minutes, they feed on the old, desiccated mesocarp of these fruits by ripping open the woody pods longitudinally. No infructescence or pod is spoiled and dropped before it has been eaten out completely. Especially in this time of food scarcity, spider monkeys tend to eat very economically. At 8.00 h, all three travel back over 100 m. Then the second female splits off while mother and son are feeding on young leaves of a low tree. Following this, the mother and son rest in the middle part of the canopy for about two consecutive hours. At 10.15 h, they feed briefly on young leaves of *Pachira insignis*. From 10.25 - 10.35 and 10.45 - 10.55 h, they feed on the fruits of another *Dimorphandra . pullei*. After a short travel bout, they eat the flowers of *Guarea grandifolia* for 26 minutes, broken by a rest of 15 minutes. From 11.45 - 12.15 h, mother and son travel slowly and feed on a few flowers of Bignoniaceae lianes. From 12.15 - 13.10 h, both animals rest high up in an emergent tree. When they continue on their way, they meet the other female again. Some greeting vocalizations are heard, then all three feed on young leaves of *Pachira insignis*, a common tree in this region which is restricted to pina swamp forest along creeks. For one hour they feed without interruption on these young leaves by tearing the apical part of the

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leaflets off the costa by their teeth. From 14.15 - 15.45 h, all three rest, the second female in a nearby tree. From 15.45 h on, they feed continuously for 40 minutes on the flowers of a *Guarea grandifolia* tree. After a rest of 20 minutes, mother and son travel to the same sleeping tree as used the previous night and enter the crown by leaping. The second female stays back, and feeds on the flowers of a nearby *Guarea grandifolia* for another ten minutes. She enters the sleeping tree at 17.00 h. She sits down at the same place as the previous night, five meters above mother and son, who are sitting side by side. The juvenile is then nursed for five minutes while he is lying between his mothers knees. The time now is 17.15 h and the monkeys are ready to sleep, lying in forks of branches in the late afternoon sun.

Today, neither long calls nor barking duets were heard and no other subgroups were encountered. The observed animals fed on a total of 14 different food plants belonging to 10 species, of which, three; were very important: *Dimorphandra pullei*, two fruiting trees; *Guarea grandifolia*, three flowering trees; *Pachira insignis*, young leaves of two trees. Not including the data from faeces, a total of three feeding records were made for fruits, five for flowers and six for young leaves. Total feeding time was 3½ hours of which three hours were spent on the three most important species. Total resting time between 6.00 - 18.45 h was seven hours, and total travel distance was 700 m.

Comparing these two days which are typical for each season, the following differences are most striking. Day range length during the long wet season can be more than six times day range length during the long dry season. During the long wet season, total resting time is much less and total feeding time is much more. Also, the sleeping tree is left much earlier and entered much later in the wet season than in the dry season. The diet in the dry season includes a much higher percentage of flowers and young leaves than during the wet season. In the dry season, the monkeys feed very economically and activity is kept to a minimum. In general, subgroups are smaller during the long dry season and fewer encounters take place with other subgroups. The monkeys are also more silent.

4.2.1. **Foraging techniques.** In general, individual feeding activity within a subgroup was closely synchronized. When feeding

for prolonged periods of time on the same food source before traveling to another, the first feeding bout was usually similar for all members of the subgroup and consisted of eating at high speed. Later, short resting bouts could alternate with short feeding bouts, which did not invariably occur simultaneously for all subgroup members involved. Juveniles spent less time feeding than adults, spending the extra time playing either alone or with other juveniles and/or adults.

Usually, the daily itineraries and activity patterns of a subgroup were determined by a so-called leading female or sometimes shared by two leading females. The latter occurred quite rarely and only over short periods of time. Each female seemed to have somewhat different foraging routes in mind, resulting in frequent fission and fusion. The route connecting the principal food plants was the shortest one possible, both in geographical and ecostructural sense, and the leading female usually did not hesitate. It appeared that she had roughly mapped out in her mind the foraging route for a particular day early in the morning or perhaps even the day before. Another observation which may help in interpreting this remarkable behavioral pattern is the fact that a leading female that temporarily joins another subgroup led by another female and following a completely different route, could not readily relocate her planned route after splitting off. For this reason, she engaged in some apparently inappropriate behavior such as retracing earlier travel routes and revisiting certain food sources, or traveling back and forth.

When a foraging subgroup was relatively large (four or more independently locomoting animals), the monkeys tended to spread their attention over different food sources at any given point in time, thus avoiding possible agonistic interactions. This type of foraging seems to be possible only when food supply is abundant and one or more other food sources are likely to be nearby. During the long wet season, the average subgroup size observed was therefore larger.

Spider monkeys live in medium-size, loosely associated groups which fragment into subgroups of varying size and composition, and roam independently in the same general area. The only persistent association is that of a female and her offspring up to four years of age. All other members of the group will join a subgroup only

temporarily and then switch to another or go their own way. Temporary, solitaries are frequently observed, especially during the long dry season.

A leading female appeared to know a certain part of the home range the best and this area is referred to as her "core area". Leading females were often observed in their "core areas" checking fruit sources that were soon to become available. On a number of such occasions a leading female was seen going off the route in order to check a food source with unripe fruit, testing the fruit, dropping it and then returning to the rest of the subgroup. Some days, this behavior was observed especially during the late afternoon, when the rest of the subgroup was playing or traveling ahead towards the sleeping tree. The behavior was not performed every day but occurred at least every fourth day. In this way important food plants which were approaching the edible stage could be incorporated at the right moment into the female's pre-planned foraging route. If this interpretation of foraging behavior is correct, the knowledge of a leading female becomes most impressive, especially since the phenological picture is constantly changing and a foraging route involves a very large number of plants dispersed over a wide area.

The unusual social structure of spider monkeys seems to be a highly efficient adaptation to exploiting available mature-fruit sources, especially since other group members can rapidly learn about food by conspecific cueing (Slatkin and Kiester, 1974). Since mature-fruit sources are patchily distributed and the fruits can only be obtained for short periods of time and in relatively small amounts, the optimal foraging strategy seems to be a core-area system of leading fermales, with whom other group members may join temporarily to exchange knowledge on available food sources.

4.2.2. **Feeding techniques.** In general, fruits are found at or near the periphery of tree crowns. Spider monkeys tend to feed by suspension and are seldom seen picking a fruit and carrying it to a bough or branch before consuming it. Fruits are picked with one hand. Many fruits are swallowed whole, but when the outer layer is tough the fruit is normally opened with the teeth and then eaten. Few manipulations were observed when spider monkeys fed on fruit. This may be related to lack of a functional thumb. When fruits are small or compound, spider monkeys may eat them by removing

part or all of the infructescence, holding it with the hand (s) and snapping off the fruitlets with the mouth (e.g., in *Alchorneopsis*, *Hyeronima*, *Pourouma*, *Oenocarpus* and *Guettarda*). Some fruits are only chewed for the juice (e.g., in *Geissospermum*) or for the soft outer layer which is scraped off with the teeth (e.g., in *Couepia*, *Licania* and *Ceiba*). Manipulation of fruit parts with particular fingers was rarely observed. Pulp and seedlets of *Clusia grandiflora* are scraped out of the locules with two fingers. Pods are ripped open allong the suture (s) with the teeth and eaten out, while both valves are held in the hands (e.g., in *Inga*). Bivalved fruits dehiscing at full maturity, such as those of *Virola*, are bitten just before opening, while the fruit is held with both hands. At this mature stage, the fruit is easily opened by applying pressure. After pulling the valves apart with the hands or with hands and teeth, the monkey swallows both stone and aril. When feeding on young seeds, spider monkeys bite out part of the fruit-wall so that the seed(s) can be removed for eating.

To reach some food items, such as the infructescences of *Philodendron scandens* and the aerial-root tips of *Philodendron*, spider monkeys pull up several meters of stem or aerial root while sitting on a branch. Once a spider monkey was seen sitting on a bough and looking down along a bunch of hanging stems of a *Philodendron scandens*. It first pulled up the wrong stem and, then the right one to obtain the fruiting spadix. Breaking off branches to feed on their infructescences, a common behavior of capuchin monkeys, was observed very rarely and seemed to occur rather by accident than by intent.

Leaves selected as food were always young leaves and usually ocurred at the periphery of the tree crown. Leaves would be eaten either directly or after they were torn off twig or stem. Selective feeding on particular leaf parts was observed in many cases. Parts of the lamina were ripped off the costa with the teeth, or only the apex of the leaf was bitten off. Young shoots and leaves still rolled up in the sheath were also eaten, and sometimes the base of the petiole was preferred.

Flowers occur mostly at the periphery of crowns and usually were eaten directly by pulling the flowering twig or stem towards the mouth or by picking the flowers themselves with one hand. In

many cases only the corolla was bitten off and eaten, the rest of the flower remaining attached to the peduncle, stem or twig. Sometimes, all or part of the inflorescence was broken off with the hand before it was eaten. Some flower species were selected only for the tips of stamens, style and/or stigma, others for the sticky central body of staminodes, the honeycup or the thickened perianth.

Bark was eaten by biting off pieces with the teeth, chewing for a while and ingesting the pulpy mass. The bark eaten was usually decaying or rotten. Most of the trees from which bark was selected were apparently healthy. However, in certain places, such as the edges of scars and water-filled holes, the bark was more or less decaying because of continuous contact with rain water. Frequently, places on the underside of boughs which were obviously affected by regularly flowing rain water were chosen. These places were often hard for the monkeys to reach and so required much effort. Inconvenient postures had to be adopted such as hanging by all five extremities under a thick, horizontal bough. Many of these particular patches appeared to have been used for several years and their exact location was apparently known from earlier visits. It is worth noting that of 11 species of tree providing a source of bark for the spider monkeys in the study area, 10 species provided the monkeys with another food item as well (eight for fruit, two for flush leaves). Only *Nectandra kunthiana* provided only bark, but it was not observed fruiting during the study period and might well provide the monkeys with edible fruits at certain times. Selective feeding on bark may be important for the monkeys, since several tree species are known to have poisonous bark (e.g., *Vataireopsis speciosa*). Restricting bark-eating to well-known species may be advantageous as it may limit the chance of error. Also, use of the same bark feeding sites over a long period of time may help in avoiding dangerous errors, especially if barks (as opposite to fruits and flowers) are as difficult to differentiate for the monkeys as they were for the observer.

The method of drinking from tree holes resembles very much the drinking behavior of siamangs and gibbons as described by Chivers (1974) and Ellefson (1974). Water-filled holes are usually found at the junction of branches or places where a branch or bough is broken off and the wood is rotten. These holes are filled with water most of the year and play an important role as a water source, es-

pecially during the long dry season. The monkey dips its hand into the hole, raises it rapidly to the mouth, lifting up the elbow in order to suck the water running off the back of the hand. This action is sometimes repeated over 80 times in a row. Water was seen being taken in the same manner from the beakers formed by the tightly imbricate leaf bases of big Bromeliads growing epiphytically on boughs. During the long wet season, drinking was observed rarely as the juicy fruits which make up the main part of the diet apparently contain enough water.

4.2.3. **Feeding heights.** *Ateles* is primarily an animal of the upper levels of the forest. Its main foods, nutritious large-seeded fruits, are usually found in the upper periphery of canopy crowns. Of a total of 6,105 feeding minutes, recorded for 30 days evenly spread over the year, 77.2% was spent in the upper levels of the forest. 22.8% of this time was spent in emergents (30 m or more) and 54.4% in the upper part of the camopy (25-30 m). The lower levels of the canopy and the understory were relatively unimportant, with 16.4% spent in the middle part (20-25 m) and 5.6% in the lower part of the canopy (15-20 m). Ateles was rarely seen feeding in the understory (3-15 m), this stratum accounting for only 0.8% of total feedling time.

4.2.4. General feeding postures. Locomotion and postural behavior of Ateles p. paniscus has been studied in depth by Mittermeier (1978) in the Voltzberg study area. Some of the results concerning locomotion during feeding and general feeding postures will be mentioned briefly here. For detailed description refer to Mittermeier (1978).

Climbing, especially "horizontal climbing", appeared to be the most important locomotion pattern during feeding. It is typefied by irregular limb use. Most locomotion takes place on twigs and branches, with twigs playing a greater role during feeding than during travel. Twigs are the most important supports in feeding postures since most of the feeding activities take place at the periphery of tree crowns. Feeding postures can be divided into three major categories: sitting, standing and suspensory. Sitting and standing postures are above branch, with the animal's weight on the support. Suspensory postures are those in which the major support is above or to the side. Most often they involve three limbs as support, the

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tail couting as a limb, in addition to the limb used to grasp food. Sitting and suspensory postures were the most important, while bipedal, tripedal and quadrupedal standing postures contributed 10-15%. A vertical clinging posture is occasionally used, and on rare occasions *Ateles* will feed in a reclining position.

4.2.5. Food selectivit. In general, daily itineraries appeared to be made up of direct lines between subsequent sleeping trees, and were determined by several trees, lianas or groups of trees which were important in providing the monkey's food at that time. Spider monkeys were rarely seen visiting a particular food plant more than once a day. Only when the same sleeping tree was used on consecutive nights were some food sources, especially those occurring near this sleeping tree, used a second time.

Ripe fruits were usually selected from a distance by sight. Sometimes, as in the case of *Sacoglottis cydonioides, Brosimum parinarioides* and *Clarisia racemosa*, the monkey would inspect the fruit by sniffing or biting it softly, since the external properties of these fruits do not give a definite indication of the stage of maturity.

Affected and wormy fruits were often recognized without being opened, even when they were marked only by very inconspicuous insect holes. There is also evidence for the selective feeding on tastier fruits from different trees of the same species. Form example, spider monkeys fed only on some of the simultaneously fruiting trees of the species *Spondias mombin*. The selected trees turned out, without exception, to produce sweet-tasting fruits, whereas the neglected ones carried bitter-tasting fruits. Given the fact that *Ateles paniscus* was found one of the main dispersal agents of the large seeds of Spondias mombin, in this way it may provide selective pressure for sweet-tasting flesh in this species.

4.2.6. Temporal patterning of food choice. Spider monkey day ranges appeared to be determined mainly by certain food sources, here referred to as *primary food sources*. These sources usually produce large, relatively fast-ripening (or in the case of leaves, rapidly flushing) crops of relatively nutritious food items, enough for at least three independently locomoting members of a subgroup to feed on together. Normally, feeding bouts on foods in this category are relatively long. Most of the species are available every year, but crops can fail during some years. Examples of primary food sources

are: *Ceiba, Protium, Tetragastris, Guarea, Virola, Achrouteria* and *Ecclinusa*.

Secondary food sources are those producing smaller, slow-ripening crops of relatively nutritious foods, available for prolonged periods but at any moment offering a meal to only one or two independently locomoting animals. Examples are: *Duguetia, Monstera* (infructescence), *Philodendron* (infructescence), *Hylocereus* (inflorescence, infructescence), *Jacaratia, Clusia, Leretia, Strychnos, Cecropia, Passiflora, Moutabea* and *Paullinia*. These food sources will be used only by one or two members of a subgroup on its way from one primary food source to another. Normally, feeding bouts are short.

Tertiary food sources are defined as reliable sources mostly available for prolonged periods of time, sometimes even for several months or longer, providing relatively low-nutrient secondary food. These sources usually occur throughout the home range and may be used either by the whole subgroup or by members of a subgroup on their way from one primary food source to another. Feeding bouts vary in length, but may be quite long. Examples of tertiary food sources are: *Philodendron* (leaves, shoots and aerial roots), *Licania* (bark), *Eperua* (leaves), *Pterocarpus* (leaves), *Norantea* (flowers), *Bellucia* (fruits), *Carapa* (leaves), *Cecropia* (leaves) and *Peperomia* (shoots). Crops of tertiary food sources never fail and the monkeys can depend on them every year.

As an introduction to the materials on variation in food choice, I present outlines of food choice and foraging routes performed by a spider monkey subgroup during four consecutive days in both December 1977 and April 1978. These months are chosen for comparison because of strikingly different availability of preferred food. Also, during both periods of observation, a particular leading female and her juvenile son were observed continuously, and were found to determine fully the ranging behavior of all individuals joining ther subgroup during the observation period. In tables VII and VIII, all food species and food items used by a soider monkey subgroup during four consecutive days in both December 1977 and April 1978 are listed, as are the amount of feeding time for each food item and species and the category to which each food source belongs. The corresponding daily itineraries of the subgroup are mapped in figures 20 and 21.

During four consecutive days of observation in December, primary food sources accounted for 87% of total feeding time, whereas feeding on secondary and tertiary food sources made up only 2% and 11% respectively. During four consecutive days of observation in April, primary food sources accounted for 86% of total feeding time, whereas feeding on secondary and tertiary food sources only made up 12% and 2% respectively.

4.2.7. **Diurnal variation in food choice.** Spider monkeys appeared to select for variety of food. As shown in tables VII and VIII, a spider monkey subgroup used on average 14 different food items each day in December and in April. These items represented only about a quarter of the total monthly number of food items used. Among these, three or four food items were considered most important based on the amount of feeding time and the estimated total weight of food ingested. Duration of the feeding visit to these three or four primary food sources could be long but never exceeded two hours. Most feeding visits to other food sources were short, ranging between one and 15 minutes.

Daily patterns of food use could be distinguished. Fruits were eaten throughout the day, but there were usually two feeding peaks: early in the morning and late in the afternoon. A third peak might occur around midday (between 11.00-13.00 h) (Van Roosmalen, in prep.). Leaf-eating occurred throughout the day in the period July-January and increased during the course of the day. From January to July, however, it mainly occurred in the late afternoon. This pattern may be explained as follows. Fruit-eating requires more energy expenditure for suspensory behavior in the periphery of crowns than does leaf-eating. When fruits are abundant (from January to July) and activity budgets correspondingly high, it seems likely that the monkeys prefer to leave the easy activity of eating young leaves for the late afternoon when they are more tired. On the other hand, increase of leaf-eating in spider monkeys is correlated with decrease in extent and rate of ranging (for example, see table VII, December 5). Feeding on flowers occurred throughout the day in the period July-January, and increased during the course of the day in January and February. Flowers of Bignoniaceae and Cactaceae (e.g., *Hylocereus*), however, were especially consumed in the morning when the corolla has just opened. Feeding on bark and rotten palm sheaths

was more frequently observed during the morning, with a peak bet-
ween 10.00-12.00 h. The consumption of other food items, such as
honey, insects, aerial roots and pseudobulbs occurred infrequently
throughout the day, and the sample size is too small for determi-
ning general patterns.

4.2.8 Variation in food choice between days. Diet changed
considerably from day to day. Spider monkeys usually exploited the
food sources of a particular part of the home range in a two to four-
day cycle. The cycling pattern shifted constantly at variable rate,
depending on the kind and the availability of present food sources.
In general, primary food sources, which are most responsible for de-
termining the cycling pattern, are ripening or flushing over relati-
vely short periods of time. Some of these sources provide an entire
subgroup enough to feed on day after day. If not exploited by the
monkeys, the mature fruits or infructescences either open their val-
ves and become available to birds (e.g., *Tetragastris, Laetia, Viro-
la*) or drop to the ground (e.g., *Bagassa, Brosimum*). Consequently,
when such a preferred food source becomes available, a leading
spider monkey female will include it in her itinerary almost every
day (table VII, e.g., *Bagassa guianensis* and *Brosimum parinarioi-
des*; table VIII, e.g., *Tetragastris altissima* and *T. panamensis*). In
this way, these particular food sources may play a central role in
daily ranging behavior for some time. Most primary food sources,
however, neither have dehiscent fruit nor do they drop a fruit crop
in a short period of abundance. Rather, they produce mature fruit
more gradually. Food sources of the latter kind may be visited once
every two to four days (e.g., *Spondias, Inga, Styrax*). In the meanti-
me, enough fruits can ripen and become available for the entire sub-
group to feed on at a next visit. Solitary ranging animals may visit
some of these sources in the interval between visits of a larger
subgroup led by a dominant female, but the relatively small
amount of food eaten by these animals probably does not affect
the ranging pattern. In general, secondary food sources, which
usually ripen slowly, are not visited more than once every two
days. Most intervals between subsequent visits appeared to be
longer than this, often ranging from three to eight days or more,
depending on the food species. Tertiary food sources usually
produce enough for short feeding visits every day, but since most

Table VII. Food choice and feeding time for a spider monkey subgroup during four consecutive days in December 1977. The food sources listed correspond with those mapped in figure 20; (I) stands for primary, (II) for secondary, and (III) for tertiary food sources.

Species	Food item	Food category	Feeding time (min.)
December 2			
1. Bagassa guianensis	infructescense	I	74
2. Brosimum parinarioides	infructescense	I	117
3. Inga pezizifera	pods checked only		
4. Philodendron acutatum	y. leaves, shoots	III	3
5a. Philodendron scandens	shoots	III	4
b. Coussapoa latifolia	infructescense	I	4
6a. Philodendron acutatum	aerial-root tips	III	3
b. Paullinia sphaerocarpa	y. seeds	II	1
7. Inga sp.	pods checked only		
8a. Eschweilera congestiflora	y. seeds + aril	II	3
b. Hillia illustris	flowers	III	2
9. Philodendron acutatum	aerial-root tips	III	2
10. Sacoglottis cydonioides	bark	III	2
11. Inga alba	bark	III	2
12a. Gesneriaceae indet.	y. leaves	III	11
b. Tabebuia serratifolia	y. leaves	III	12
13. Achrouteria pomifera	fruit	I	41
14. Couratari stellata	bark	III	2
15. Ceiba pentandra	y. leaves	I	8

Weather: sunny; heavy rain from 14.36-15.00 and 17.00-19.00 h
Observation time: 5.48-17.00 h
Day range size: 1.500 m
Total food species used: 15
Total food items used: 18
Total feeding time: 291 minutes (244 on primary, 4 on secondary and 43 on tertiary food sources)
Most important food species calculated in feeding time: Brosimum parinarioides (117 min.), Bagassa guianensis (74 min.), Achrouteria pomifera (41 min.)
Subgroup size and composition: 5.48-13.38 h - 4 (2♀♀ 1♂ 1 ♂)
13.38-17.00 h - 7 (+2 ♀♀ 1II)

Species	Food item	Food category	Feeding time (min.)
December 3			
1. Cecropia sciadophylla	infructescence	II	5
2. Cecropia sciadophylla	infructescence	II	2
3. Bagassa guianensis	infructescense	I	17
4. Pouteria sp. (400)	y. seeds	I	8
5. Vataireopsis speciosa	y. leaves	I	3
6. Bagassa guianensis	infructescence	I	9
7a. Peperomia glabella	shoots	III	3
b. Ficus guianensis	figs	I	94
c. Ceiba pentandra	y. leaves	I	3
8. Xylophragma	flowers	III	3

Weather: sunny; heavy rain from 11.25-12.00 and 12.07-12.35 h
Observation time: 5.40-13.00 h, then lost contact

Table VII (Continued)

Species	Food item	Food category	Feeding Time (min.)

December 3

Day range size: 900 m(+ 1,600 m hypothetic)
Total feeding time: 147 minutes (134 on primary, 7 on secondary and 6 on tertiary food sources)
Most important food species calculated in feeding time: Ficus guianensis (94 min.), Bagassa guianensis (26 min.)
Subgroup size and composition: 5.40-8.50 h - 4 (2♀♀ 1♂ 1J3♂)
8.50-13.00 h - 3 (1♀ left subgroup)

December 4

Species	Food item	Food category	Feeding Time (min.)
1. Bagassa guianensis	infructescense	I	29
2. Brosimum parinarioides	infructescence	I	32
3. Bellucia grossularioides	fruit	III	11
4. Ampelocera edentula	y. leaves	III	1
5. Sacoglottis cydonioides	bark	III	1
6. Trichilia quadrijuga	fruit	I	18
7. Dimorphandra pullei	frut	I	10
8. Vantanea	fruit	II	8
9. Achrouteria pomifera	fruit	I	10
10. Xylophragma seemannuanum	flowers	III	8
11. Coussapoa asperifolia	infructescence	II	2
12. Cordia sagotti	fruit	I	5
13. Achrouteria pomifera	fruit	I	4
14. Clarisia racemosa	fruit	I	5
15. Ceiba pentandra	y. leaves	I	37
16. Inga leiocalycina	bark	III	5
17. Guatteria chrysopefala	fruit	I	12
18. Achrouteria pomifera	fruit	I	6
19. Dimorphandra pullei	fruit	I	9
14. Clarisia racemosa	fruit	I	8
20. Licaria canella	y. leaves	III	4
21. Apeiba echinata	flowers	III	1
22. Xylophragma seemannianum	flowers	III	4

Weather: sunny; heavy rain from 16.45-19.30 h
Observation time: 5.40-16.45 h
Day range size: 1,250 m
Total food species used: 18
Total food items used: 18
Total feeding time: 227 minutes (185 on primary, 7 on secondary and 35 on tertiary food sources)
Most important food species calculated in feeding time: Ceiba pentandra (37 min.), Brosimum parinarioides (32 min.), Bagassa guianensis (29 min.)
Achrouteria pomifera (20 min.), *Dimorphandra pullei* (19 min.)
Trichilia quadrijuga (18 min.)
Subgroup size and composition: 5.40-12.15 h - 6 (3♀♀ 1♂ 1J2o, 1J3♂)
12.15-16.45 h - 3 (2♀♀ 1J2o)

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Table VII (Continued)

Species	Food Item	Food category	Feeding Time (min.)
December 5			
1. Vataireopsis speciosa	y. leaves	I	55
2. Ceiba pentandra	y. leaves	I	41
3. Achrouteria pomifera	fruit	I	33
4. Achrouteria pomifera	fruit	I	18
5. Bagassa guianensis	infructescence	I	16
6. Ampelocera edentula	y. leaves	III	2
7. Bellucia grossularioides	fruit	III	10
8. Bagassa guianensis	infructescense	I	35

Weather: sunny; heavy rain from 11.35-11.50, 13.48-14.37 and 17.15-18.45 h
Observation time: 5.45-17.10 h
Day range size: 850 m
Total food species used: 6
Total food items used: 6
Total feeding time: 210 minutes (198 on primary, 0 on secondary and 12 on tertiary food sources)
Most important food species calculated in feeding time: Vataireopsis speciosa (55 min.), *Achrouteria pomifera* (51 min.), *Bagassa guianensis* (51 min.), *Ceiba pentandra* (41 min.)
Subgroup size and composition: 3 (1♀, 1♂, 1J3♂)

of these food sources are not really preferred by the monkeys and occur throughout the home range, they do not significantly affect daily ranging pattern. However, some tertiary food sources may be important, particularly during the long dry season when fruits are scarce.

Leading females each tend to exploit different parts of the home range (core areas), except when a fruit excess occurs. This pattern is shown in tables VII and VIII. Only two females belonging to the part of the group followed in December and April were leading females. Both were accompanied by a juvenile and were leading a subgroup consisting mainly of a male and/or one or more females with or without offspring. During the observation time in December, which is a period of relative scarcity of preferred fruits, both leading females rarely joined subgroups and obviously exploited different parts of the group's range. In April, both females frequently joined subgroups and then followed roughly similar itineraries, while feeding on somewhat different food sources. This pattern was made possible by the excess of preferred fruit in this period of the year.

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Table VIII. Food choice and feeding time for a spider monkey subgroup during four consecutive days in April 1978. The food sources listed correspond with those mapped in figure 21; (I) stands for primary,(II) for secondary,and (III) for tertiary food sources.

Species	Food item	Food category	Feeding time (min.)
April 23			
1. Tetragastris altissima	fruit	I	9
2. Tetragastris panamensis	fruit	I	25
3. Tetragastris panamensis	fruit	I	39
4. Styrax cf. fanshawei	fruit	I	28
5. Cecropia sciadophylla	infructescence	II	14
6. Ecclinusa sp.	fruit	I	4
7. Cayaponia ophthalmica	fruit	II	2
8. Guettarda acreana	fruit	II	4
9. Sterculia excelsa	y. seeds	II	2
10. Cecropia sciadophylla	infructescence	II	1
11. Coussarea paniculata	fruit	II	1
12. Geissospermum sericeum	fruit (juice)	I	7
13. Rheedia macrophylla	fruit	II	7
14. Guarea grandifolia	fruit	I	9
15. Geissospermum sericeum	fruit (juice)	I	5
16. Indet. (liana)	y. leaves	III	4
17. Prieurella sp.	fruit	I	10
18. Termites	termites	III	4
19. Cecropia sciadophylla	infructescence	II	6
20. Philodendron acutatum	y. leaves	III	2

Weather: sunny; no rain
Observation time: 10.25-18.20 h
Day range size: 1,900 m
Total food species used: 15
Total food items used: 15
Total feeding time: 183 minutes (136 on primary, 37 on secondary and 10 on tertiary food sources)
Most important food species calculated in feeding time: Tetragastris panamensis (64 min.), *Styrax aff fanshawei* (28 min.), *Tetragastris altissima* (25 min.), *Cecropia sciadophylla* (21 min.)
Subgroup size and composition: 10.25-17.00 h - 5 (3♀♀, 1J3♂1I1)
after 17.00 h - 6 (1♂ joined subgroup)

Species	Food item	Food category	Feeding time (min.)
April 24			
1. Tetragastris altissima	fruit	I	69
2. Clusia scrobiculata	fruit	II	6
3. Tetragastris panamensis	fruit	I	2
4. Tetragastris panamensis	fruit	I	44
5. Guarea grandifolia	fruit	I	1
6. Mendoncia hoffmannseggiana	fruit	I	15
7. Guarea grandifolia	fruit	I	13
8. Celastraceae indet.	fruit	II	8
9. Cayaponia rigida	fruit	II	16
10. Guarea grandifolia	fruit	I	6
11. Guarea grandifolia	fruit	I	35

Habitat...

Table VIII (Continued)

Species	Food item	Food category	Feeding Time (min.)
April 24			
12. Guarea grandifolia	fruit	I	9
13. Guarea grandifolia	fruit	I	4
14. Moutabea guianensis	fruit	II	4
15. Strychnos tomentosa	fruit	II	3
16. Inga alba	bark	III	6
17. Strychnos tomentosa	fruit	II	6
18. Guarea grandifolia	fruit	I	4
19. Inga alba	bark	III	4
20. Guarea grandifolia	fruit	I	4
21. Spondias mombin	fruit	I	15
22. Guarea grandifolia	fruit	I	15

Weather: sunny; no rain
Observation time: 5.40-18.10 h
Day range size: 2,680 m
Total food species used: 11
Total food items used: 11
Total feeding time: 289 minutes (236 on primary, 43 on secondary and 10 on tertiary food sources)
Most important food species calculated in feeding time: Guarea grandifolia (91 min.), Tetragastris altissima (69 min.), Tetragastris panamensis (46 min.)
Subgroup size and composition: 5 (2♀♀, 1♂, 1J♂, 1Jl)
from 14.20-16.20 h · 3 (♀ + Il lost contact but joined subgroup again)

April 25			
1. Guarea grandifolia	fruit	I	7
2. Tetragastris altissima	fruit	I	16
3. Tetragastris panamensis	fruit	I	16
4. Ficus trigonata	figs	I	2
5. Clusia scrobiculata	fruit	II	3
6. Tetragastris panamensis	fruit	I	9
7. Guarea grandifolia	fruit	I	6
8. Tetragastris panamensis	fruit	I	2
9. Cecropia sciadophylla	infructescence	II	6
10. Styrax aff. tanshawei	fruit	I	14
11. Tetragastris panamensis	fruit	I	3
12. Tetragastris altissima	fruit	I	29
13. Pachira insignis	y. seeds	II	1
12. Tetragastris altissima	fruit	I	41
11. Tetragastris panamensis	fruit	I	4
14. Ficus pertusa	figs	I	9
15. Heteropsis jenmani	infructescence	II	6
16. Pachira insignis	flowers	II	2
17. Guarea grandifolia	fruit	I	12
18. Guarea grandifolia	fruit	I	12
19. Geissospermum sericeum	fruit (juice)	I	15
20. Guarea grandifolia	fruit	I	5
21. Inga alba	bark	III	1

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Table VIII (continued)

Species	Food item	Food category	Feeding Time (min.)
April 25			
22. Inga bourgoni	fruit	I	8
23. Moutabea guianensis	fruit	II	5
24. Spondias mombin	fruit	I	13
19. Geissospermun sericeum	fruit (juice)	I	8
17. Guarea grandifolia	fruit	I	2
20. Guarea grandifolia	fruit	I	4
25. Guarea grandifolia	fruit	I	4
26. Guarea grandifolia	fruit	I	1
27. Guarea grandifolia	fruit	I	3
12. Tetragastris altissima	fruit	I	95
28. Guarea grandifolia	fruit	I	3

Weather: sunny. heavy rain from 13.54-14.04, 14.20-14.35 and 18.05-18.25 h.
Observation time: 5.35-17.35 h
Day range size: 2,850 m
Total food species used: 15
Total food items used: 16
Total feeding time: 365 minutes (343 on primary, 21 on secondary and 1 on tertiary food sources)
Most important food species calculated in feeding time: Tetragastris altissima (181 min.), *Guarea grandifolia* (59 min.), *Tetragastris panamensis* (34 min.), *Geissospermum sericeum* (23 min.)
Subgroup size and composition: 5.35-8.00 h - 5 (2♀♀, 1♂ 1J3♂)
    8.00-17.30 h - 7 (1♀ + 1J2♀ joined subgroup)

Species	Food item	Food category	Feeding Time (min.)
April 26			
1. Guarea grandifolia	fruit	I	4
2. Cayaponia rigida	fruit	II	7
3. Inga edulis	pods checked only		
4. Virola surinamensis	fruit	I	25
5. Clusia grandiflora	fruit	II	2
6. Clusia grandiflora	fruit	II	1
7. Guarea grandifolia	fruit	I	1
8. Tetragastris panamensis	fruit	I	5
9. Spondias mombin	fruit	I	11
10. Tetragastris panamensis	fruit	I	6
11. Tetragastris panamensis	fruit	I	6
12. Tetragastris altissima	fruit	I	5
13. Guarea grandifolia	fruit	I	8
14. Bagassa guianensis	infructescence	I	7
15. Spondias mombin	fruit	I	12

Weather: rainy all day (from 6.05 h on)
Observation time: 5.45-9.10 h and 12.36-13.30 h
Total feeding time: 100 minutes (90 on primary, 10 on secondary and 0 on tertiary food sources)
Most important food species calculated in feeding time: Virola surinamensis (25 min.), *Spondias mombin* (23 min.), *Tetragastris panamensis* (17 min.), *Guarea grandifolia* (13 min.).
Subgroup size and composition: 5.45-9.10 h - 5 (2♀♀, 1♂ 1J3♂)
    12.36-13.30 h - 7 (1♀ 1J2♀ joined subgroup)

Habitat... 97

APRIL 23
APRIL 24
APRIL 25
APRIL 26

NORTH

* Sleeping tree
• Cat. I food plant used
○ Cat II or III food plant used

300
meter
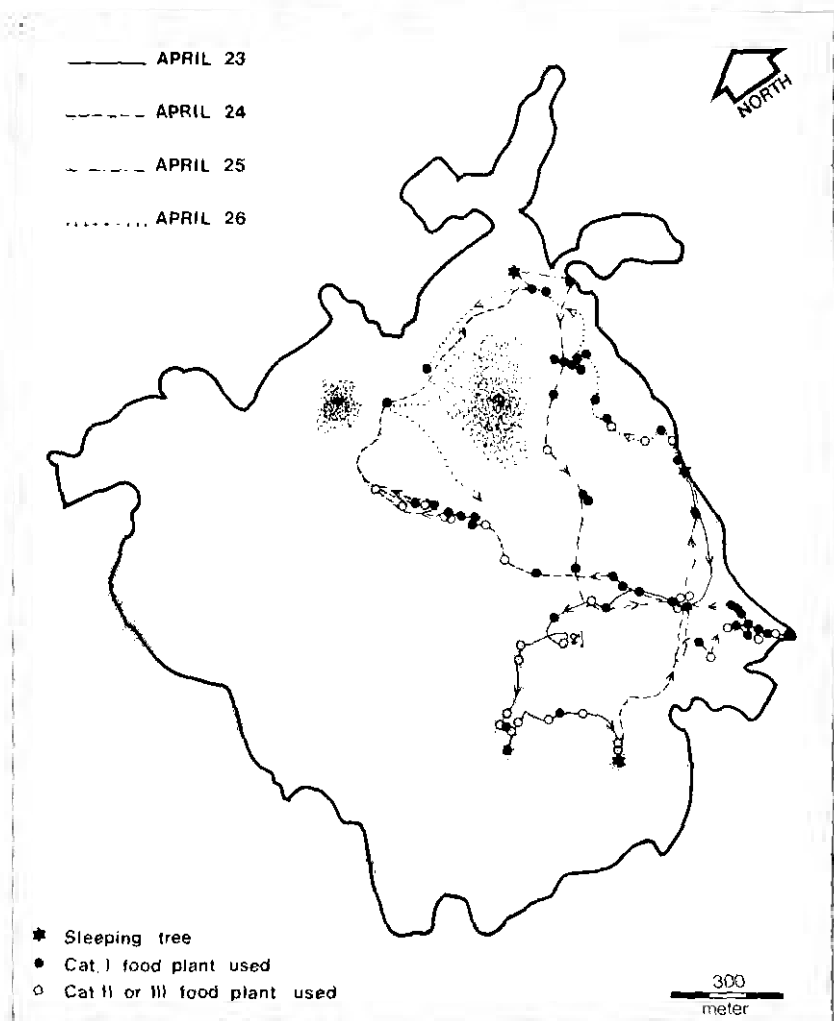
Figure 21 Routes followed by a spider monkey subgroup led by a certain female on four consecutive days in April 1978. The food sources used are indicated and correspond with those given in table VIII. In this figure, I only indicate whether a food source belongs to category I or to category II or III.

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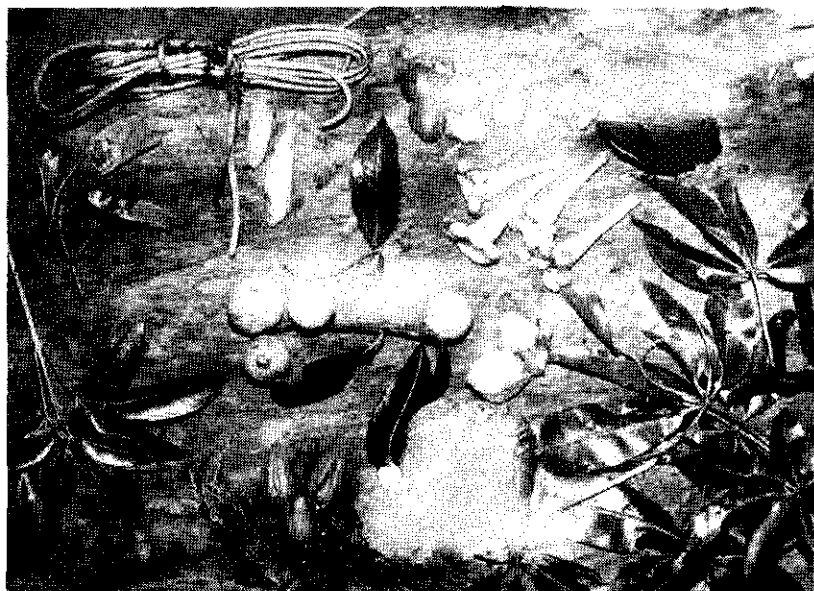
Figure 22 Food choice by a spider monkey subgroup on December 2 (A) and December 3, 1977 (B). The food species are listed in table VII. Note the great number of tertiary food sources (category III) in day-sample A, and the lack of nutritious, large-seeded fruits at this time of year.

Figure 23 Food choice of a spider monkey subgroup on April 24 (A) and April 25, 1978 (B). The Food species are listed in table VIII. Note the great number of primary food sources (category I) and the lack of tertiary food sources (category III) in both day-samples. The fruits are mainly of the nutritious, large-seeded type at this time of year.

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4.2.9. **Monthly variation in food choice.** In figure 24, monthly variation in food choice of *Ateles p. paniscus* is shown graphically. It should be emphasized that total observation time for each month of the year was kept roughly equal. The striking variation in samples per month is due to the fact that activity patterns of the spider monkeys varied greatly, and this is positively correlated with fruit supply and negatively with the amount of leaves and flowers eaten. In August, for example, a total of only 45 feeding records were collected. This was related to long resting periods and few feeding bouts concentrating on a small number of food plants. A total of only 24 food species was used during August, whereas in the period September-June between 41 and 61 food species were used each month.

Fruits account for a relatively low percentage (less than 60%) of total feeding records for each month during the first part of the long dry season (July, August and September). This period is characterized by a striking decline in the availability of edible fruits. In contrast, during the period January-July, fruits account for a high percentage of total feeding records, with a maximum in May and June (over 95%), and ripe fruits with a maximum in March and April (over 91%). Young seeds were eaten in all months except for July and October, but they contribute very low percentages for most months (fig. 24). However, relatively high percentages of seed predation are found in May (14.4%) and June (8.8%), around the peak of the long wet season. By ingesting many protein and fat-rich young seeds during this period, the monkeys seem to stock up on energy for the coming months of food scarcity. Surinam Bushnegroes and Amerindians have noted this, and prefer to hunt spider monkeys during these months when the animals are said to be at their fattest.

Flowers are eaten throughout the year, but account for only a very low percentage (0.5.-3.0%) of total feeding records during the long wet season (March-July). However, flowers contribute a considerable part of total feeding records during the long dry season (July-December), with a peak in September (28.1%) in the middle of the dry season. A minor peak is reached in February (6.3%) during the short dry season.

Flush leaves are also eaten throughout the year, but account for only a very low percentage (3.0% or less) of total feeding re-
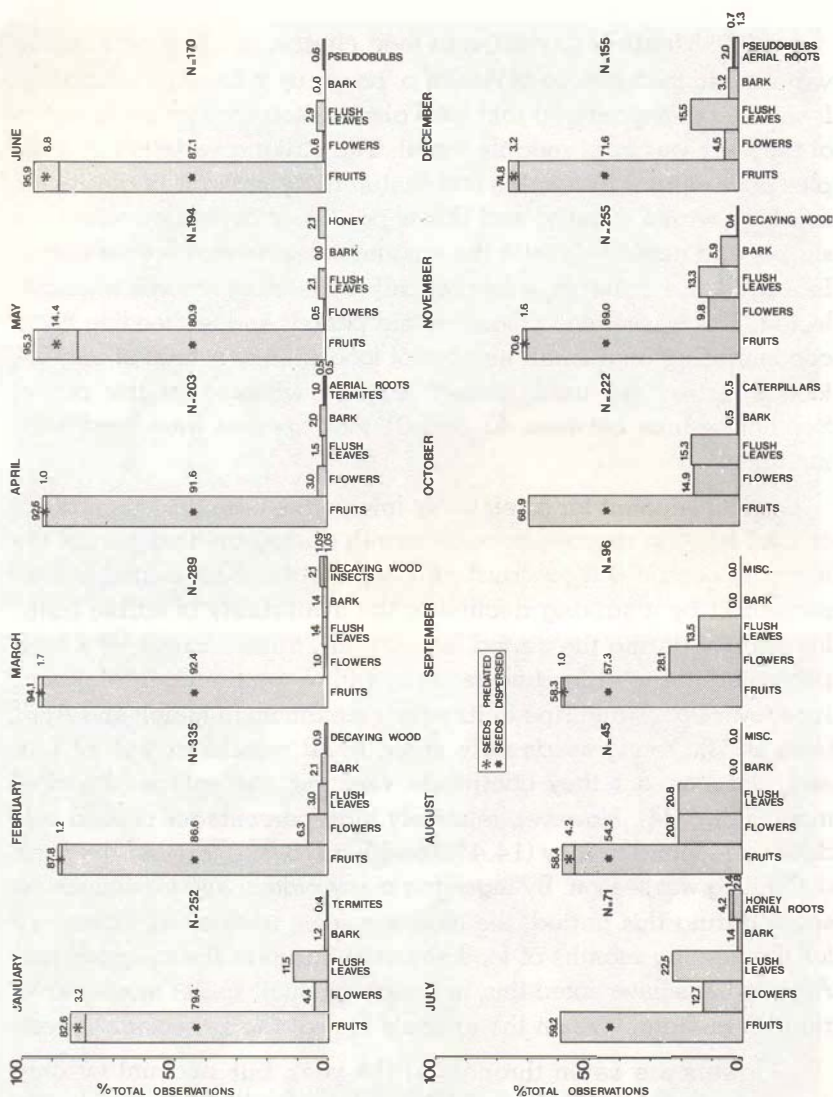
Figure 24 Monthly variation in food choice by a spider monkey group in the Voltzberg study area, expressed as percentage of the total number of feeding observations for each category.

cords during the months February-July. Flush leaves contribute relatively high percentages of total feeding records during the period July-February, that is from the start of the long dry season through the short wet season.

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Spider monkeys rarely fed on bark (0.0-2.1%). However, in November, feeding on bark accounted for 5.9%, and in December for 3.2% of total feeding records. With the exception of July, bark-eating was not observed during the period May-October. Decaying wood and rotten palm sheaths were eaten only in February, March and November, but at very low frequencies. In February and March, these account for about 1%, and in November for only 0.4% of total feeding records.

Aerial roots were eaten only in April, July and December, accounting for 0.5, 2.8 and 1.3% respectively of the total number of feeding records for each month.

Pseudobulbs were eaten only during June and December, accounting for 0.6 and 0.7% of total feeding records.

Honey was eaten only in May and July, accounting for 2.1 and 1.4% of total feeding records.

Insects appeared to be eaten only during part of the year, particularly in March. Termites were eaten during January, March and April, and accounted for 0.4, 0.35 and 0.5% respectively of total feeding records. Caterpillars were eaten only in March and October, accounting for 0.7 and 0.5%.

During the months July, August and September (the period of low fruit supply), the monkey compensates its diet with relatively high percentages of both flowers and flush leaves (fig. 25). When fruit abundance is highest (during the period March-July), both flowers and flush leaves play a minor role in the spider monkey's diet.

The monthly diet of *Ateles p. paniscus* in the Voltzberg study area is given in detail and illustrated in Figures 26-37. All food items used are depicted and ranked according to the total number of feeding records for each item. The plant part actually eaten is also mentioned. Seeds and stones are usually drawn as well. The drawings show monthly diversity of food choice, and the relative importance for each food item in a particular month is given by the number of feeding records and its location in the drawing: the more centrally located, the greater the importance.
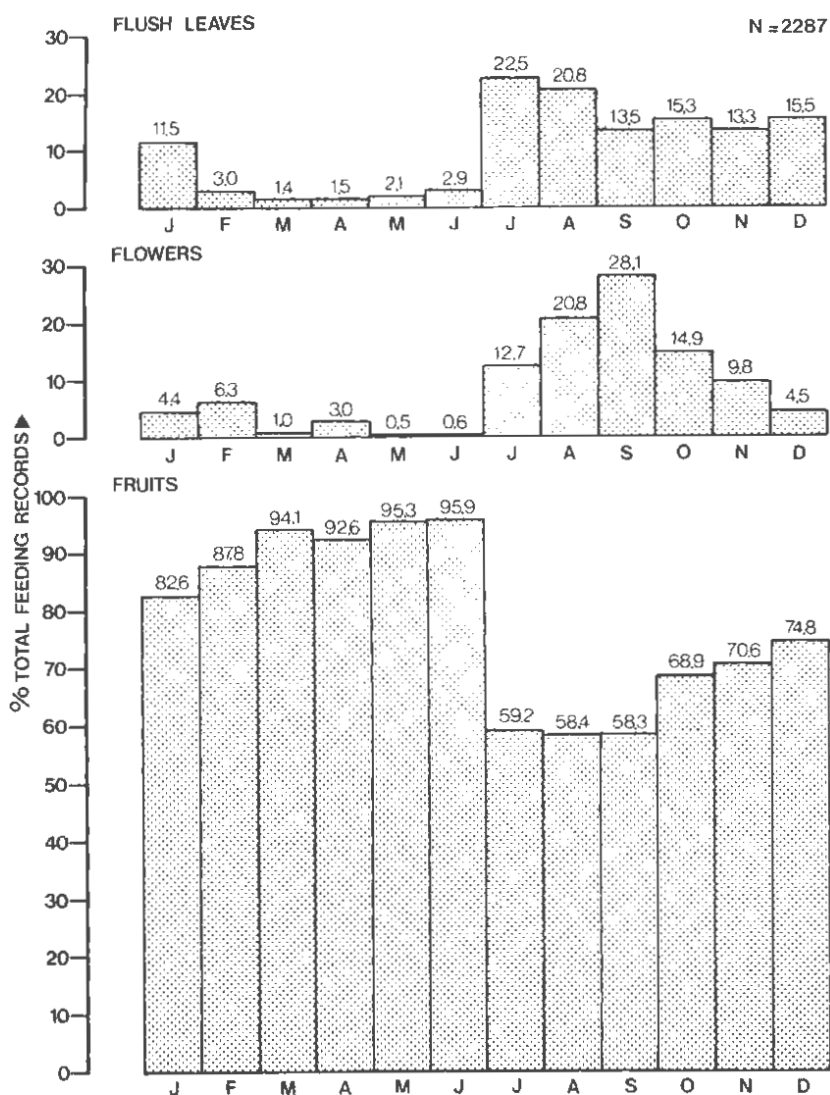
Figure 25 Comparison of monthly percentages of the total number of feeding records for flush leaves, flowers and fruits eaten by *Ateles p. paniscus* in the Voltzberg study area during the present study.

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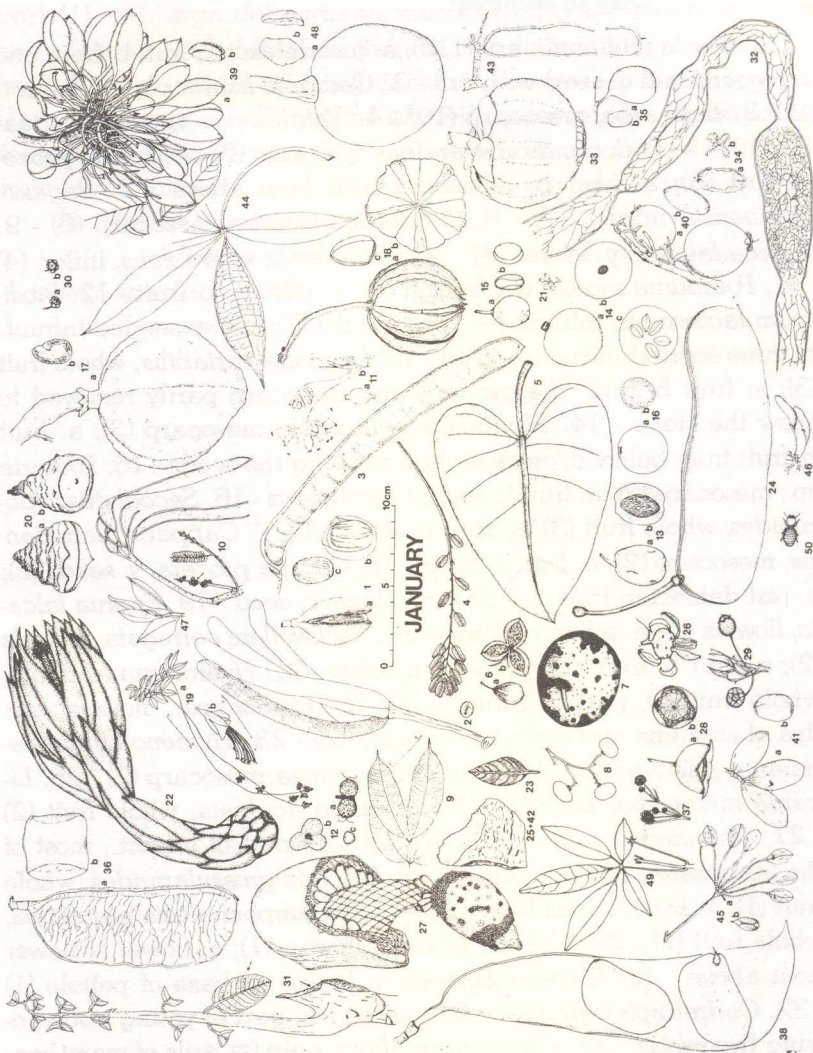
Figures 26-37 Monthly diet of *Ateles p. paniscus* in the Voltzberg study area. The species of food plant and other food items are ranked according to the total number of feeding records collected for each month of the year (in parentheses). In addition, the part actually eaten is mentioned. When necessary, an explanation of the corresponding drawing of a food item is added. The drawings show monthly diversity of food choice, whereas the relative importance of a food item in a particular month is given by its location in the drawing. The more centrally located, the greater the importance.

+ = fruiting less than once every year; y. = young; inflor. = inflorescence; infruct. = infructescence

Fig. 26. Diet in January.

1. *Virola melinonii,* aril (110); a. just dehiscing fruit b. fruit, one valve removed c. seed with aril - 2. *Cecropia sciadophylla,* infruct. (20) 3. *Inga alba,* mesocarp (10) - 4. *Vataireopsis speciosa,* y. leaves (10) - 5. *Philodendron scandens,* y. leaves (9) - 6. *Laetia procera,* aril (8); a. fruit b. dehiscing fruit from above - 7. *Bagassa guianensis,* infruct. (7) - 8. *Cordia lomatoloba,* mesocarp (6) - 9. *Eperua falcata,* y. leaves (4) - 10. *Piptadenia suaveolens,* inflor. (4) - 11. *Pourouma mollis,* whole fruit (4); a. infruct. b. fruit - 12. *Brosimum lactescens,* infruct. (= pseudofruit) (3); a. two-seeded infruct. b. three-seeded infruct. c. seed - 13. *Drypetes variabilis,* whole fruit (3); a. fruit b. fruit, the exocarp and mesocarp partly removed to show the stone - 14. *Moutabea guianensis,* mesocarp (3); a. fruit b. fruit from below c. cross section showing the seeds - 15. *Pouteria* sp., mesocarp (3); a. fruit b. seed, lateral views - 16. *Sacoglottis cydonioides,* whole fruit (3); a. fruit b. stone - 17. + *Capparis maroniensis,* mesocarp (2); a. fruit b. seed - 18. *Carapa procera,* y. seeds (2); a. just dehiscing fruit b. fruit from above c. seed - 19. *Eperua falcata,* flowers (2); a. inflor. b. flower - 20. *Eschweilera corrugata,* y. seeds (2); a. fruit b. fruit obliquely from below - 21. *Hyeronima laxiflora,* whole fruit (2); part of infruct. - 22. *Hylocereus* sp.a., flowers, esp. tips of stamens and style, and stigma (2) - 23. *Hymenolobium petraeum,* y. leaves (2) - 24. *Inga cinnamomea,* mesocarp (2) - 25. *Licania micrantha,* bark (2) - 26. *Pereskia aculeata,* whole fruit (2) - 27. *Philodendron acutatum,* infruct. (2); part of infruct., most of the fruits eaten by the monkey - 28. *Bellucia grossularioides,* whole fruit (1); a. fruit b. fruit from above - 29 *Campomanesia aromatica,* whole fruit (1) - 30. *Carapa procera,* flowers (1); a. flower b. flower from above - 31. *Carapa procera,* y. leaves + base of petiole (1) - 32. *Cedrelinga cateniformis,* y. seeds (1); part of young pod showing two seeds - 33. *Clusia grandiflora,* pulp (= arils of many seedlets) (1) - 34. *Combretum rotundifolium,* y. seeds (1); a. fruit b. fruit from above. 35. *Copaifera guianensis,* aril (1); a. fruit b. seed - 36. *Dioclea macrocarpa,* y. seeds (1); a. pod b. seed - 37. *Enterolobium schomburgkii,* inflor. (1) - 38. *Eperua rubiginosa,* y. seeds, esp. plumula (1); pod, one valve removed, showing the seeds - 39. *Ephedranthus guianensis,* mesocarp (1); a. infruct. b. seed - 40. *Eugenia macrocalyx,* whole fruit (1); a. infruct. b. seed - 41. *Gnetum urens,* perigonium or whole fruit (1); a. infruct. b. seed - 42. *Inga alba,*

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bark (1) - 43. *Inga thibaudiana*, mesocarp (1) - 44. *Jacaratia spinosa*, y. leaves - 45. *Malmea obovata*, whole fruit (1); a. part of infruct. b. seed - 46. *Norantea guianensis*, flowers, esp. the honeycups (1); part of inflor. 47. *Peperomia glabella*, y. leaves (1) - 48. *Strychnos tomentosa*, mesocarp (1); a. fruit b. seed, lateral views - 49. Tabebuia serratifolia, y. leaves (1) - 50. *Termites*, whole insects (1)

In total: 50 food items

45 food plant species   *252 feeding records*

1 insect species
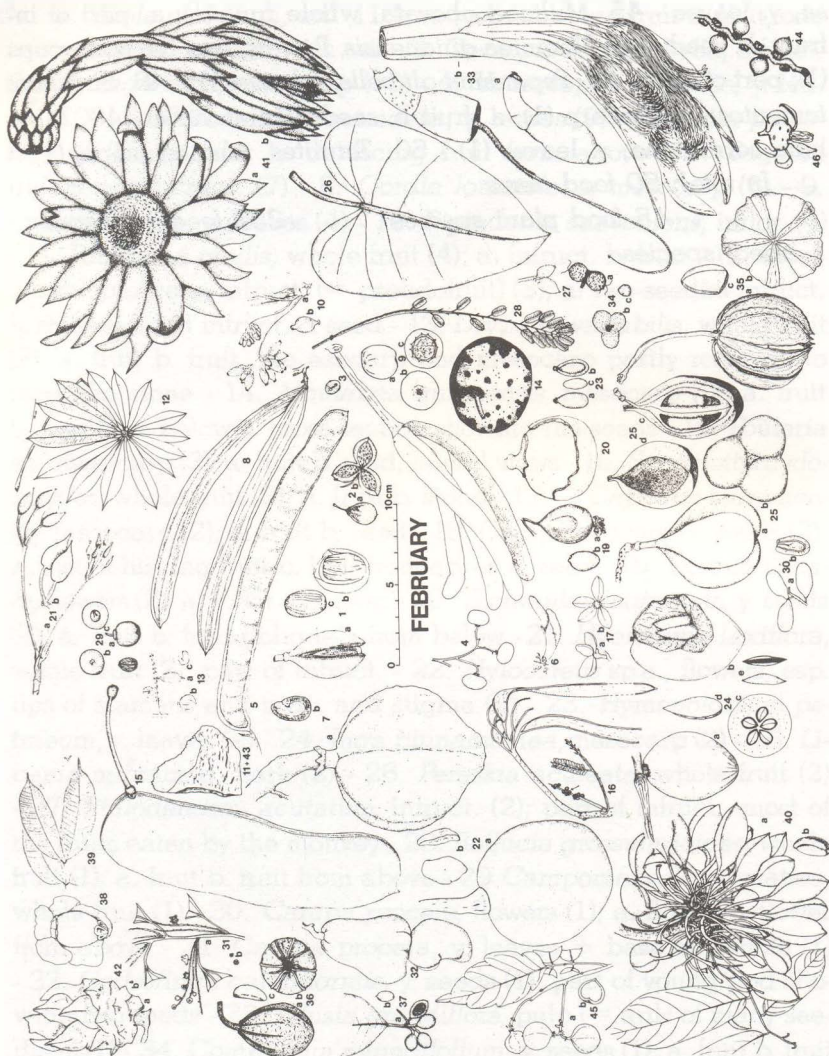
Fig. 27. Diet in February

1. *Virola melinonii*, aril (105); a just dehiscing fruit b. fruit, one valve removed c. seed with aril - 2. *Laetia procera* pulp (= arils of many seedlets) (32); a. fruit b. dehiscing fruit from above - 3. *Cecropia sciadophylla*, infruct. (25) - 4. *Cordia lomatoloba*, mesocarp (22) - 5. *Inga alba*, mesocarp (21) - 6. *Norantea guianensis*, flo-

wers,esp. the honeycups (15); part of inflor. - 7. +*Capparis maro-niensis*, mesocarp (12) a. fruit b. seed - 8. *Inga edulis*, mesocarp (9) - 9. *Ampelocera edentula*, mesocarp (8); a. fruit b. fruit from below c. cross section, showing one stone - 10. *Pourouma mollis*, whole fruit (7); a. infruct. b. fruit - 11. *Licania micrantha*, bark (6) - 12. *Cecropia sciadophylla*, y. leaves (5) - 13. *Paullinia acuminata*, aril (5); a. infruct. b. other type of fruit c. seed with aril - 14. *Bagassa guianensis*, infruct. (4) - 15. Inga cinnamomea, mesocarp (4) - 16. *Piptadenia suaveolens*, inflor. (4) - 17. *Quassia simarouba*, mesocarp (4); a. fruit b. fruit from above - 18. *Attalea Maripa*, decaying and rotten sheaths of long before shed leaves (3) - 19. *Cayaponia oph-thalmica*, mesocarp (3); a. fruit b. seed - 20. *Licania majuscula*, exocarp + mesocarp (3); fruit the outer layer partly scraped off by the monkey, showing the big stone - 21. *Pourouma minor*, whole fruit(3); a. young infruct. b. mature fruits - 22. *Strychnos tomentosa*, mesocarp (3); a. fruit b. seed, lateral views - 23. *Prieurella qua-drijuga*, aril (3); a. fruit b. longitudinal section c. seed - 24. *Ecclinusa* sp., y. seeds and mesocarp (2); a. fruit b. fruit partly opened by the monkey, showing some young seeds c. cross section d., e. seed, lateral views - 25. *Paullinia spicata*, aril (2); a. fruit b. fruit from above c. fruit, one valve removed d. valve from inside - 26. *Philodendron scandens*. y. leaves (2) - 27. *Pourouma sp., whole fruit (2); part of infruct.* - 28. *Vataireopsis speciosa*, y. leaves (2) - 29. *Vitex stahelii*, whole fruit or mesocarp only (2); a. fruit b. fruit from above c. fruit from below - 30. *Abuta grandifolia*, mesocarp (1); a. part of infruct. with two types of fruit b. stone - 31. *Alchorneopsis floribunda*, whole fruit (1); a. infruct. b. seed - 32. *Anacardium giganteum*, pseu-dofruit (= pedicel) (1) - 33 *Pachira insignis*, flowers + floral buds (1); a. floral bud b. flower - 34. *Brosimum lactescens*, infruct. (1); a. two-seeded b. three-seeded infruct. c. seed - 35. *Carapa proce-ra*, y. seeds (1); a. just dehiscing fruit b. fruit from above c. seed - 36. *Cheiloclinium hippocrateoides*, mesocarp (1); a. fruit b. fruit from below c. seed - 37. *Chrysophyllum auratum*, mesocarp (1); a. infruct. b. seed - 38. *Clusia scrobiculata*, pulp (= arils of many seed-lets) (1) - 39. *Eperua falcata*, y. leaves (1) - 40. *Ephedranthus guia-nensis*, mesocarp (1); a. infruct. b. seed - 41. *Hylocereus* sp. a., flowers, esp. tips of stamens and style, and stigma (1); a. flower from above b. flower, lateral view - 42. *Hylocereus* sp. b., whole fruit (1); a. fruit b. seed - 43. *Inga alba*, bark (1) - 44. *Oenocarpus bacaba*,

whole fruit (1); part of infruct. - 45. *Paullinia sphaerocarpa*,y. seeds + aril (1); a. infruct. b. valve from inside - 46. *Pereskia aculeata*, whole fruit (1)

In total: 46 food items   335 feeding records
                44 food plant species

Van Roosmalen
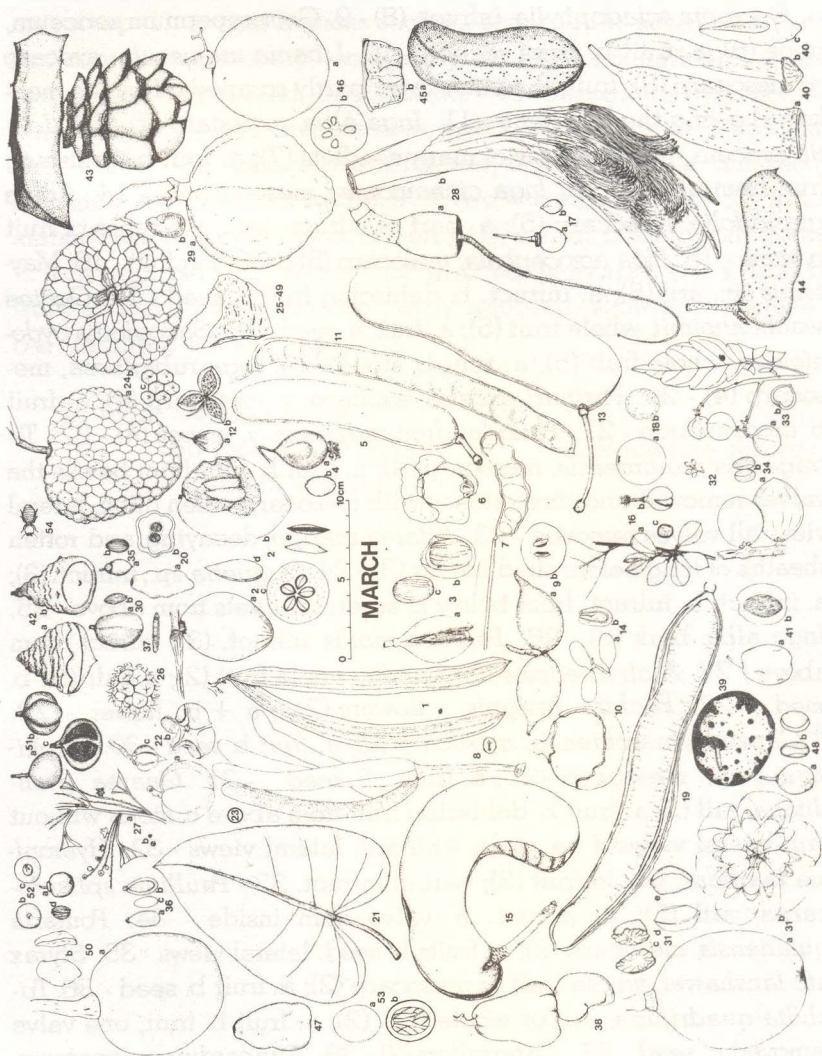
Fig. 28. Diet in March

1. *Inga edulis*, mesocarp (44) - 2. *Prieurella sp.*, mesocarp (38); a. fruit b. fruit partly opened by the monkey, showing some seeds c. cross section d., e. seed, lateral views - 3. *Virola melinonii*, aril (24); a. just dehiscing fruit b. fruit, one valve removed c. seed with aril - 4. *Cayaponia ophthalmica*, mesocarp (14); a. fruit b. seed - 5. *Inga bourgoni*, mesocarp (13) - 6. *Clusia scrobiculata*, pulp (=

arils of many seedlets) (10) - 7. *Inga leiocalycina*, mesocarp (9) - 8. *Cecropia sciadophylla*, infruct. (8) - 9. Geissospermum sericeum, juice (8); a. fruit b. cross section - 10. *Licania majuscula*, exocarp + mesocarp (8); fruit, the outer layer partly scraped off by the monkey, showing the big stone - 11. *Inga alba*, mesocarp (7) - 12. *Laetia procera*, pulp (= arils of many seedlets (7); a. fruit b. dehiscing fruit from above - 13. *Inga cinnamomea,* mesocarp (6) - 14. *Abuta grandifolia*, mesocarp (5); a. part of infruct. with two types of fruit b. stone - 15. *Inga acrocephala;* mesocarp (5) dehiscing fruit - 16. Maytenus sp., aril (5); a. infruct. b. dehiscing fruit c. seed - 17. *Ocotea wachenheimii,* whole fruit (5); a. fruit b. seed - 18. *Sacoglottis cydonioides*, whole fruit (5); a. fruit b. stone - 19. *Inga rubiginosa*, mesocarp (4) - 20. *Parinari excelsa*, exocarp + mesocarp (4); a. fruit b. cross section - 21. *Philodendron scandens,* y. leaves (4) - 22. *Tetragastris panamensis*, mesocarp (4); a. fruit b. fruit from below, the valves removed and three stones with mesocarp eaten out c. lateral view, all valves removed - 23. *Attalea maripa*, decaying and rotten sheaths of long before shed leaves (3) - 24. *Duguetia* sp., infruct.(3); a. infruct. b. infruct. from below c. several fruitlets from above - 25. *Inga alba*, bark (3) - 26. *Perebea mollis*, infruct. (3); infruct. from above - 27. *Alchorneopsis floribunda*, whole fruit (2); a. infruct. b. seed - 28. *Pachira insignis,* flowers (2) ; a + b. flower - 29. + *Capparis maroniensis, mesocarp (2); a. fruit b. seed - 30. Amphizoma* sp. mesocarp (2) ; a. fruit b. seed - 31. *Guarea grandifolia*, aril (2) a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d+e. stone with aril, lateral views - 32. *Hyeronima laxiflora*, whole fruit (2); part of infruct. 33 - *Paullinia sphaerocarpa*, aril (2); a. infruct. b. valve from inside - 34. *Pouteria guianensis*, mesocarp (2); a. fruits b. seed, lateral views - 35. *Styrax* aff. *fanshawei*, whole fruit or mesocarp (2); a. fruit b. seed - 36. *Trichilia quadrijuga*, aril or whole fruit (2); a. fruit b. fruit, one valve removed c. seed - 37. *Caterpillars*(2) - 38. *Anacardium giganteum*, pseudofruit (= pedicel) (1) - 39. *Bagassa guianensis*, infruct. (1) - 40. *Couratari guianensis*, y. seeds (1); a. fruit without operculum b. columella with operculum c. seed - 41. *Drypetes variabilis*, whole fruit (1); a. fruit b. fruit, the exocarp and mesocarp partly removed to show the stone - 42. *Eschweilera corrugata*, y. seeds (1); a. fruit b. fruit obliquely from below - 43. *Hylocereus*sp. a., whole fruit (1) - 44. *Inga* cf. *capitata*, mesocarp (1) - 45. *Tanaecium noctur-*

num, y. seeds (1); a. fruit b. seed - 46. *Parahancornia fasciculata* mesocarp (1); a. fruit b. cross section, showing the seeds - 47. *Parinari campestris*, exocarp + mesocarp (1) - 48. *Pouteria* sp., mesocarp (1); a. fruit b. seed, lateral views - 49. *Sacoglottis cydonioides*, bark (1) - 50. *Strychnos tomentosa*, mesocarp (1); a. fruit b. seed, lateral views. - 51. *Tetragastris altissima*, mesocarp (1); a. one-seeded fruit b. more-seeded fruit c. fruit, two valves removed - 52. *Vitex stahelii*, whole fruit or mesocarp only (1); a. fruit b. fruit from above c. fruit from below d. stone - 53. *Iriartea exorrhiza* (1); a. fruit b. fruit, exocarp and mesocarp partly removed, showing the stone - 54. *Termites*, whole insects (1).

In total: 54 food items

        50 food plant species   289 feeding records
        2 insect species

Fig. 29. Diet in April

1. *Guarea grandifolia*, aril (35); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views - 2. *Tetragastris panamensis*, mesocarp (19); a. fruit b. fruit from below, the valves removed and three stones with mesocarp eaten out c. lateral view, all valves removed - 3. *Tetragastris altissi-*

ma, mesocarp (14); a. one-seeded fruit b. more-seeded fruit c. fruit, two valves removed - 4. *Spondias mombin*, mesocarp (12); a. fruit b. stone - 5. *Inga bourgoni*, mesocarp (10) - 6. *Prieurella sp.*, mesocarp (8); a. fruit b. fruit, partly opened by the monkey, showing some seeds c+d. seed, lateral views e. cross section - 7. *Cecropia sciadophylla*, infruct. (7) - 8. *Geissospermum sericeum*, juice (7); a. fruit b. cross section - 9. *Inga edulis*, mesocarp (7) - 10. *Cayaponia rigida*, whole fruit (6); infruct. - 11. *Clusia scrobiculata*, pulp (= arils of many seedlets) (6) - 12. *Inga acrocephala*, mesocarp (5) - 13. *Helicostylis tomentosa*, infruct. (4); a. infruct from above b. infruct. obliquely from below - 14. *Inga alba*, bark (4) - 15. *Moutabea guianensis*, mesocarp (4); a. fruit b. fruit from below c. cross section showing the seeds - 16. *Protium neglectum*, mesocarp (4); a. more-seeded fruit b. one-seeded fruit - 17. *Cayaponia ophthalmica*, mesocarp (3); a. fruit b. seed - 18. *Pachira insignis*, flowers (2) - 19. *Clusia grandiflora* pulp (= arils of many seedlets) (2) - 20. *Coussarea paniculata*, whole fruit (2); infruct. - 21. *Ficus trigonata*, whole figs (2) - 22. *Inga leiocalycina*, mesocarp (2) - 23. *Laetia procera*, pulp (=arils of many seedlets) (2); a. fruit b. dehiscing fruit from above - 24. *Protium polybotryum*, mesocarp (2); part of infruct. - 25. *Strychnos tomentosa*, mesocarp (2); a. fruit b. seed, lateral views - 26. *Styrax aff. fanshawei*, whole fruit or mesocarp only (2); a. fruit b. seed - 27. *Trichilia martiana*, aril or whole fruit (2); a. infruct. b. seed - 28. *Virola surinamensis*, aril (2); a. part of infruct. with dehiscing fruits b. seed - 29. *Bagassa guianensis*, infruct. (1) - 30. *Bellucia grossularioides*, whole fruit (1); a. fruit b. fruit from above - 31. *Species c.* (Bignoniaceae), flowers (1) - 32. *Pachira insignis*, y. seeds (1); young fruit - 33. *Cheiloclinium cognatum*, (young) seeds (1); a. fruit b. seed - 34. *Cheiloclinium anomalum*, mesocarp (1); a. fruit b. fruit from below - 35. *Cynometra marginata*, y. leaves (1); a. leaf bud b. y. leaf - 36. *Drypetes variabilis*, whole fruit (1); a. fruit b. fruit, exocarp and mesocarp partly removed to show the stone - 37. *Duguetia sp.*, infruct. (1) a. infruct. b. several fruitlets from above - 38. *Ficus pertusa*, whole figs (1) - 39. *Guarea grandifolia*, flowers (1); a. part of inflor. with floral buds b. flower - 40. *Guettarda acreana*, whole fruit (1); a. infruct. b. seed - 41. *Hylocereus sp.* a., flowers, esp. tips of stamens and style, and stigma (1) - 42. *Inga alba*, mesocarp (1) - 43. *Inga stipularis*, mesocarp (1) - 44. *Licania densiflora*, exocarp + mesocarp (1) - 45. *Mendoncia hoff-*

mannseggiana, mesocarp (1); a. fruit b. fruit, the bracts removed
c. stone - 46. *Philodendron acutatum,* tips and epiderm of aerial
roots (1); part of aerial root - 47. *Philodendron acutatum,* y. leaves
(1) - 48. *Philodendron scandens,* y. leaves (1) - 49. Heteropsis jen-
mani, infruct. (1); part of infruct., several fruitlets eaten off - 50.
Platonia insignis, aril (1); a. fruit b. seed - 51. *Pouteria guianensis,*
mesocarp (1); a. fruits b. seed, lateral views - 52. *Rheedia macrophyl-
la,* aril (1); a. fruit b. cross section c. seed - 53. *Termites,* whole in-
sects (1)

In total: 53 food items
48 food plant species   *203 feeding records*
1 insect species

Fig. 30. Diet in May

1. *protium polybotryum*, mesocarp (24) — 2. *Tetragastris panamensis*, mesocarp (21); a. fruit b. fruit from below, the valves removed and three stones with mesocarp eaten out c. lateral view, all valves removed — 3 *Couratari stellata*, young seeds + base of columella (13); a. fruit b. seed c. columella + operculum — 4. *In-*

ga. cf. *capitata*, mesocarp (11) — 5. *Protium neglectum,* mesocarp
(11); a. more-seeded fruit b. one-seeded fruit–6. *Tetragastris altissi-
ma,* mesocarp (9); a. one-seeded fruit b. more seeded fruit c. fruit,
two valves removed — 7. *Guarea grandifolia,* aril (8); a. fruit b. de-
hiscing fruit from above c. stone without aril, lateral views d. stone
wich aril, lateral views — *Maytenus* sp., aril (8); a. infruct. b. dehis-
cing fruit c. seed — 9. *Clarisia racemosa,* whole fruit (6); a+b. two
types of fruit c. seed — 10. *Eschweilera poiteaui,* y. seeds + aril
(6); a. fruit opened, the seeds removed b. fruit, partly opened by
the monkey, showing one seed c. seed with aril — 11. *Dicranosty-
les guianensis,* mesocarp (5): a. infruct. b. one valve from inside c.
seed — 12. *Helicostylis tomentosa,* infruct. (5); a. infruct. from abo-
ve b. infruct. obliquely from below — 13. *Inga bourgoni,* mesocarp
(4) — 14. *Inga pezizifera,* mesocarp (4) — 15. *Maripa scandens,*
y. seeds (4); a. fruit b. seed — 16. *Sacoglottis cydonioides,* whole
fruit (4); a. fruit b. stone — 17. *Honey* (4) — 18. *Cheiloclinium po-
dostemmum,* mesocarp (3); a. fruit b. fruit from below c. cross sec-
tion, showing the seeds d. seed — 19. *Duguetia* sp., infruct. (3);
a. infruct. b. infruct. from below c. several fruitlets from above —
20. *Spondias mombin,* mesocarp (3); a. fruit b. stone — 21. *Virola
surinamensis,* aril (3); a. dehiscing fruits b. seed, the aril removed
— 22. *Prieurella* sp., mesocarp (2) a. fruit b. fruit, partly opened
by the monkey, showing some seeds c. cross section d+e. seed, la-
teral views — 23. *Eperua falcata,* y. seeds esp. the plumula (2); a.
fruit, one valve removed b. plumula — 24. *Hylocereus* sp. a, flower,
esp. tips of stamens and style, and stigma — 25. *Inga acrocephala,* me-
socarp (2); dehiscing pod — 26. *Monstera adansonii,* infruct. (2);
infruct., several fruits at the base eaten by the monkey — 27. *Mou-
tabea guianensis,* mesocarp (2); a. fruit b. fruit from below c. cross
section, showing the seeds — 28. *Oenocarpus bacaba,* whole fruit
(2); part of infruct. — 29. *Philodendron scandens,* y. leaves (2) —
30. *Styrax* aff. *fanshawei,* whole fruit or mesocarp (2); a. fruit b. seed
— 31. *Carapa procera,* y. seeds (1); a. dehiscing fruit b. y. seed c.
fruit from above — 32. *Cayaponia ophthalmica,* mesocarp (1); a.
fruit b. seed — 33. *Cayaponia rigida,* whole fruit (1); infruct. — 34.
Cheiloclinium cognatum, (young) seeds (1); a. fruit b. seed — 35.
Amphizoma sp, mesocarp (1); a. fruit b. seed — 36. *Dia-
lium guianense,* aril (1); part of infruct. — 37. *Dipteryx odorata,* y.
leaves (1) — 38. *Eschweilera corrugata,* y. seeds + aril (1); a. fruit

b. fruit obliquely from below — 39. *Euterpe oleracea*, whole fruit (1); a. part of infruct. b. stone — 40. *Ficus gomelleira*, whole fig (1); a. fig, lateral view b. fig, from below c. fig from above — 41. *Geissospermum sericeum*, juice (1); a. fruit b. cross section — 42. *Jacaratia spinosa*, whole fruit (1); a. fruit b. seed — 43. *Leonia glycycarpa*, mesocarp (1); a. fruit b. seed — 44. *Malmea obovata*, whole fruit (1); a. infruct. b. seed — 45. *Mendoncia hoffmannseg-giana*, mesocarp (1); a. fruit b. fruit, the bracts removed c. stone, lateral views — 46. *Parkia nitida*, inflor., esp. the stamens and styles of the fertile flowers at the top (1); a. inflor. b. sterile flowers c. ferti-le flowers d. leaflet — 47. *Rheedia macrophylla*, aril (1); a. fruit b. cross section showing the seeds c. seed — 48. *Iriartea exorrhiza* (1); a. fruit b. fruit, the exocarp and mesocarp partly removed, showing the big stone.

In total: 48 food items

       47 food plant species   194 feeding records
       1 honey
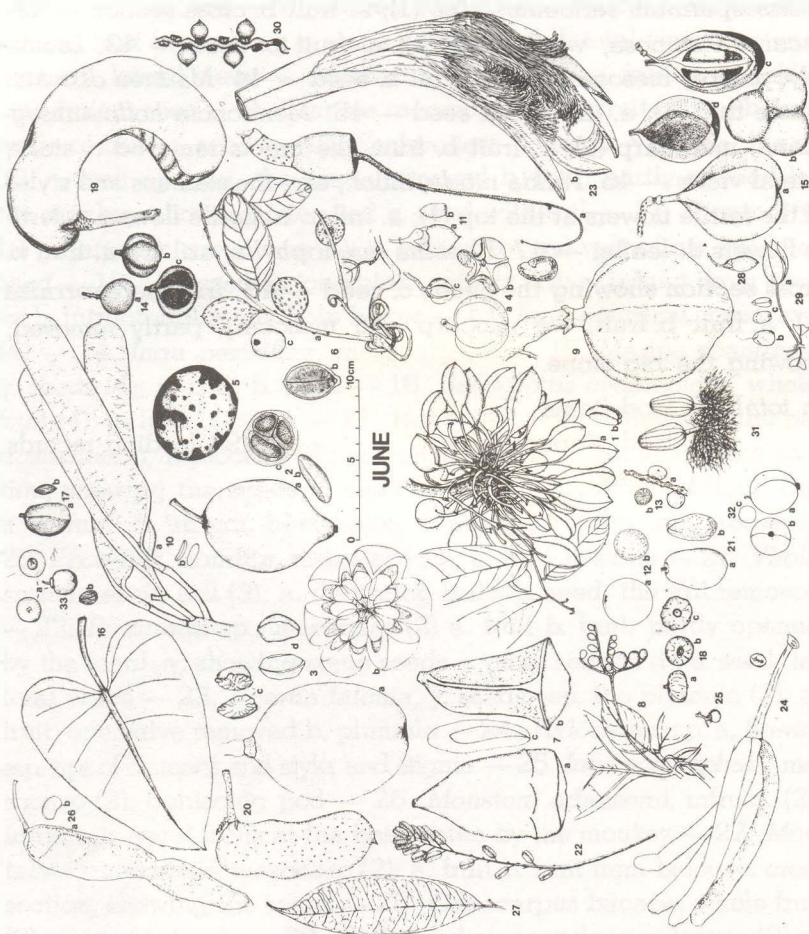
Fig. 31. Diet in June

1. *Ephedranthus guianensis*, mesocarp (29); a. infruct. b. seed
— 2. *Rheedia macrophylla*, aril (20); a. fruit b. seed c. cross section, showing the seeds — 3. *Guarea grandifolia*, aril (17); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views — 4. *Tetragastris panamensis*, mesocarp (11); a. fruit b. fruit from below, the valves removed and three

stones with mesocarp eaten out c. lateral view, all valves removed
— 5. *Bagassa guianensis*, infruct. (10) — 6. *Dicranostyles guianen-
sis*, mesocarp (10); a. infruct. b. valve from inside c. seed — 7. *Cou-
ratari stellata*, y. seeds + columella (9); a. fruit b. columella +
operculum c. seed — 8 *Guettarda acreana*,. whole fruit (7); infruct.
— 9. *Capparis maroniensis*, mesocarp (6); a. fruit b. seed — 10.
Dimorphandra pullei, desiccated mesocarp (5); a. part of infruct.
b. seed, lateral views — 11. *Maripa scandens*, y. seeds (5); a. fruit
b. seed — 12. *Sacoglottis cydonioides*, whole fruit (5); a. fruit b.
stone — 13. *Euterpe oleracea*, whole fruit (4); a. part of infruct. b.
stone — 14. *Tetragastris altissima*, mesocarp (4); a. one-seeded fruit
b. more-seeded fruit, two valves removed — 15. *Paullinia spicata*,
aril (3); a. fruit b. fruit from above c. fruit, one valve removed, sho-
wing the seeds d. valve from inside — 16. *Philodendron scandens*,
y. leaves (3) — 17. *Amphizoma sp.*, mesocarp (2); a. fruit
b. seed — 18. *Ficus gomelleira*, whole fig (2); a. fig, lateral view
b. fig. from below c. fruit from above - 19. *Inga acrocephala*, mesocarp
(2); dehiscing pod — 20. *Inga cf. capitata*, mesocarp (2) — 21. *Spon-
dias mombin*, mesocarp (2); a. fruit b. stone — 22. *Vataireopsis spe-
ciosa*, y. leaves (2) — 23. *Pachira insignis*, flowers, esp. the tips
of stamens and style (1); a+b. flower — 24. *Cecropia latiloba*
infruct. (1) — 25. *Cordia panicularis*, whole fruit (1) — 26. *Inga co-
riacea*, mesocarp (1); a. fruit b. seed — 27. *Maquira guianensis*,
y. leaves (1) — 28. *Maripa glabra*, y. seeds (1) — 29. *Mendoncia
hoffmanseggiana*, mesocarp (1); a. fruit b. fruit, the bracts removed
c. stone, lateral views — 30. *Oenocarpus bacaba*, whole fruit (1);
part of infruct. 31. — *Species a.* (Orchidaceae), pseudobulbs (1) —
32. *Trymatococcus paraensis*, whole fruit (1); a. fruit b. fruit from
above c. seed — 33. *Vitex stahelii*, whole fruit or mesocarp (1); a.
fruit, different views b. stone.

In total: 33 food items   170 feeding records
          33 food plant species
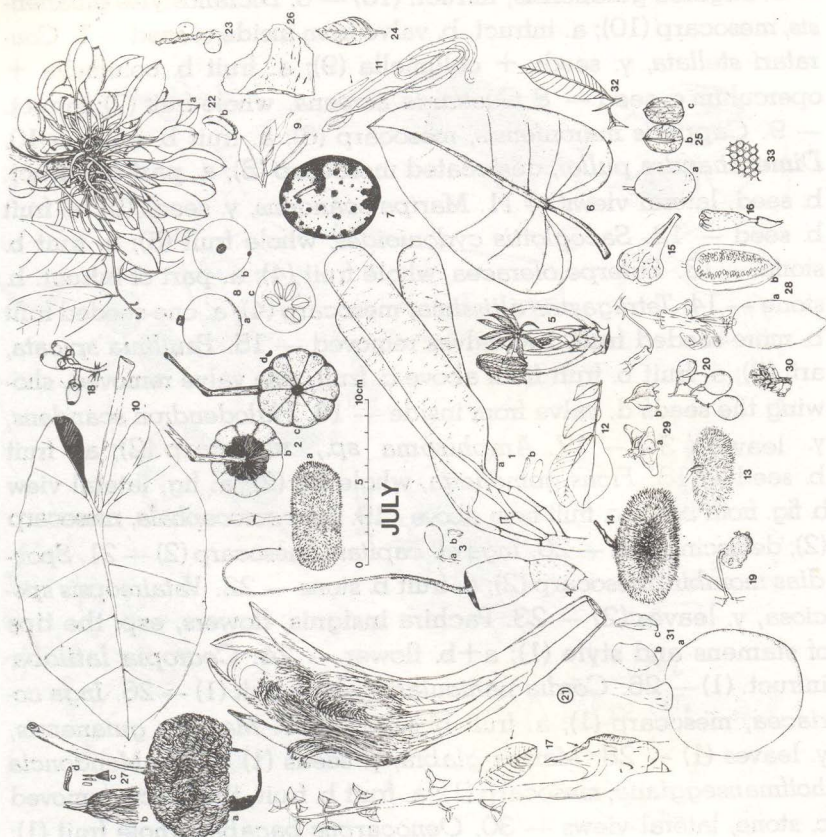
Fig. 32. Diet in July

1. *Dimorphandra pullei*, desiccated mesocarp (16); a. part of infruct. b. seed, lateral views — 2. *Apeiba echinata*, mesocarp (6); a. fruit b. fruit from below, the exocarp removed c. fruit from above, the exocarp removed d. seed — 3. *Minquartia guianensis*, whole fruit (6); a. fruit b. stone — 4. *Pachira insignis*, flowers, esp. tips of stamens and style (4); a+b. flower — 5. *Pachira in-signis* y. leaves (3); part of shoot with y. leaves — 6. *Philodendron scandens*, y. leaves (3) — 7. *Bagassa guianensis*, infruct. (2) — 8. *Moutabea guianensis*, mesocarp (2); a. fruit b. fruit from below c. cross section, showing the seeds — 9. *Peperomia glabella*, y. leaves (2); shoot with y. leaves — 10. *Philodendron acutatum*, y. lea-

ves (2) — 11. *Philodendron scandens,* tips of aerial roots (2) — 12. *Pithecellobium jupunba,* y. leaves (2) — 13. *Apeiba glabra,* mesocarp (1); fruit 14. *Apeiba schomburgkii,* mesocarp (1); fruit — 15. *Species a.* (Bignoniaceae), flowers (1); corolla — 16. *Species b.* (Bignoniaceae), flowers (1); flower — 17. *Carapa procera,* y. leaves + base of petiole (1) — 18. *Clusia* sp., floral buds (1); floral buds — 19. *Coussapoa asperifolia,* pistillate inflorescences (1); inflor. — 20. *Dialium guianense,* aril (1); part of infruct.— 21. *Dioscorea* cf *trifida* y. leaves (1); no drawing — 22. *Ephedranthus guianensis,* mesocarp (1); a. infruct. b. seed — 23. *Euterpe oleracea,* whole fruit (1); part of infruct. — 24. *Hymenolobium petraeum,* y. leaves (1); leaflet — 25. *Leretia cordata,* whole fruit (1); a. fruit b+c. stone, lateral views — 26. *Licania micrantha,* bark (1) — 27. *Parkia nitida,* inflor., esp. the stamens and styles of the fertile flowers at the top (1); a. inflor. b. sterile flowers c. fertile flowers d. leaflet - 28. *Passiflora glandulosa,* whole fruit (1); a. fruit b. longitudinal section, showing the seeds — 29. *Paullinia tricornis,* aril (1); a+b. two types of fruit — 30. *Philodendron scandens,* infruct. (1); part of infruct. — 31. *Strychnos tomentosa,* mesocarp (1); a. fruit b+c. seed, lateral views — 32. *Virola melinonii,* y. leaves (1) — 33. *Honey* (1).

In total: 33 food items

    29 food plant species   71 feeding records
     1 honey
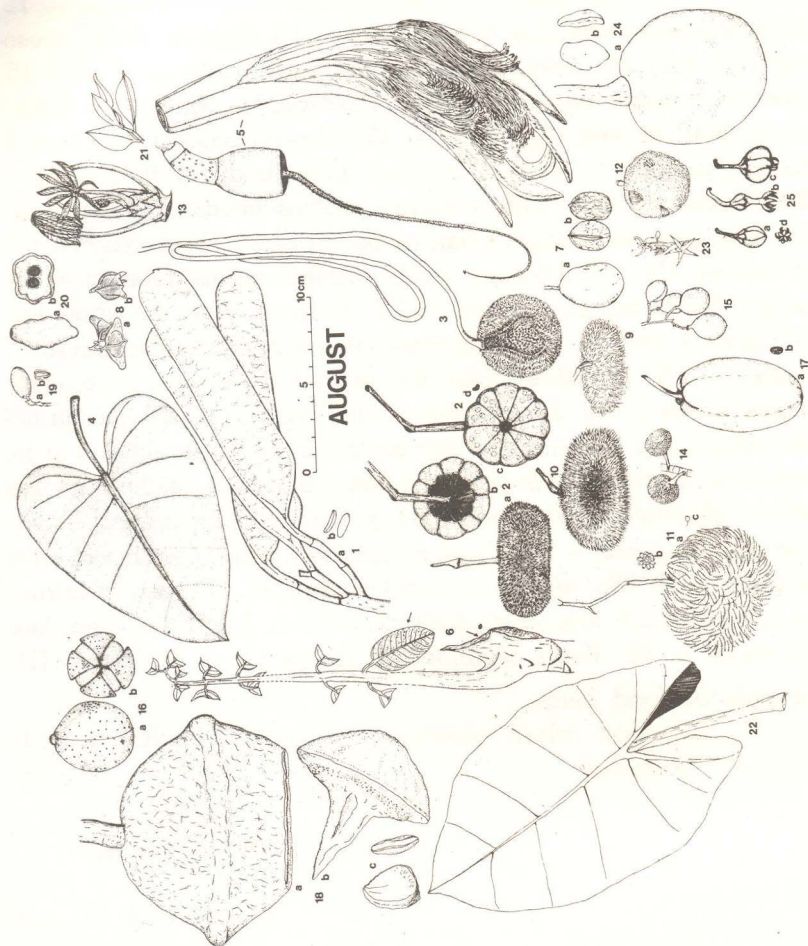
Fig. 33. Diet in August

1. *Dimorphandra pullei*, desiccated mesocarp (6); a. part of infruct. b. seed, lateral views — 2. *Apeiba echinata*, mesocarp (5); a. fruit b. fruit from below, the exocarp removed c. fruit from above, the exocarp removed d. seed — 3. *Parkia pendula*, inflor., esp. the tips of flowers (5); inflor., part of the flowers eaten by the monkey — 4. *Philodendron scandens*, y. leaves (4) — *Pachira insignis*, flowers (2) — 6. *Carapa procera*, y. leaves (2) — 7. *Leretia cordata*, whole fruit (2); a. fruit b. stone, lateral views — 8. *Paullinia tricornis*, aril (2); a+b. two types of fruit — 9. *Apeiba gla-*

bra, mesocarp (1); fruit — 10. *Apeiba schomburgkii*, mesocarp (1); fruit — 11. *Apeiba tibourbou*, mesocarp (1); a. fruit b. several seedlets with mesocarp c. seedlet — 12. *Bagassa guianensis*, y. infruct. (1) — 13. *Pachira insignis*, y leaves (1); shoot with young leaves — 14. *Coussapoa angustifolia*, infruct. (1) — 15. *Dialium guianense*, aril (1); part of infruct. 16. *Guarea kunthiana*, aril (1); a. fruit b. dehiscing fruit from above — 17. *Jacaratia spinosa*, whole fruit (1); a. fruit b. seed — 18. *Lecythis davisii*, mesocarp (1); opened fruit b. operculum c. seed, lateral views — 19. *Minquartia guianensis*, whole fruit (1); a. fruit b. stone — 20. *Parinari excelsa*, exocarp + mesocarp (1); a. fruit b. cross section — 21. *Peperomia glabella*, y. leaves (1) — 22. *Philodendron acutatum*, y. leaves (1) — 23. *Sterculia excelsa*, flowers (1); part of inflor. — 24. *Strychnos tomentosa*, mesocarp (1); a. fruit b. seed, lateral views — 25. *Symphonia globulifera*, flowers (1); a. floral bud b. flower, the petals removed c. flower d. stigma from above.

In total: 25 food items   45 feeding records
         24 food plant species
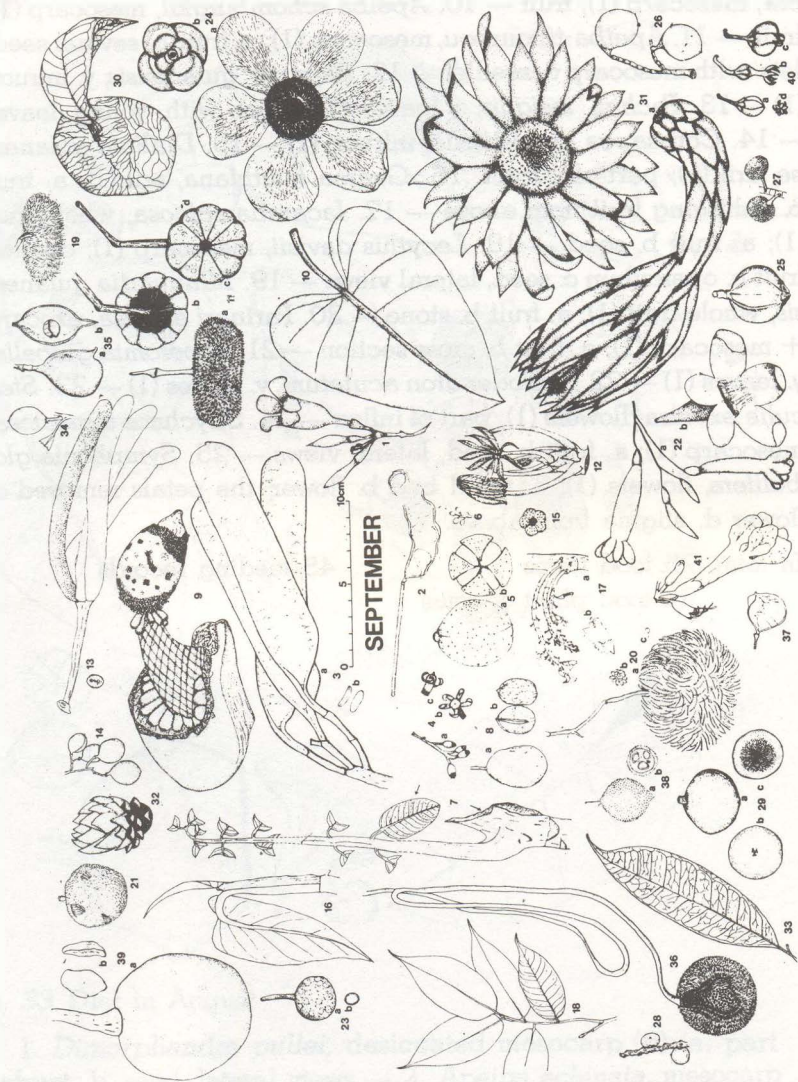
Fig. 34. Diet in September

1. *Adenocalymna* sp., flowers (11); part of inflor. — 2. *Inga leio-calycina*, mesocarp (9) — 3. **Dimorphandra pullei**, desiccated mesocarp (7); a. part of infruct. b. seed, lateral views — 4. *Guarea grandifolia*, flowers (7); a. part of inflor. with floral buds b. flower from above c. flower, lateral view — 5. *Guarea kunthiana*, aril (6);

a. fruit b. dehiscing fruit from above — 6. *Hyeronima laxiflora*, whole
fruit (5); part of infruct. — 7. *Carapa procera*, y. leav... + base of
petiole (3) — 8. *Leretia cordata*, whole fruit (3); a. fruit b. stone,
lateral views — 9. *Philodendron acutatum*, infruct. (3); infruct., most
of the fruits eaten by the monkey — 10. *Philodendron scandens*, y.
leaves (3) — 11. *Apeiba echinata*, mesocarp (2); a. fruit b. fruit from
below, the exocarp removed c. fruit from above, the exocarp remo-
ved d. seed — 12. *Pachira insignis*, y. leaves (2); shoot with y.
leaves — 13. *Cecropia sciadophylla*, infruct. (2) — 14. *Dialium
guianense*, aril (2); part of infruct. — 15. *Guazuma ulmifolia*, who-
le fruit or mesocarp (2); fruit from above — 16. *Heteropsis jenma-
nii*, tips of shoots + y. leaves (2); shoot with y. leaves — 17.
Platymiscium ulei, flowers (2); a. inflor. b. flower — 18. *Pterocarpus
officinalis*, y. leaves (2); y. leaf — 19. *Apeiba glabra*, mesocarp (1);
fruit — 20. *Apeiba tibourbou*, mesocarp (1); a. fruit b. several seeds
with some mesocarp c. seed — 21. *Bagassa guianensis*, y. infruct.
(1) — 22. *Arrabidaea corallina*, flowers (1); a. part of y. inflor. b.
opened corolla, obliquely from above — 23. *Brosimum parinarioi-
des*, infruct. (= pseudofruit) (1); a. infruct. b. seed — 24. *Clusia
platystigma*, male flowers, esp. central body of staminodes (1); a.
flower from above, showing the central body of staminodes b. flo-
wer from below, the petals removed, showing bracteola and sepals
— 25. *Clusia purpurea*, pulp (= many seedlets with aril) (1); fruit
— 26. *Copaifera epunctata*, aril (1); infruct. — 27. *Coussapoa an-
gustifolia*, infruct. (1) — 28. *Euterpe oleracea*, whole fruit (1); part
of infruct. — 29. *Ficus insipida*, whole fig (1); a. fig b. fig from abo-
ve c. cross section 30. *Helicostylis pedunculata*, infruct. (1); infruct.,
one leaf attached — 31. *Hylocereus* sp. a., flowers, esp. tips of sta-
mens and style, and stigma (1); a. flower b. flower from above —
32. *Hylocereus* sp. b., flowers, esp. the tips (1); flower, the tip eaten
by the monkey — 33. *Maquira guianensis*, y. leaves (1) — 34. *Mi-
cropholis guyanensis*, mesocarp — 35. *Ormosia paraënsis*, y. seeds
(1); a. fruit b. fruit, one valve removed, showing the mimetic seed
— 36. *Parkia pendula*, inflor. esp. the tips of flowers (1); inflor. with
part of peduncle, part of the flowers eaten by the monkey — 37.
Peltogyne venosa, aril (1); fruit — 38. . *Rheedia benthamiana*, aril
(1); a. fruit b. cross section showing the seeds — 39. *Strychnos to-
mentosa*, mesocarp (1); a. fruit b. seed, lateral views — 40. *Sympho-
nia globulifera*, flowers (1); a. floral bud b. flower, the petals removed

c. flower d. stigma from above — 41. *Tabebuia serratifolia*, flowers (1); part of inflor., the corolla of one flower eaten by the monkey.

In total 41 food items   96 feeding records
          41 food plant species

Fig. 35. Diet in October

1. *Ecclinusa guianensis*, mesocarp (71); a. fruit b. cross section, showing the seeds — 2. *Dimorphandra pullei*, desiccated mesocarp (24); a. part of infruct. b. seed, lateral views — 3.. *Achrouteria pomifera*, mesocarp (17); a. fruit b. fruit from below c. seed, lateral views d. cross section, showing the seeds — 4. *Guarea gran-*

difolia, flowers (11); a. part of inflor. with floral buds b. flower from above c. flower, lateral view — 5. *Philodendron scandens*, y. leaves (10) — 6. *Arrabidaea corallina*, flowers (9); a. part of y. inflor. b. opened corolla, obliquely from above — 7. *Abuta grandifolia*, mesocarp (7); a. part of infruct. with two types of fruit b. stone — 8. *Hylocereus sp.* a., flowers, esp. tips of stamens and style, and stigma (5) — 9. *Pterocarpus officinalis*, y. leaves (5); y. leaf — 10. *Bagassa guianensis*, y. infruct. (4) — 11. *Helicostylis pedunculata*, infruct. (4); infruct., one leaf attached — 12. *Vataireopsis speciosa*, y. leaves (4) — 13. *Carapa procera*, y. leaves + base of petiole (3) — 14. *Adenocalymna sp.*, flowers (2) — 15. Anomoctenium granulosum y. leaves (2); no drawing — 16. *Pachira insignis*, y. leaves (2); shoot with y. leaves — 17. Dipteryx odorata,y leaves (2); y. leaf- 18. *Ephedranthus guianensis*, mesocarp (2); a. infruct. b. seed — 19. *Hylocereus s.p.* b., flower, esp. the tip (2); flower, the tip eaten by the monkey — 20. *Parkia nitida*, mesocarp (2); infruct., few fruits left — 21. *Strychnos tomentosa*, mesocarp (2); a. fruit b. seed, lateral views — 22. *Virola melinonii*, aril (2); a. dehiscing fruit b. fruit, one valve removed, showing the seed with lacerate aril c. seed — 23. *Ampelocera edentula*, y. leaves (1); y. leaf — 24. *Apeiba echinata*, flowers (1); a. floral bud b. flower c. flower, the sepals and petals removed — 25. *Apeiba glabra*, mesocarp (1); fruit — 26. *Bellucia grossularioides*, whole fruit (1); a. fruit b. fruit from above — 27. *Anomoctenium granulosum*, flowers, esp. the corolla (1) — 28. *Brosimum lactescens*, infruct. (= pseudofruit) (1); a. two-seeded infruct. b. three - seeded infruct. c. seed — 29. *Carapa procera*, flowers (1); a. flower b. flower from above — 30. *Clarisia racemosa*, whole fruit (1); a+b. two types of fruit c. seed — 31. *Paullinia sp.*, whole fruit (1); infruct. — 32. *Paullinia sp.*, y. leaves (1); no drawing — 33. *Fagara sp.*, y. leaves (1); y. leaf — 34. *Ficus nymphaeifolia*, whole fig (1); a. figs and leaves, strongly reduced b. fig. — 35. *Goupia glabra*, whole fruit (1); infruct. — 36. *Guarea grandifolia*, aril (1); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views — 37. *Guatteria chysopetala*, whole fruit (1); infruct. — 38. *Gustavia hexapetala*, mesocarp + funicle (1); a. fruit from below b. seed, lateral views — 39. *Not identified species* (Loranthaceae), y. leaves (1) — 40. *Moutabea guianensis*, mesocarp (1); a. fruit b. fruit from below c. cross section, showing the seeds — 41. *Parinari excelsa*, exocarp + mesocarp (1); a. fruit

b. cross section — 42. *Philodendron acutatum*, y. leaves (1) — 43. *Quassia simarouba*, bark (1) — 44. *Tabebuia serratifolia*, flowers (1); part of inflor., the corolla of one flower eaten by monkey — 45. *Tabebuia serratifolia*, y. leaves (1); y. leaf — 46. *Unonopsis glaucopetala*, whole fruit (1); a. fruit b. seed, lateral views — 47. *Vitex stahelii*, whole fruit or mesocarp only (1); a. fruit b. fruit from above c. fruit from below d. stone — 48. *Caterpillars*, whole insects (1)

In total 48 food items

    43 food plant species   222 feeding records

     1 insect species

Fig. 36. Diet in November

1. *Achrouteria pomifera*, mesocarp (31); a. fruit b. fruit from be-low c. cross section, showing the seeds d. seed, lateral views — 2. *Guatteria chrysopetala*, whole fruit (18); infruct. — 3. *Brosimum lactescens*, infruct. (11); a. two-seeded infruct. b. three-seeded infruct. c. seed — 4. *Coussapoa latifolia*, infruct. (11); a. twig infruct., strongly reduced b. infruct. — 5. *Ceiba pentandra*, y. leaves (10); y. leaf, the apical part of the leaflets eaten — 6. *Philodendron acutatum*,

infruct. (10); part of infruct., most of the fruits eaten by the monkey — 7. *Bagassa guianensis*, infruct. (9) — 8. *Vataireopsis speciosa*, y. leaves (9) — 9. *Ficus gardneriana*, whole fig (8); a. fig b. from above — 10. *Ampelocera edentula*, flowers (7); part of inflor. — 11. *Dimorphandra pullei*, desiccated mesocarp (7); a. part of infruct. b. seed, lateral views — 12. *Guarea grandifolia*, aril (7); a. fruit b. dehiscing fruit from above c. stone without aril, lateral views d. stone with aril, lateral views — 13. *Bellucia grossularioides*, whole fruit (6); a. fruit b. fruit from above — 14. *Brosimum parinarioides*, infruct. (6); a. y. infruct. b. mature infruct. c. seed — 15. *Licania micrantha*, bark (6) — 16. *Cordia sagotii*, whole fruit (5); a. fruit b. fruit from below c. stone — 17. *Ecclinusa guianensis*, mesocarp (5); a. fruit b. cross section, showing the seeds c. seed — 18. *Carapa procera*, flowers (4); a. flower b. flower from above — 19. *Couepia caryophylloides*, exocarp + mesocarp (4); a. fruit b. stone — 20. *Peperomia glabella*, y. leaves (4) — 21. *Unonopsis glaucopetala*, whole fruit (4); a. infruct. b. seed, lateral views — 22. *Virola melinonii*, aril (4); a. just dehiscing fruit b. fruit, one valve removed c. seed with aril — 23. *Cecropia sciadophylla*, infruct. (3) — 24. *Ceiba pentandra*, floral buds + flowers (3); inflor. — 25. *Clarisia racemosa*, whole fruit (3); a+b. two types of fruit c. seed — 26. *Gnetum urens*, perigonium or whole fruit (3); a. infruct. b. seed — 27. *Apeiba echinata*, flowers (2); a. floral bud b. flower c. flower, the sepals and petals removed — 28. *Bagassa guianensis*, y. infruct. (2) — 29. *Anomoctenium granulosum*, y. leaves (2); no drawing — 30. *Anomoctenium granulosum*, y. seeds (2); a. fruit b. suture c. fruit, one valve removed, showing the seeds d. seed — 31. *Carapa procera*, y leaves + base of petiole (2); leaf — 32. *Ceiba pentandra*, exocarp of y. fruits (2); a. y. fruit b. seed — 33. *Ficus broadwayi*, whole fig (2); a. fig b. fig from above c. cross section — 34. *Gustavia hexapetala*, mesocarp + funicle (2); a. fruit from below b. seed, lateral views — 35. *Inga alba*, bark (2) — 36. *Pereskia aculeata*, flowers (2) — 37. *Pterocarpus officinalis*, y. leaves (2); leaf — 38. *Talisia squarrosa*, mecocarp (2); a. infruct., one fruit eaten out by the monkey b. seed — 39. *Trichilia surinamensis*, whole fruit (2); a. fruit b. fruit, two valves removed c. seed — 40. *Abuta grandifolia*, mesocarp (1); a. part of infruct. with two types of fruit b. stone — 41. *Ampelocera edentula*, y. leaves (1) — 42. *Apeiba glabra*, mesocarp (1); fruit — 43. *Attalea maripa*, decaying and rotten sheaths (1) — 44. *Xyloph-*

ragma seemannianum, flowers (1) — 45. Cedrela odorata, y. seeds + columella (1); a. y. fruit b. mature fruit c. seed — 46. Coussapoa angustifolia, infruct. (1) — 47. Dimorphandra pullei, bark (1) — 48. Stizophyllum inaequilaterum, flowers (1) — 49. Eperua falcata, flowers (1) — 50. Euterpe precatoria, whole fruit (1); a. fruit from below b. stone — 51. Zanthoxylum rhoifolium. (1); leaf — 52. Ficus malacocarpa, whole fig (1); a. infruct. b. fig from above — 53. Ficus trigona, whole fig (1); a. twig infruct., strongly reduced b. infruct. c. fig. from above — 54. Guarea grandifolia, flowers (1); a. part of inflor. b. flower from above c. flower, lateral view — 55. Hyeronima laxiflora, bark (1) — 56. Inga leiocalycina, bark (1) — 57. Licania majuscula, bark (1) — 58. Licania micrantha, y. leaves (1) — 59. Licaria canella, y. leaves (1) — 60. Nectandra kunthiana, bark (1) — 61. Norantea guianensis, flowers, esp. the honeycups (1); part of inflor. 62. Operculina hamiltoni, y. seeds (1); a. floral bud b. flower from above c. seed — 63. Parkia nitida, mesocarp (1); infruct., two fruits left — 64. Philodendron scandens, y. leaves (1) — 65. Pithecellobium jupunba, bark (1) — 66. Qualea dinizii, flowers (1); flower — 67. Sacoglottis cydonioides, bark (1) — 68. Tabebuia capitata flowers (1); part of inflor. — 69. Trymatococcus oligandrus, whole fruit (1); a. fruit b. fruit from above — 70. Vitex stahelii, whole fruir or mesocarp only (1); a. fruit b. fruit from above. c. fruit from below d. stone.

In total 70 food items   255 feeding records
        45 food plant species

Fig. 37. Diet in December

1. *Bagassa guianensis*, infruct. (20) — 2. *Clarisia racemosa*, whole fruit (14); a+b. two types of fruit c. seed — 3. *Guatteria chrysopetala*, whole fruit (13); infruct. — 4. *Achrouteria pomifera*, mesocarp (11); a. fruit b. from below c. cross section, showing the seeds d. seed, lateral views — 5. *Vataireopsis speciosa*, y. leaves (9) — 6.

Vitex stahelii, whole fruit or mesocarp only (8); a. fruit b. fruit from above c. fruit from below d. stone — 7. *Brosimum parinarioides*, infruct. (7); a. y. infruct. b. mature infruct. c. seed — 8. *Inga alba*, mesocarp (6); fruit — 9. *Bellucia grossulariodes*, whole fruit (5); a. fruit b. fruit from above — 10. *Xylophragma seemannianum*, flowers (4); part of inflor. — 11. *Ceiba pentandra*, y. leaves, esp. the apical part of the leaflets (4); leaf — 12. *Dimorphandra pullei* desiccated mesocarp (4); a. part of infruct. b. seed, lateral views — 13. *Cecropia sciadophylla*, infruct. (3) — 14. *Ceiba pentandra*, exocarp of y. fruits (3); a. y. fruit b. seed — 15. *Trichilia surinamensis*, whole fruit (3); a. part of infruct. b. dehiscing fruit from above — 16. *Ampelocera edentula*, y. leaves (2) — 17. *Cedrela odorata*, y. seeds + columella (2); a. y. fruit b. mature fruit c. seed — 18. *Cordia sagotii*, whole fruit (2); a. fruit b. fruit from below c. stone — 19. *Coussapoa latifolia*, infruct. (2); a. twig with infruct., strongly reduced b. infruct. — 20. *Philodendron acutatum*, aerial roots esp. the tips (2); part of aerial root, — 21. *Philodendron acutatum*, infruct. (2); infruct., part of the fruits eaten by the monkey. — 22. *Philodendron acutatum*, y. leaves (2) — 23. *Sacoglottis cydonioides*, bark (2) — 24. *Unonopsis glaucopetala*, whole fruit (2); a. infruct. b. seed, lateral views — 25. *Apeiba echinata*, flowers (1); a. floral bud b. flower c. flower, the sepals and petals removed — 26 *Anomoctenium granulosum*, y. leaves (1); no drawing — 27. *Couratari stellata*, bark (1) — 28. *Coussapoa asperifolia*, infruct. (1) — 29. *Eschweilera congestiflora*, y. seeds + aril (1); a. fruit b. fruit, the operculum removed c. seed — 30. *Ficus guianensis*, whole fig (1); with infruct. — 31. *Ficus citrifolia*, whole fig (1); infruct. — 32. *Not identified species* (Gesneriaceae), y. leaves (1) — 33. *Guarea grandifolia*, aril (1); a. fruit b. dehiscing fruit from above, showing the stones c. stone without aril, lateral views d. stone with aril, lateral views — 34. *Hillia illustris*, flowers, esp. the corolla (1); corolla — 35. *Hylocereus* sp. a., flowers, esp. the tips of stamens and style, and stigma (1); a. flower from above b. flower just before opening — 36. *Inga alba*, bark (1) — 37. *Inga leiocalycina*, bark (1) — 38. *Vantanea parviflora*, exocarp + mesocarp (1); a. fruit b. stone — 39. *Licania majuscula*, exocarp + mesocarp (1); fruit, the exocarp and mesocarp partly scraped off the monkey — 40. *Licaria canella*, y. leaves (1) — 41. *Maquira guianensis*, y. leaves (1) — 42. *Species b.* (Orchidaceae), pseudobulbs (1) — 43. *Paullinia sphaerocarpa*, y. seeds (1); a. in-

fruct. b. valve from inside — 44. *Peperomia glabella*, y. leaves (1) — 45. *Pereskia aculeata*, flowers (1) — 46. *Philodendron scandens* y. leaves (1) — 47. *Pouteria* sp., y. seeds (1); a. y. fruit b. cross section c. y. seed — 48. *Tabebuia serratifolia* y. leaves (1); y. leaf.

In total 48 food items   155 feeding records
          45 food plant species

4.2.10. *Monthly variation in food supply.* Phenological data for many trees and lianes, and particularly for those producing food for *Ateles*, were collected continuously over a period of two years in the Voltzberg study area, and scored in two-week periods of flowering and fruiting (table I). Data were gathered by continuously collecting and naming all fresh fruits, fruit parts and flowers from the forest floor and making additional observations on crowns. In general, flowering and fruiting appeared to be seasonal. One important exception is *Ficus*, as most of the species do not show any tendency to seasonality. Data on monthly variation in availability of edible flowers, flush leaves and ripe fruits are extracted from table I and shown graphically in figure 38. At the beginning of the long dry season (July/August), many trees and lianes start to flower, some after dropping their leaves. The flowering season lasts from the end of July until mid-February with a distinct peak in November, i.e., towards the start of the short wet season. A minor peak can be seen in April, at the end of the short dry season. Very few plants flower during the long wet season.

Flushing of leaves follows a somewhat similar pattern of seasonality. For most trees and lianes, flushing starts at the end of July and lasts until February, with a peak in November towards the end of the long dry season. Flushing seems to be rare from February to July.

Ripe fruits are available throughout the year, but a distinct peak can be seen in the months of March, April and May. Towards the end of the long wet season the availability of ripe fruits drops drastically, reaching a minimum in July and August. A minor peak can be seen in November at the start of the short wet season.

Most tree species tend to fruit every year and, at an individual level, usually alternate a good crop with a minor one. However, the timing of flowering and fruiting in a particular species can vary con-

siderably from year to year, perhaps because of yearly variations in timing and duration of the different seasons and/or differences in rainfall. A shift of one to two months and sometimes even more is not unusual (e.g., Pachira insignis was flowering in 1977 from mid-June to mid-August, and in 1978 from March to May). Moreover, individuals of some species seem to fruit only once every two
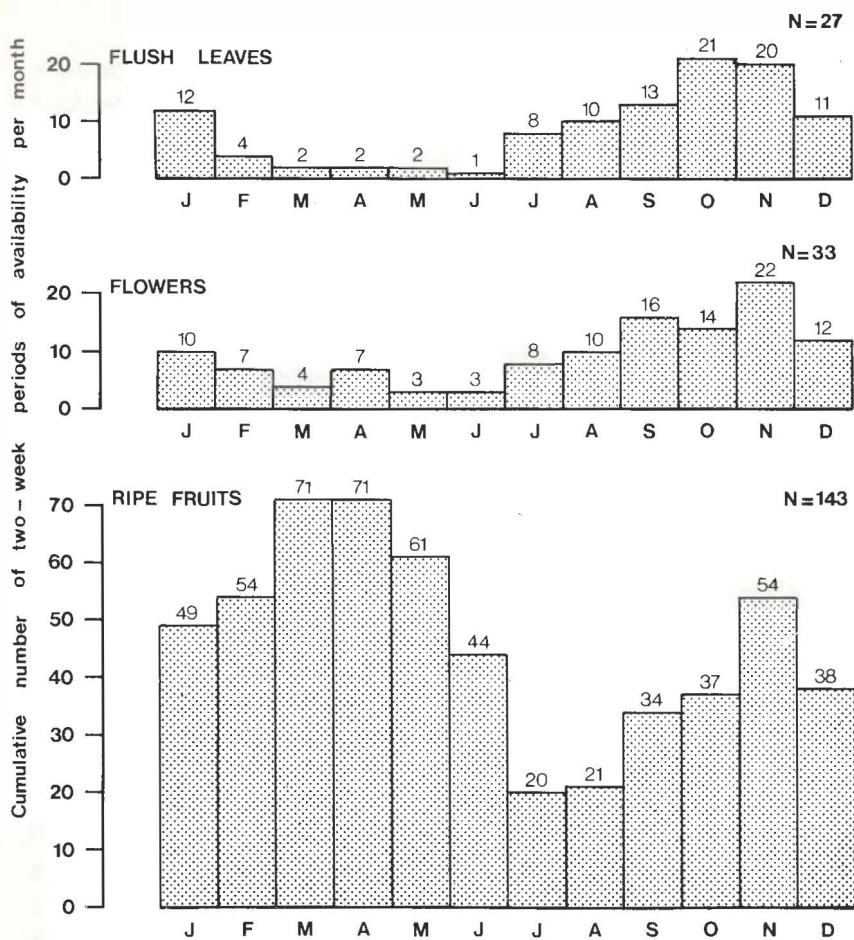
Figure 38 Monthly variation in availability of edible flowers, flush leaves and ripe fruits for spider monkeys in the Voltzberg study area during the present study. Data are expressed as the sum of two-week periods in which the items were available. Only those species were taken into account for which phenological data were collected systematically throughout the year (33 specis of flower, 27 species of leaf and 143 species of fruit; see table I).

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years, or even once every three to four years (e.g., *Hymenolobium*). Some years the whole fruit crop of a species may fail for some reason (e. g., *Minquartia guianensis* in 1977; *Capparis maroniensis* in 1978). Many lianes seem to fruit without any tendency to seasonality (e.g., *Strychnos, Ficus, Moutabea guianensis*), and some trees (e.g., *Guarea grandifolia, Ficus*) and lianes (e.g., *Ficus, Abuta grandifolia*) fruit about twice a year.

In some species, fruits are present for prolonged periods (e.g., *Capparis maroniensis*, 4 1/2 months; *Dimorphandra pullei*, 7 months; *Licania majuscula*, 5 months; *Virola melinonii*, 5 1/2 months) since fruiting is not synchronized at an individual level. Other species provide the monkeys with ripe fruits for only 10-14 days (e.g., *Ampelocera edentula*, several *Ficus species.*).

4.2.11. *Food supply and food choice.* Table IX compares the monthly supply of food items with the food choice observed. Data are extracted from Table I and Figures 26-37. Food items not included are bark, decaying wood, pseudobulbs, honey and insects because their availability seems to be either permanent or hard to determine. From June to October, during the end of the long wet season and the first part of the long dry season, food supply is lowest and the monkeys seem to exploit just about all available food items. In contrast, during December and January in particular, a food excess seems to exist in terms of percentages of food items not exploited (17.3 and 15.0%, respectively). The foods neglected during December are mainly flowers, and during January, they are young seeds and low-nutrient fruits of minor overall importance. However, when all food items are considered to be equally preferred by spider monkeys, comparing food supply and food choice in this way does not provide information about the real food excess. Spider monkeys prefer ripe fruits over all other foods. In Table X, the food supply is expressed both as the total number of two-week periods of availability of fruits and as the total number of potential edible-fruit bearing plants in the area for each month of the year. During December and January, the months apparently providing the monkeys with an excess of food items (Table IX), the supply of preferred ripe fruits is still rather low. This forces the monkey to eat considerable amounts of young leaves and flowers (Fig. 25). In contrast, in the period March-July (and in April, May and June in par-

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ticular) preferred food species obviously provide the monkeys with an excess of ripe fruits. This results in enormous amounts of spontaneously-falling unexploited fruits when species such as *Guarea grandifolia, Tetragastris altissima, Protium polybotryum, Capparis, maroniensis, Spondias mombin* and *Virola melinonii* are producing large crops. In this period the monkeys eat very low percentages of leaves and flowers (Fig. 25). The supply of fruits and young seeds is extremely low in the period July-November, in July and August in particular. This is obviously a period of food scarcity for the spider monkeys. When crops of certain species fail (as was the case in 1976), the monkeys suffer from food shortage.

Table IX. Food supply compared with food choice for each month of the year, expressed as the total number of food items. the food excess is expressed as the percentage of food items not exploited. Not included are bark, decaying wood, pseudobulbs, honey and insects.

Month	Total number of food items		% Food items
	available	eaten	not exploited
January	53	45	15.0
February	47	42	10.6
March	49	48	2.0
April	54	51	5.6
May	51	47	7.8
June	32	32	0.0
July	31	31	0.0
August	24	24	0.0
September	39	38	2.6
October	50	46	8.0
November	66	60	9.9
December	52	43	17.3

4.3 Ateles as a Specialized Frugivore

Among frugivores, three major categories are distinguishable in relation to fruits and seeds eaten:

1. *Total frugivores* (Morton, 1973), *specialized frugivores* (McKey, 1975) or *specialists*

2. *Partial frugivores* (Morton, 1973), *opportunistic frugivores* (McKey, 1975) or *generalists*

3. *Seed-eaters* or *seed-predators.*

Ateles can be considered one of the most prominent specialized frugivores in the Neotropics. Specialists are best characterized

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Table X. Food supply for a group of spider monkeys in the Voltzberg study area, expressed as the comulative number of two-week periods of availability for fruits (A), young seeds (B) and both (A+B), and as the total number of potential ripe-fruit sources (C), young-seed sources (D) and both (C+D) for each month of the year. Data on availability and numbers of potential food sources are extracted from Table I.

Month	Total number of two-week periods of availability for			Total number of fruit sources for		
	ripe fruits A	young seeds B	fruits A+B	ripe fruits C	young seeds D	fruits C+D
January	49	19	68	412	429	841
February	54	9	63	480	213	693
March	71	7	78	641	209	850
April	71	3	74	1,298	344	1,642
May	61	12	73	1,213	719	1,932
June	44	5	49	1,086	205	1,291
July	20	0	20	175	0	175
August	21	1	22	143	6	149
September	34	2	36	200	12	212
October	37	2	39	253	12	265
November	54	3	57	487	7	494
December	38	10	48	364	23	387

as animals that derive most of their supplies of carbohydrate, lipid and protein from fruits throughout the year. They, therefore, are restricted to the tropics. In the Neotropics several cotingids (e.g., the bellbird, the cock-of-the-rock), the oilbird, several trogons (e.g., the quetzal), guans, most toucans, kinkajous, howler monkeys, woolly monkeys (*Lagothrix* spp.) and woolly spider monkeys (*Brachyteles arachnoides*) also belong to this category.

Generalists are characterized as animals that mainly utilize fruits as a quickly harvestable source of carbohydrates, organic acids, water and possibly minerals that does not interfere much with the harvesting of proteins and lipids from other resources such as insects and meat (Morton, 1973). Generalists may be primarily or partial insectivorous or carnivorous. The majority of Neotropical birds and monkeys belong to this category, among them trumpeters, curassows, chachalacas, quails, tinamous, woodpeckers, caciques, tanagers, oropendulas, orioles, manakins, trushes, woodwarblers, tyrant flycathers, squirrel monkeys, capuchin monkeys and callitrichid monkeys. Other mammals such as marsupials, coatis, raccoons and tayras also fall into this category.

Seed-eaters derive most of their supplies of lipid and protein from seeds eaten in a young or mature stage. Pre-dispersal (arboreal) seed predation is performed especially by doves, grosbeaks, buntings, sparrows, finches, parakeets, parrots, macaws, tree porcupines, squirrels and saki monkeys (*Chiropotes* and *Pithecia*), whereas *post-dispersal (terrestrial) seed predation is performed most* notably by rodents such as acouchis, agoutis, pacas, spiny rats and rice rats. Among the insects, bruchid weevils are notorious seed predators.

In general, fruits eaten by specialists are characterized by a firm, dense edible part (aril or mesocarp) surrounding the seed or stone and containing a relatively high portion of fat and protein, and also by having a single or only few large seeds (e.g., *Virola, Ocotea, Oenocarpus, Protium, Tetragastris*). In contrast, fruits ingested by a wide variety of generalists generally have juicy, watery flesh and contain many small seeds (e.g., *Carica, Cecropia, Ficus, Jacaratia, Loreya, Miconia, Passiflora*). Fruits predated for the mature seeds after dispersal are usually dry, have only a minuscule aril attached to the seed, or else have a thin layer of mesocarp surrounding the seed or stone. The seeds are in some way protected against pre-dispersal predation by a thick, woody, dehiscent or indehiscent exocarp or by a tough, bony or woody endocarp, (e.g., *Andira, Astrocaryum, Attalea, Bertholletia, Carapa, Couepia, Eschweilera, Lecythis, Licania, Mora, Pachira, Vouacapoua*).

By means of comparative morphological analysis of 1,567 different fruits of Surinam woody plants above 1.5 m in height, Van Roosmalen (in prep.), estimates that dispersal by wind (anemochory) takes place in 10.6% of the species, by water in 5.2%, by the plant itself (autochory) in 0.3%, by specialists and scatter-hoarding rodents in 41.9% and by generalists (together with specialists) in 42.1%. Thus, about 84% are zoochorically dispersed in some way.

Three coevolutionary patterns may be distinguished between fruits and dispersal agents (as categorized above):

I. Large-seeded nutritious fruits seem to have coevolved with specialized frugivores as their principal dispersal agents. As McKey (1975) pointed out, the evolution of adaptations to specialized frugivory has resulted in generally increased dispersal quality, which means that the chance to survive and to grow to maturity per pro-

pagule is greater than in both other seed dispersal strategies mentioned below. Specialists are more dependent on fruits as food, so one may expect that these animals possess a better ecological knowledge, especially of available fruit sources (as is demonstrated in *Ateles,* with their well-developed spatial and temporal memory for particularly nutritious fruit sources). The plant may rely on the regular visitation of specialists to the fruit-crop, and therefore the chance that mature fruits remain on the plant and become rotten, desiccated or predated after spontaneously falling to the forest floor is minimized. Furthermore, the quality of dispersal depends on the treatment of the seeds in the gut of the dispersal agent. Seeds adapted to dispersal by ingestion (*endozoochory*) have protection against the rough chemistry and/or physics experienced in the guts of animals. This defense may be a hard seed coat or endocarp. Many specialists have thin-walled, often small stomachs with little muscularization, reflecting the relatively small amount of mechanical breakdown necessary for digestion of fruit flesh (Jenkins,1969). Another adaptation in many specialists, especially in birds, is the habit of regurgitating larger seeds just after the surrounding edible part has been removed in the stomach (Skutch, 1944; Snow, 1961, 1962, 1970; McKey, 1975). Both these features mean that seeds ingested by specialized frugivores will receive a gentle treatment within the gut. Spider monkeys do not regurgitate seeds, but when eating large-seeded fruits they do not masticate much and seldom destroy seeds with the teeth. Theoretically, coevolution with specialists would involve the possibility of evolving relatively soft seeds which are not protected by a tough of endocarp. Indeed, this pattern of coevolution may be seen in many representatives of the family Lauraceae, which produce nutritious fruits containing one vulnerable seed that is protected from exploitation by generalists and seed-eaters by means of its size and by containing toxic compounds. This family figures strongly in the diets of a number of specialized frugivores (Snow, 1971). However, it does not in the diet of *Ateles* in the Voltzberg area because most representatives of this family here measure less than 12 m in height. Finally, large seeds have a greater store of reserves than small seeds, and therefore the number of safe sites in a habitat is positively correlated with the increase in seed size. In some environments, selection favors an increase in seed size and a corresponding decrease in seed number

(Janzen, 1969). If larger seeds are evolved, the plant has to produce a fruit nutritious enough to attract specialized frugivores capable of ingesting large seeds. The high nutritive content of these large-seeded fruits is notable, and this coevolutionary pattern may be demonstrated in families such as Burseraceae, Capparaceae, Loganiaceae, Meliaceae, Myristicaceae, Palmae, Sapindaceae and Sapotaceae, all of which produce important fruits for *Ateles*.About 80% of the 166 plant species producing edible fruits that are eaten by *Ateles p. paniscus*, are of this nutritious and large-seeded type. In contrast, juicy, unnutritious and small-seeded fruits such as those of *Bellucia, Campomanesia, Ficus, Guettarda, Hylocereus, Jacaratia, Passiflora, Pereskia* and *Trymatococcus* only make up about 20% of the total number of fruit species eaten by *Ateles*. Moreover, these fruits were usually exploited only incidentally on the way from one nutritious fruit source to another, and appear to never significantly influence the daily foraging route. Also, food sources of this kind were not regularly revisited (table IV).

II. Many animals feed primarily on insects and/or meat, and only utilize fruits as a source of water, organic acids and carbohydrates (Morton, 1973). Plants depending on generalists for their dispersal may be able to attract them with relatively inexpensive, low-or unnutritious fruits (e.g., berries). Generalists will choose to ingest a berry with small seeds rather than a protein-and fat rich fruit with a large seed, as long as proteins and lipids can be derived more easily from other resources (e.g., insects). Furthermore, most nutritious fruits are protected against exploitation by generalists by a strong attachment of edible layer to seed coat or endocarp and/or a toxic seed coat or endosperm. When the fruit is small, the outer layer is thin and leathery, facilitating swallowing of the whole fruit (e.g., many Melastomataceae, Myrtaceae, Rubiaceae, *Cecropia, Coussapoa* and *Ficus*). In larger fruits of this type, the outer layer is easily penetrable (e.g., *Carica, Jacaratia, Hylocereus* and *Passiflora*) or dehiscent (e.g., *Carpotroche, Clusia, Phenakospermum* and *Stenosolen*). The seed coat or endocarp is always very tough in fruits of this category, so the seeds are protected against the rough chemistry and mechanical breakdown in the gut of at least some of the numerous generalists that exploit them. Seeds of this kinds are mostly the so-called 'dormant' seeds, which can wait sometimes for years (or even decades, e.g., *Carica*) for a chance to germinate. Germi-

nation in some species is induced by strong fluctuations in soil temperature (e.g., *Cecropia*, Boerboom and Holthuyzen, 1980), as may occur in edge habitats, secondary formations and high forest following treefalls. Several plants with fruits of this kind are true pioneers (e.g., *Carica*, *Cecropia*, *Ficus*, *Miconia*, *Passiflora*, *Phenakospermum* and *Solanum*). An advantage of this seed dispersal strategy may be the greater quantity of dispersal delivered by a wide array of generalists and the longivety of seeds. However, this may come at the cost of decreased dispersal efficiency, since many seeds will be destroyed in the guts of certain animals. In addition, visitation of the fructifying plant is irregular and unreliable, the majority of seeds will fall to the ground and be predated under the parent plant, and the store of reserves is minimal. Furthermore, the range of habitats is restrictive.

III. The third zoochorical dispersal strategy found in Neotropical plants is that performed by scatter-hoarding rodents. This strategy is based on predator-satiation. The seeds are usually large and edible, and crops are mass-ripening. The seeds fall in quantity and are partly buried by scatter-hoarders effectively protecting them from predation by bruchid weevils. This coevolutionary pattern between fruits and dispersal agents is demonstrated in many Bombacaceae (e.g., *Pachira*), Lecythidaceae (e.g., *Bertholletia*, *Eschweilera*, *Lecythis*), Leguminosae (e.g., *Andira*, *Vouacapoua*), Meliaceae (e.g., *Carapa*) and Palmae (e.g., *Astrocaryum*, *Attalea*, *Mauritia*). The advantages of this strategy are the relatively low investment in edible layer, the great store of reserves in the seeds, the regularity and reliability of visitation by scatter-hoarders and the storage of seed in the proper habitat. Disadvantages may be the high pre-and post-dispersal predation loss, the high investment in nutritive seeds and the clumped appearance of seedlings and full-grown trees.

Since a specialized frugivore must extract a balanced diet from the fruits available at any one time, its existence may require overlapping fruiting seasons. This pattern may be shown in the case of the spider monkey. Most nutritious fruits eaten by *Ateles p. paniscus* have a definite fruiting season. Many of the fruiting seasons are quite long and overlap broadly. Most Burseraceae, for example, fructify for 2-3 1/2 months, *Capparis maroniensis* for 4 1/2 months, *Dimorphandra pullei* for 7 months, many *Inga* species for 2-3

months, *Strychnos tomentosa* for 7 1/2 months, *Guarea grandifolia* for 4 months, *Moutabea guianensis* for 4 months, *Euterpe* species for two months, *Oenocarpus bacaba* for two months, *Apeiba* species for 2-3 months, *Virola melinonii* for 5 1/2 months and *Licania majuscula* for 5 months. In most nutritious-fruit producing plants exploited by spider monkeys, the length of the fruiting season is determined by the individual plants of the species not fruiting simultaneously and by the spread of fruit maturing within one plant. The fruiting seasons were determined for 62 species producing nutritious fruit at the Voltzberg study site. Of these, 52 fruited for periods ranging from two to eight months. Spreading of fruit production over a long period of time, has the advantage that less strenuous demands are being made on the small community of dispersal agents. Plants following this strategy have their own reliable subset of dispersal agents, shared with relatively few other plants. In contrast, 14 of the 20 species producing low-or unnutritious fruit fruited for periods of less than two months (range 10-40 days). Since each species with a broad-niched fruit utilizes a large proportion of the available dispersal agents when it is fruiting, there will be strong selection for fruiting seasons of such species to be displaced in relation to one another, as has been clearly observed in *Ficus*. Alternatively, the fruiting periods will be spread over extremely long periods of time, as has been observed in *Cecropia* and *Bellucia*. Plants dispersed by scatter-hoarders are usually mass-ripening, and at an individual level are producing crops only once every two or three years.

In summary, *Ateles*, as an important dispersal agent, shows many features of coevolution with nutritious, large-seeded fruits, and at least fills the niche of similarly adapted animals in the past. The high-quality dispersal offered by spider monkeys, which is offered by few other specialized frugivores, compensates the plant for the cost of producing crops ob nutritious fruits, but severely limits the number of propagules. In general, the fruiting seasons of these plant species are long, since the small number of dispersal agents may be easily overloaded by a mass-ripening fruit crop, and the existence of the dispersal agent may require that several species of fruit, each providing different nutrients, have broadly overlapping fruiting seasons.

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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, someti-

mes 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, four 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 bet-

ween 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 recognized 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 accompa-

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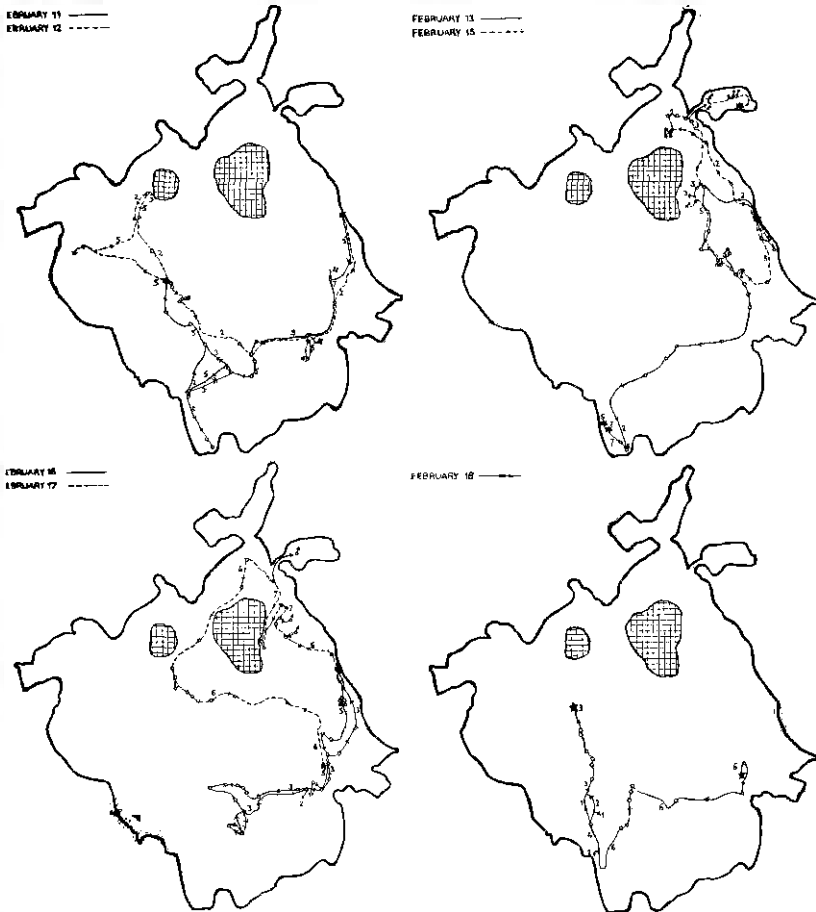
Figure 39 Daily travel paths and the pattern of temporary associations with the female (with juvenile) leading the frequently-changing subgroup on February 11, 12, 13, 15, 16, 17 and 18, 1978. Subgroup size, food plants and sleeping trees used are indicated. See for details figures 3g A,B, C, and D.

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
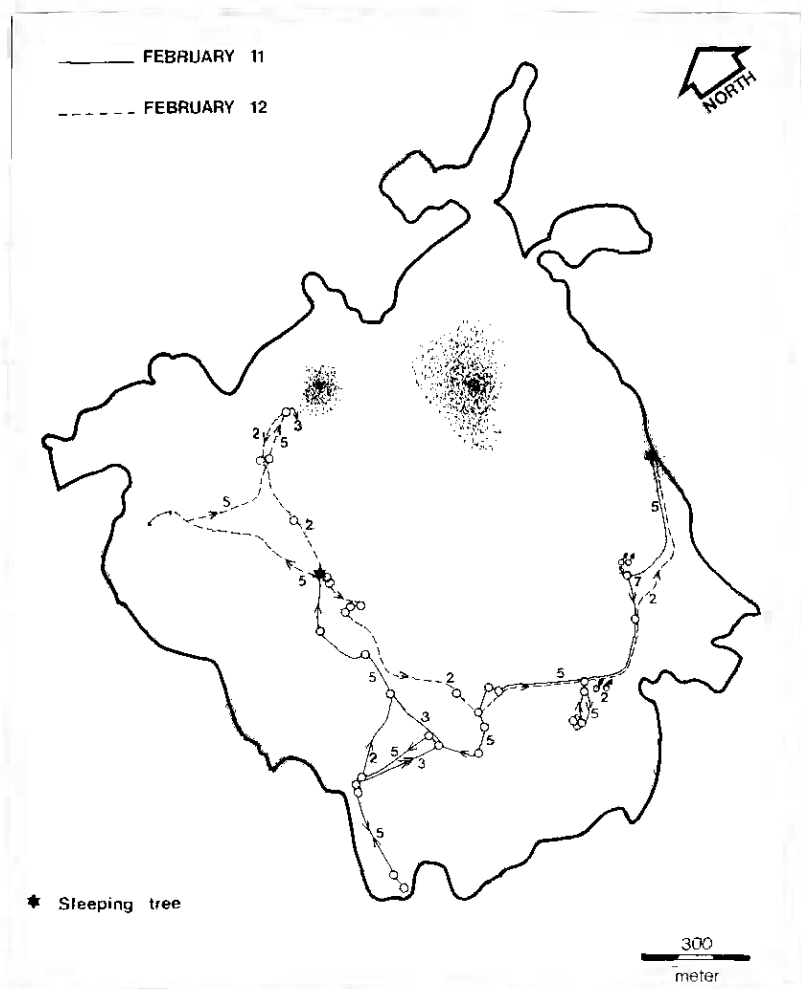
and its mother are considered a single unit. Thus, in these calcula-
tions six adults are involved: two leading females, two non-leading
females and two males. The figures, given in table XI, clearly show
a tendency for adults to assemble into subgroups containing at least
one leading females thoughout the year, except for the months July
and August (39.0 and 40.5%, respectively) which represents a pe-
riod 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).

FEBRUARY 13

FEBRUARY 15

NORTH

★ Sleeping tree

300
meter
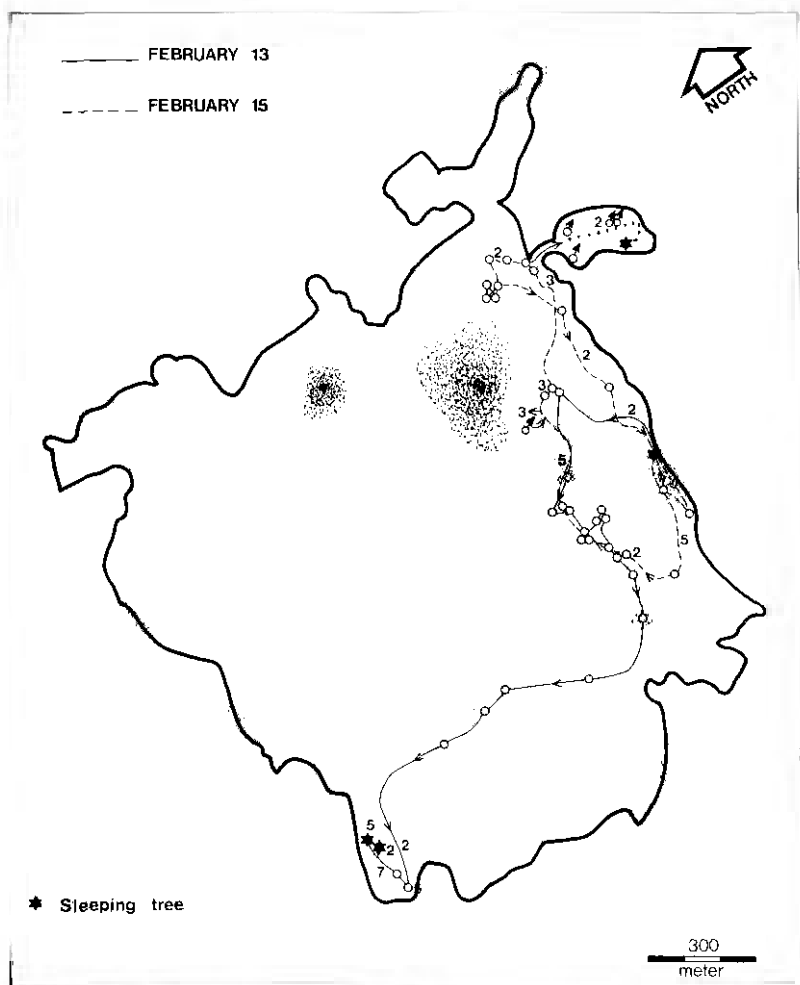
In table XII, all subgroup sizes and compositions observed in the study group during one year of intensive study are listed and their frequencies are expressed in terms of cumulative observation time (minutes) and percentage of total observation time (i.e., 1,061 hours). For this purpose, infants were 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%,

FEBRUARY 16

FEBRUARY 17

NORTH

* Sleeping tree

300
meter
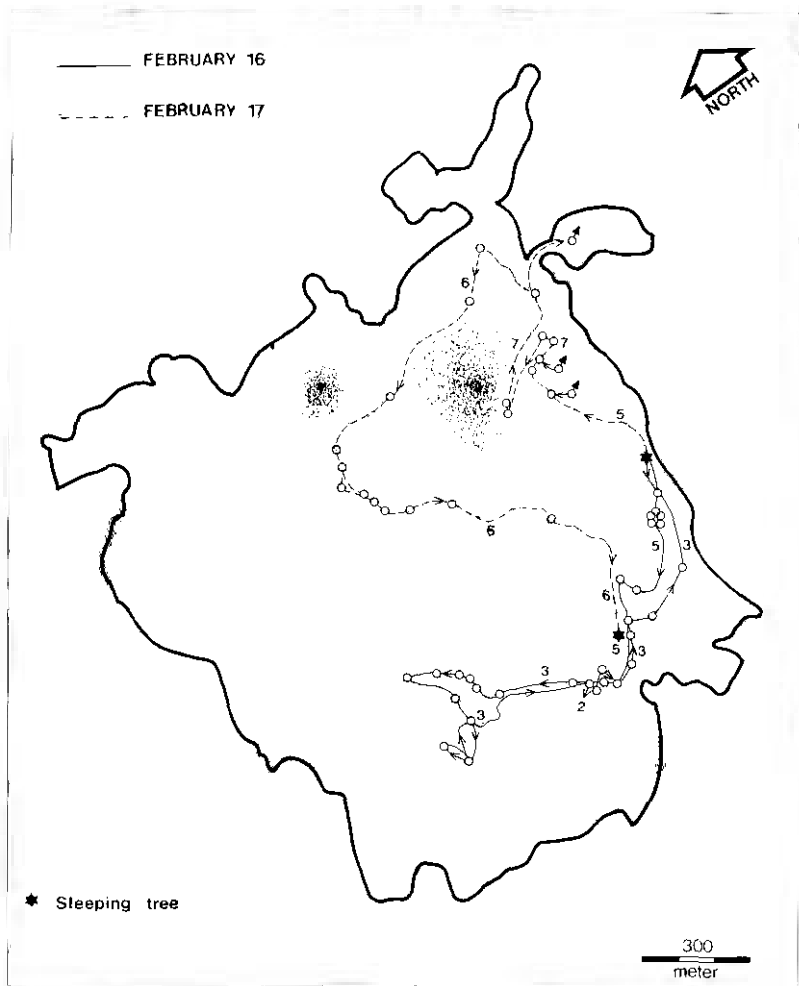
respectively). A subgroup of three individuals was observed most frequently (28.0%), followed by subgroups of two and four individuals (19.1 and 18.6%, respectively). Solitary ranging animals were seen with a frequency of 6.2%, but they may be underestimated because of their being harder to detect. Subgroups 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.

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Sleeping tree

300
meter
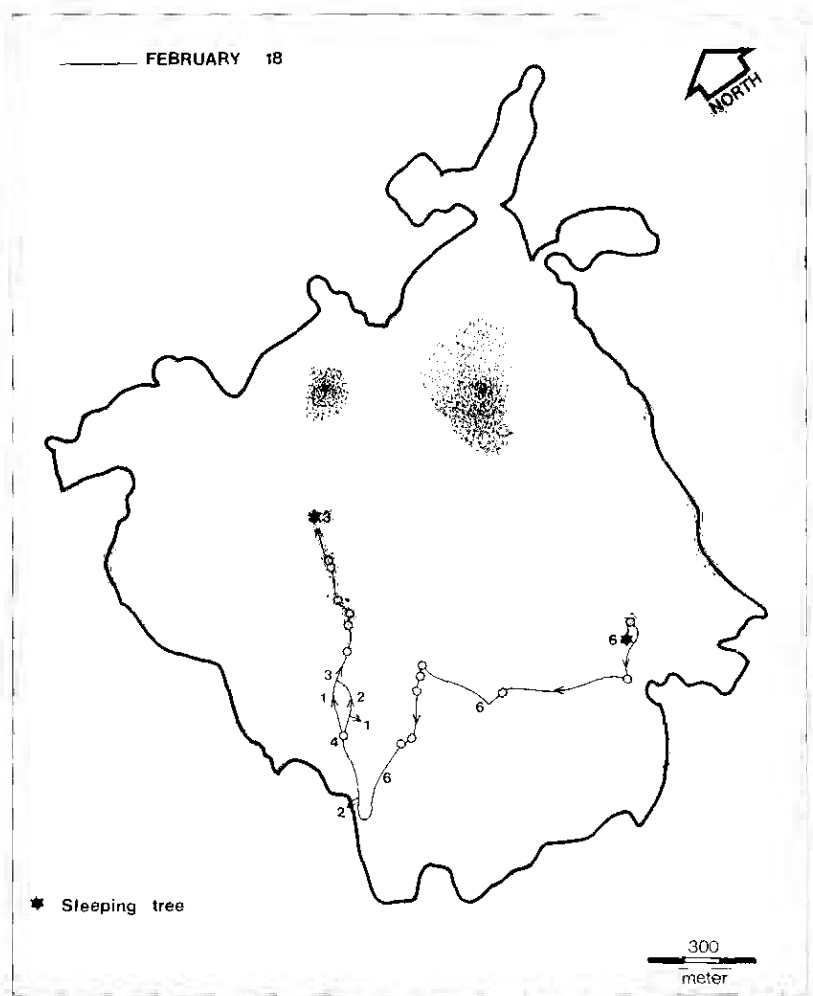
The subgroup composition most frequently observed was the combination ♂ ♀ +J (18.5%), followed by that of ♂ ♀ ♀ +J (12.3%). The subgroup compositions ♀ +J (8.9%) and ♀ ♀ +J (8.6%) were also common. Solitary ranging males were observed with the same frequency (i.e. 3.1%) as solitary ranging females with 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
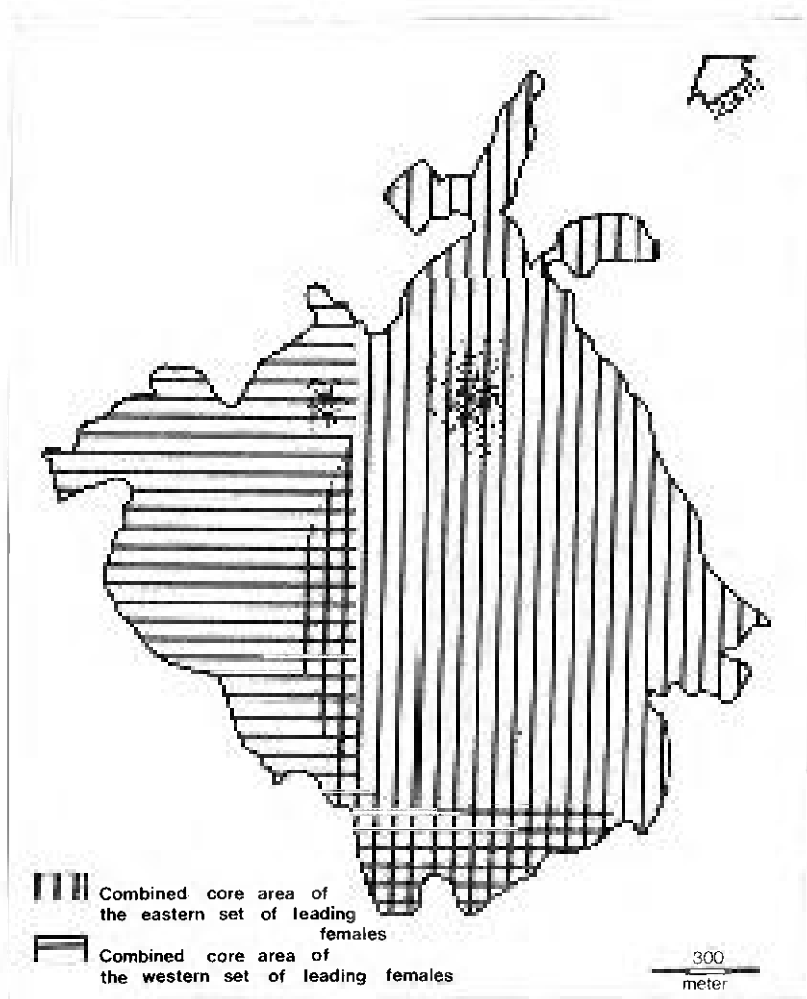
Figure 40 Distribution of combined core area of both sets of leading females within the spi-
der monkey group range. The combined core area of the western set of leading
females corresponds with the core area of male ♂2, the combined core area of
the eastern set of leading females corresponds roughly with that of male ♂1 and
male ♂3. Male ♂3 was found most frequently in the core-area overlap zones whe-
re every group female could be encountered regularly.

of 6.1% and mainly involved a receptive female. A subgroup con-
sisting of at least one male together with other animals was obser-·
ved with a frequency of 70.9%. A subgroup of only two males made

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

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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 local 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%

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(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 ($\male$ 1), one of middle age ($\male$ 2) and a young male 6-7 years of age ($\male$3).

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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 ($\male$1) was the highest ranking, followed by male $\male$2, male $\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, $\male$1 and $\male$2, each used approximately the combined core area of a set of leading females, the eastern and western set, respectively. The young male ($\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 $\male$2, was observed most frequently in a subgroup led by the mother of the juvenile-3 male, whereas male $\male$3 alternately joined a subgroup led by a female of the eastern set or, less often of the western set.

Both male $\male$2 and male $\male$3 were seen visiting the male $\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 agita-

ted 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 minimal 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

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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
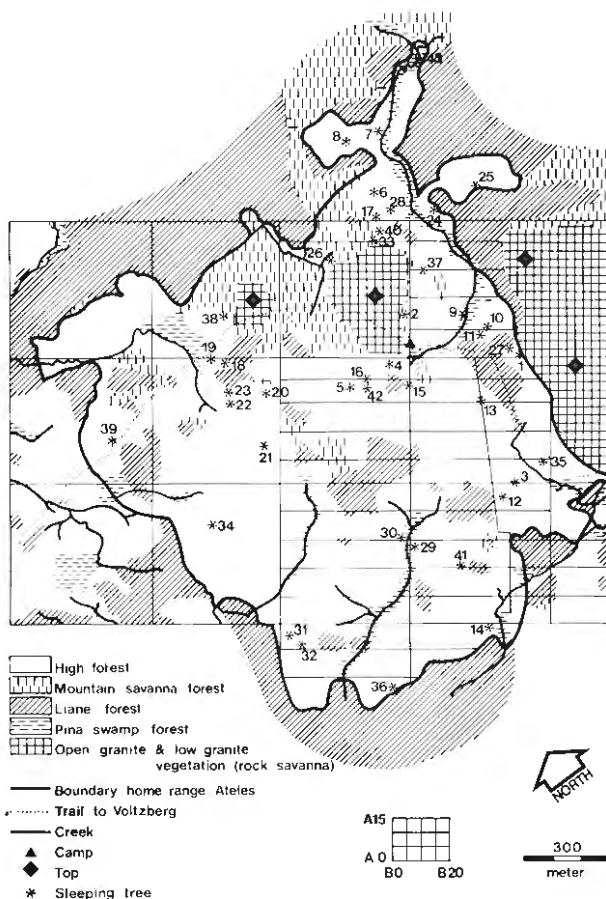
Figure 41 Location and species of sleeping trees used by members of the spider monkey group in the Voltzberg study area:

1. *Hymenolobium flavum* 2. *Hymenolobium petraeum* - 3. *Enterolobium schom-burgkii* - 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*.

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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.

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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

initiated sexual activity by moving rapidly towards a particular male, presenting her genitalia, and then sitting in his lap. When a male didn't react by initiating the copulatory position, the female rushed away through the tree crown, sat down somewhere else, and after several minutes attempted a second or third time before the male locked his hindlegs around her torso. Consortship involving one or two males and a receptive female usually was not secluded from the other members of the group, particularly not in case of leading females. However, for copulating the pair sometimes sought seclusion. The reason for this is probably strong harrassment from the juvenile. Several times, a receptive mother of a juvenile separated from a subgroup just after entering a food tree when the juvenile paid full attention to foraging. In these cases, the male immediately followed the female, and the pair copulated undisturbed 100-200 m away from the rest of the subgroup.

Receptive females appeared to choose a mate. This was best demonstrated when a receptive female that ranged in a subgroup without males reacted to male long calls by immediately altering her direction of travel and rushing towards the calling male. After meeting the male, presentation and copulation followed. Once, a leading female responding to calls by male ♂ 3 met male ♂ 1 about halfway along her route and advertised and copulated with him. However, before ejaculation took place, she broke of, rushed to male ∴3, and copulated with him.
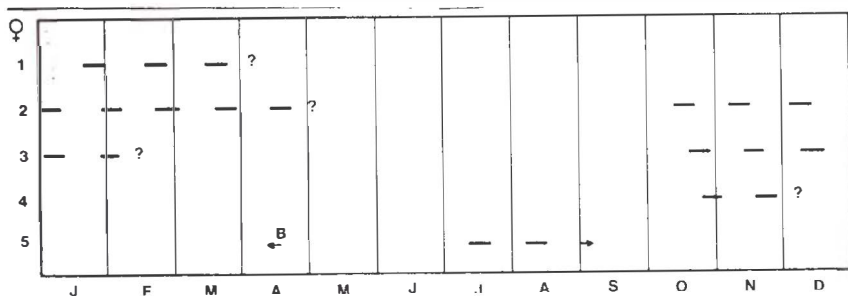
Figure 42 Estrus periods in five adult females belonging to the spider monkey study group, as observed from May 1977 to May 1978. 1, 2 and 4 are leading females; 1 and 2 were accompanied respectively by a juvenile-2 female and a juvenile-3 male; 3 and 5 are non-leading females without offspring. B = birth;? = observations not continued.

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 upper-leg 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.

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6. CONSERVATION

Ateles is threatened by hunting, live capture and habitat destruction (Grimwood, 1969; Freese, et al., 1976; Hernández-Camacho and Cooper, 1976; Mittermeier, 1977; Mittermeier and Coimbra-Filho, 1977).

For several reasons, spider monkeys are extremely vulnerable to hunting. Locally, they form an important food item, as they are large and good to eat. The size and noisy habits make them rather easy to locate, track and hunt. They defend themselves from human intruders by means of an aggressive branchshaking and dropping display. This behavior affords a hunter shooting an entire subgroup out of a tree crown. In addition, they show a very low reproductive rate. Females do not give birth before the age of five and, thereafter, only once every three to four years. Spider monkey social structure makes them even more vulnerable to hunting, as the group's survival may well depend on the few leading females having the best temporal and spatial knowledge of food sources. Unfortunately, for purposes of life capture, particularly the females carrying an infant will be shot. The infants serve a local pet market. Finally, population density is originally rather low (i.e., 7.1 individuals per Km^2.

Habitat destruction is another threat to spider monkey's survival. *Ateles* are largely restricted to undisturbed, most heterogeneous lowland rainforests which are going to disappear quickly all over their range.

In general, *Ateles* is an extremely vulnerable primate that shows little or no adaptability to human intrusion. In Amazonia, hunting is the main cause of decline. In Central-America, it is primarily threatened by habitat destruction. In Surinam, most of the interior is still undisturbed, making the outlook for conservation fairly good. At the moment, Surinam parks and nature reserves protect as much as 5,304 km^2 of rain forest habitat in the interior, most of them in remote and uninhabited areas. When the infrastructure of the interior shall be improved in the near future, the protection of these areas will be a major problem to conservationists. Hunting pressure will increase and illegal lumber extraction will threaten these areas too.

Unfortunately, a number of tree species providing spider monkeys, among other animals, with safe sleeping sites and food, produce commercially valuable timber. For these reasons, the national parks and nature reserves will be best protected by so-called buffer zones surrounding them. These areas should lack an infrastructure which, in general, enables more than incidental hunting and logging.

As pointed out before, for many canopy trees and lianas spider monkeys play an important, sometimes perhaps vital role in seed dispersal and escape from seed predation. Local extinction of spider monkeys alone may strongly affect primary forest composition and structure and may cause forest degradation. Unfortunately, this will be noticeable a long time after, since these processes take place gradually.

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7. DISCUSSION

The relation between feeding behavior and social organization.

Several authors have tried to find relationships between habitat in which primate species are found and social organization (Crook and Gartlan, 1966; Eisenberg, *et al.*, 1972; Jolly, 1972; Altmann, 1974; Clutton-Brock, 1974; Struhsaker, 1969; Wilson, 1975). These have met with only very limited success. Results are better when use of environment is correlated with aspects of social organization (Clutton-Brock and Harvey, 1977; Milton and May, 1976). As Rasmussen (1981) points out, proximate studies form nearly the entire data base for primate socioecology (e.g., the studies contained in the volume "Primate Ecology" edited by Clutton-Brock, 1977), whereas only few researchers directly measure effects of environment or use of environment on social interactions. The "social" of primate socioecology is largely missing. Therefore, autecological field studies describing diet, phenology of food plants, food supply, distribution of food, foraging behavior and social behavior *throughout the year* and in great detail are urgently needed. The present study may serve as an exemple, as will be discussed below.

Spider monkey food specialization involves nutritious (lipid-rich), mostly single – and large-seeded, mature fruits, which as a rule are available for relatively long periods of time but in small quantities at any given time in a single food plant. This type of fruit seems to have evolved in parallel with the frugivorous animals dependent on it and providing the plant with proper seed dispersal (McKey, 1975). These plants invest much more energy per propagule in a lipid-rich flesh than do plants with watery (sugar-rich), small-seeded berries and figs, or dry, wind-dispersed fruits. The latter generally produce large, mass-ripening fruit crops in order to satiate seed predators and to use a wide array of dispersers feeding on the fruits. However, seed dispersal offered to lipid-rich fruits by animals such as spider monkeys involves regular prolonged utilization, a gentle treatment by the disperser's mouth and gut (and some including quicker germination after defecation, e.g. in the case of stones), endochorical transport over considerable distances from the parent tree, dropping in preferred habitat and development of relatively large

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seeds with advanced growth which increases the chance of success-fully overcoming the first stage in the plant's life cycle (Van der Pijl, 1969). This strategy has many advantages for the plant but costs are relatively high. In evolutionary terms, this might have been the major reason for many high forest plants with large-seeded, lipid-rich fruits to produce asynchronous,slow-ripening fruit crops not successful every year and favoring both the specialized frugivorous animals and its own seed dispersal.

It is true that few fruits of the lipid-rich type are dropped unex-ploited on the forest floor below the parent plant. They are exploi-ted in a very efficient way by the specialized frugivores dependent upon them. This may be also an explanation for the abundance of terrestrial animals being attracted under trees in which spider mon-keys are feeding or have been feeding just before, since these much appreciated lipid-rich fruits are otherwise not available to them.

Asynchronous, prolonged and slow-ripening fruit crops that pro-vide small quantities of mature lipid-rich fruits at any given time force large-sized specialized frugivores such as spider monkeys to forage in small subgroups and with relatively short feeding bouts.

In contrast, another sympatric monkey, the bearded saki (*Chiropotes satanas chiropotes*), shows roughly similar habitat preferen-ces in horizontal and vertical distribution but feeds largely on immature seeds (Van Roosmalen *et al.*, 1981). Ripe fruits and flo-wers play only a minor role in its diet. It shows a completely diffe-rent foraging strategy and social organization even though overlap in choice of fruit species eaten between the two primates is conside-rable (i.e., *Chiropotes* fed upon a total of 78 species of fruits of which 52 were used for its young seeds; most of these fruits were exploi-ted at a mature stage by *Ateles*).

The bearded saki forages in large, multimale groups consisting of 8-30 or more animals and ranges over large areas (Ayres, 1981; Van Roosmalen, *et al.* 1981). Foraging routes appeared to be lar-gely determined by spatial distribution of certain vegetation types, subtypes or phytosociological units of lower rank that offered relati-vely high densities of few species with edible young seeds. Since the stage of immaturity does not at all seem to be critical to this monkey, seeds are available for many months and in large quanti-

ties with-in a single food source. This feature sustains the behavior pattern of foraging in large groups.

However, there is some seasonality in the supply of young seeds (Ayres, 1981). If certain vegetation types or plant associations do not offer enough to feed upon together, during the course of a day's foraging activities a group of bearded sakis may up into two or three subgroups and spread over a large area. During this time, they constantly keep mutual contact by means of their extremely loud long calls ("wiché"), while sleeping and traveling between foraging grounds is always performed cohesively by all group members.

This comparison of two sympatric primate species that largely overlap in habitat choice and choice of food species, indicates that social organization among primates may be related to very fine interspecific ecological differences such as preference for the same fruit species at different stages of development.

Comparison of spider monkeys with chimpanzees

As already noted by Cant (1977), spider monkey social organization shows a remarkable similarity with that of the chimpanzee (Pan troglodytes). Both primates live in distinguishable groups or communities, with a loose, unstable social structure within the group or community and intergroup agonistic behavior (Goodall, 1965, 1968; Reynolds and Reynolds, 1965; Klein, 1972; Bygott, 1974; Wrangham, 1975, 1977; Cant, 1977; Van Roosmalen, 1980, this study). Both in Ateles and Pan, a highly developed knowledge of available food sources seems to be present, and the assumed detailed spatial memory results in economical routes between food sources. Apparently, both species are capable of returning to certain food sources from any location within their range by the shortest possible routes (Wrangham, 1977; Van Roosmalen, 1980, this study).

The ioose, unstable social structure within the group or community seems to be prim related to food specialization (i.e. particulary mature, lipid-rich (ruits) and seasonal varium in foodpatch size. Relatively large subgroup or parties form in times of food abundance and sela small ones ave noted in times of food scarcity, perhaps as a refult of increased feeding contion (Azuma and Toyoshima 1962; Reinolds and Reinolds, 1965; Sugiyana, 1973; Nishida, 1974; Wranghan, 1975, 1977; Van Roosmalen, 1980, this study).

In both species, males perform food-calls or pant-hoots, and food-calling is positively related to food supply (Goodall, 1965, 1968; Reynolds and Reynolds, 1965; Wrangham, 1975, 1977; Van Roosmalen, 1980, this study). Reynolds and Reynolds (1965) and Eisenberg, et al. (1972) argue that the function of food-calling is to spread information about the location of food sources, and is thereby seen as altruistic. However, food-calling is least frequent when food availability is lowest and when learning about food sources would be most favorable to other group members. Wrangham (1977) points out that food-calls will tell other chimpanzees that a male has just arrived at a certain food source, which is now being depleted. When giving food long-calls, male *Ateles paniscus* often are part of relatively large subgroups and joining of subgroups usually does not take place after such food-calls.

The concept of "return time regulation" (Cody, 1974) seems to be applicable here, and directed towards other leading females not in the subgroup containing the calling male. For cropping the new growth, particularly in case of a limited amount of mature fruits, this female is told to drop this food source from her foraging route.

The relation of body size to food patch size is reflected in a relatively high degree of solitary behavoir, higher in chimpanzees, and in relatively small subgroups or parties throughout the year with the only permanent bond formed by females with their offspring. When infants and juveniles are considered together with their mothers, females with or without offspring range more frequently solitary than males, possibly related to their better knowledge of a certain "core area" (Goodall, 1965, 1968; Halperin, 1978; Van Roosmalen, 1980, this study).

Because of the flexible subgroup size in both species, aggressive and submissive behavior within a group or community is infrequent and occurs almost exclusively while feeding.

Individual adults occupy "core areas" within the group or community range, areas most frequently used in a particular part of the year (Wrangham, 1975, 1977; Van Roosmalen, 1980, this study) Male "core areas" are larger than female ones but at least in *Ateles* females possess a better knowledge of available food sources within these areas, whereas males travel more widely in times of food abundance.

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In both species co-operation between the sexes appears largely unnecessary, except during mating. Therefore, the larger subgroups or parties and wider travel by males in times of food abundance apparently signify increased reproductive effort. As Wrangham (1977) points out, reproductive competition may be expected to continue between males, since any female will be estrous in the future and will choose a male on the basis of her full knowledge of him.

Observations by Bygott (1974) and Wrangham (1975) on aggressive relations between male chimpanzees of different communities revealed that the relative size of parties is an important factor determining the outcome of the interactions. Wrangham (1975) hypothesized "that the functional consequence of territorial expansion was the acquisition of females, and tha the formation of large parties may be viewed as improving the reproductive success of a male community through its increased probability of winning territorial encounters and hence females". This hypothesis also seems to be applicable to spider monkey community. At territorial boundary conflicts, male *Ateles paniscus* performed so-called alarm long calls, thereby attracting nearby parties to the spot for sharing the long-distance agonistic behavior of shaking and breaking off twigs, branches and boughs and performing "ook-barking" towards the members of the neighboring group.

While males stay within the perimeter of the group's range, females occasionally do visit members of neighboring groups and emigration of females, particularly young non-leading females, seems to occur. Male-male dominance exists. Males cooperating in territorial defence seem to be related. This kind of social system permits males to defend large territories, including ranges of several females, by cooperating in all-male parties during territorial defence patrols and boundary conflicts with other groups (Goodall, 1965, 1968; Bygott, 1974; Wrangham, 1975, 1977; Riss and Goodall, 1977; Pusey, 1978; Van Roosmalen, 1980, this study).

8. SUMMARY

This study describes habitat and food choice of the Surinam black spider monkey, *Ateles paniscus paniscus*. It clarifies complex temporal and spatial effects of food sources on the behavior of a group of spider monkeys in a 350 ha study area in central Surinam in terms of food category, food plant identity and phenology and in terms of quantity, density and dispersion of the most important of these food sources. It recognizes the fundamental importance of mature fruit-feeding to spider monkey foraging strategy and discusses implications of diet for social behavior. From a conservation point of view, this study is essential since it emphasizes the extreme vulnerability of the spider monkey to both hunting and habitat destruction. In addition, it provides detailed information on spider monkey habitat choice and dietary requirements that is urgently needed in order to assess both potential and established protected areas. The spider monkey serves as an important "indicator" species, reflecting the degree of disturbance to Neotropical rain forests.

1. In the Voltzberg region, *Ateles paniscus* occurs at a density of 7.1 individuals per km^2, or 8.2 individuals per km^2 when only suitable habitat is considered. Biomass ranges between 0.4 and 0.5 kg/ha depending on the home range figure chosen.

Forest types found in the Raleighvallen-Voltzberg region are described structurally. Dry evergreen forest types are divided into tropical rain forest (i.e., high rain forest, low rain forest, riverbank high forest), mountain savanna forest, and liane forest. Wet forest types are divided into swamp forest and marsh forest. Finally, a xeromorphic vegetation, "rocksavanna", is distinguished.

2. The present study was conducted in the Raleighvallen-Voltzberg Nature Reserve, a 56,000 ha protected area located on the east bank of the Coppename River in central Surinam. A 350 ha study area was gridded and a vegetation map of the area was made. During the first year, the study was focussed on the synecology of all eight Surinam primates living in the area. In addition, a group of spider monkeys were habituated, data on their general behavior were collected, and the perimeter of the group's home range was roughly determined. During the second year, the study was con-

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centrated mainly on the autecology of spider monkeys. During the entire field period, the phenology of especially food plant species was monitored. In cooperation with a native tree specialist, approximately 10,000 individual trees and lianes belonging to 120 species of food plant were tagged and plotted in special maps in a 205 ha area, that was the most important part of the *Ateles* group range.

Some other localities were investigated in Surinam during the general survey, which added data to the distribution map and the habitat table.

3. Among the eight Surinam monkey species,*Ateles paniscus* is the most restricted in habitat. In the Voltzberg region, it occurs almost exclusively in high forest (92.6%), infrequently enters edge habitats (14.9%), and is found primarily in the upper levels of the canopy and in emergents (72.3%). The understory is rarely used (0.8%), and the lower extreme of its vertical range appears to be 12 meters. Among the seven major forest types available in the Raleighvallen-Voltzberg region, spider monkeys are observed only in high rain forest, mountain savanna forest, pina swamp forest and riverbank high forest.

4. A total of 207 food plant species are used, of which 68.1% are trees. The most important food plant families are Moraceae and Mimosaceae, both in terms of number of food species and percentage of total feeding records. *Ateles paniscus* is mainly frugivorous and feeds on 171 species of fruit, 33 species of flower and 28 species of leaf. Mature fruits make up 96% of the total number of fruit feeding records. Occasional feeding upon insects (i.e., termites and caterpillars) definitely takes place. The average annual food intake is 82.9% fruits, 6.4% flowers, 7.9% flush leaves, 1.7% bark and 1.0% miscellaneous (i.e., rotten palm sheaths, pseudobulbs, aerial roots, honey, insects). Monthly variation in food choice shows a strong correlation with phenology. During the first part of the long dry season (i.e., from July to September), a period of low fruit supply, the monkey compensates its diet with relatively high percentages of both flowers and flush leaves. During the long wet season (i.e., from March to June), fruit abundance results in very low percentages of both flowers and flush leaves in the diet. Ripe fruits always seem to be preferred. Young seeds play a minor overall role in the diet, except for the period May-June. By ingesting large quantities of young seeds

rich in protetin and fat during the peak of the long wet season, the monkeys seem to stock up on energy for the coming months of food scarcity (i.e., from July to October).

Foraging behavior in spider monkeys differs strikingly with the seasons. During the long wet season when fruit is abundant, activity budgets are increased. This results in large day ranges (with a maximum length of about 5,000 meters), prolonged feeding times, short resting times and daily utilization of many food sources (i.e., particularly mature fruits). Foraging often takes place in relatively large subgroups that break up and reassemble regularly, the subparties using partly different food sources but following roughly similar itineraries. During the long dry season, when fruit supply is low and food scarcity (or in some years even food shortages) exists, activity budgets are lowered to a minimum. This results in short day ranges (with a minimum of about 500 meters), prolonged resting times, short feeding times (i.e., few relatively long feeding bouts), daily utilization of only a few food sources and much higher percentages of flowers and flush leaves in the diet. Finally, mean subgroup size is decreased strongly.

Spider monkeys live in medium-sized groups that fragment into widely dispersed subgroups of varying composition. Daily itineraries and activity patterns of a subgroup are mainly determined by a so-called leading (usually older) female with or without off-spring, or sometimes by two leading females alternating responsabilities. These females appear to possess the best knowledge of certain parts of the group home range, the so-called core-areas, and seem capable of fixing beforehand an economic foraging route for the day that can include from 8 to 30 different food sources. By regularly monitoring potential food sources as to their stage of maturity and using a highly developed spatial and temporal memory, these females appear to be able to incorporate maturing food sources into their foraging routes just after they become available. The interval between subsequent visits to a particular food source appear to be species-specific and depends on the maturation rate of the fruit. In some species, the last stage of maturation passes rapidly, offering the monkeys a large enough food supply to enable an entire subgroup to feed simultaneously in the same tree. Many species, however, are exploited in 2-4 day cycles, some in 5-8 day

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or even longer cycles. Spider monkeys appear to select for variety, using daily an average of about 14 different food items that comprise about a quarter of the average monthly number of food items used. Of these, three or four food items are most important in terms of both total time spent feeding upon them and estimated weight of food ingested.

Ateles plays an important role as a dispersal agent for many plant species, and for some species it even seems to be the only seed disperser in the Voltzberg region. Endochorical seed dispersal by spider monkeys took place in 138 plant species (accounting for 93.5% of all fruit feeding records), seed dropping was recorded in 10 species (2.7%) and seed predation in 23 species (3.7%). *Ateles* belongs to the category of "specialized frugivores" that derive all or most of their supplies of carbohydrate, lipid and protein from fruits. Large-seeded, nutritious (lipid-rich) fruits seem to have evolved parallel with specialized frugivores as their principal dispersal agents, resulting in a greater quality of dispersal than that found in small-seeded, low-nutritious (sugar-rich) fruits which are usually dispersed by a wide array of both "opportunistic" and "specialized" fruit-eating animals. This coevolutionary pattern (i.e., the high nutritive content of the flesh in large-seeded fruits) may be demonstrated in families such as Burseraceae, Capparaceae, Loganiaceae, Meliaceae, Myristicaceae, Palmae, Sapindaceae and Sapotaceae, all producing important fruits for spider monkeys. Among the 166 plant species with edible fruits used by the spider monkeys in the Voltzberg region, about 80% produce lipid-rich and large-seeded fruits. Sugar-rich, small-seeded fruits (i.e., particularly berries and figs) make up only 20% of the fruit species in the diet, and are exploited only incidentally on the way from one lipid-rich fruit source to another. They almost never appear to influence the daily foraging route, and are not regularly revisited. These species often produce mass-ripening fruit crops on which the monkeys cannot greatly depend. However, the fruiting seasons of the larger-seeded fruits in general last relatively long because of more or less asynchronous fruit maturation within and between individuals of the species. This pattern may have evolved because the small number of specialized dispersal agents can be easily overloaded. The competition between these plant species for dispersal offered by a small number of dis-

persers may have evolved in lengthy, displaced, but broadly over-lapping fruiting seasons required to supply specialized frugivores the year round.

5. A group of *Ateles paniscus* usually consists of 15-20 individuals, although all members may never be observed together at the same place. A group fragments into several subgroups of varying composition, a female with offspring ranging in age from zero to about five years being the only persistent subgroup observed. The annual home range of the spider monkey study group in the Voltzberg area covers 255 hectares, of which 220 hectares offer suitable habitat. Daily travel paths range between 500 and 5,000 meters in length depending on the subgroup size and composition, the weather, the season and the distribution of particular important food sources. Sex ratio of adult males to adult females is 1 : 2(-3). The adult males of a group defend a territory with clearcut boundaries, whereas females sometimes visit neighboring groups and even may emigrate.

Spider monkey social system is characterized by its flexible grouping behavior and seems to have evolved parallel with its food choice concerning mainly lipid-rich, large-seeded fruits. The supply of this type of food varies greatly with the seasons and maturation rates within and between individual fruitings plants are generally rather slow and asynchronous. Moreover, individual mature fruits of this type are available to the monkey only for a brief period of time. After becoming, mature, most fruits soon drop to the ground or, when dehiscent, become available to birds. These food plants seldom offer enough for more than three adult spider monkeys to feed upon together. Consequently, subgroups consisting of ≤3 individuals are the most frequently encountered throughout the year. However, high densities of particular food plants fruiting during the long wet season enable spider monkeys to forage in much larger subgroups that may contain two leading females and may range in size up to nine independently locomoting individuals simultaneously using roughly the same itineraries but exploiting somewhat different food sources. As a result, during this season intragroup social interactions are much more frequent.

During the following long dry season, when lipid-rich fruit is scarce (and in some years even severe food shortages may exist),

the mean subgroup size decreases sharply. Leading-female core-areas are separated and show almost no further overlap throughout the season. Non-leading females and males still may assemble into subgroups led by a female to share ecological knowledge of food sources but they do so less frequently. Daily travel paths drop strikingly in length and the animals are more silent. Both of these factors contribute to a lower chance of mutual encounter. Activity budgets are decreased, particularly in males and non-leading females. The better knowledge of available food possessed by leading females may favor them for survival, especially during the long dry season. Also, this may be a reason why leading females seem more successful in rearing offspring than do non-leading females, and why mortality in adult males, on the basis of sex ratio, seems to be higher.

At the end of the long dry season when preferred fruit is still in low supply, relatively frequent feeding upon flush leaves and flowers again sustains foraging in larger subgroups by providing large amounts of food at a given time in large-crowned flushing or flowering food trees.

Adult males do possess core-areas and these usually are larger than those of leading females and even may include core-areas of two leading females. Adult males cooperate in territorial defence patrols and long-distance agonistic behavior (e.g., boundary conflicts). In this way, spider monkey males are able to defend more females than would be possible in a social system with cohesive bisexual groups, such as those found in many other primates.

The spider monkey social system is unusual among primates and shows the most striking similarities to that of the chimpanzee (*Pan troglodytes*). Both species are largely frugivorous, and have a loose, unstable social structure within distinguishable groups. Subgroup size varies seasonally in relation to food supply and usually is small. Individual adults occupy "core-areas" and show capacity for and continual use of a detailed, highly developed spatial memory. Dominance behavior and sexual behavior is also remarkably similar in the two species.

6. *Ateles* is a highly vulnerable primate showing little or no adaptability to human intrusion. Hunting, live capture and habitat destruction are the main threats to its survival. Spider monkeys are considered a very important component of lowland tropical rainfo-

rest ecosystem. Being one of the principal dispersal agents for plants with larger-seeded, usually lipid-rich fruits, a common phenomenon in primary forest canopy trees and lianas, local extinction of *Ateles* will probably cause long-term forest degradation. It is proposed to protect *Ateles* in national parks and nature reserves surrounded by buffer zones without an infrastructure preventing them from large-scale hunting and habitat destruction.

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Appendix

Distribution and density of main food plant and sleeping tree species in the combined core area of two leading-female spider monkeys belonging to the Voltzberg study group, whose ranging behavior was best studied. For plotting purposes, the area was subdivided in rectangular ½-hectare blocks. Shaded areas indicate non-suitable habitat (e.g., open granite, liane forest) that was not sampled. Both botanical and vernacular names (when available) are given, while the total number of individual plants plotted in the area is given in parentheses. Few species (n° 53 and 119) were very abundant locally and consequently only part of its population was plotted. Of several species, in particular lianes, only the individual plants actually seen exploited by the monkeys were plotted (n.° 25, 26, 27, 93, 115 and 116). For the purposes of this study, tagging and plotting was restricted to those individual plants, that obviously had reached "their" preferred stratum which, in general, implies the phenomenon of flowering and fruiting. Plants providing the monkeys only with edible flush leaves were plotted when reaching at least 12 meters in height, the lower limit of *Ateles* vertical range.

Besides mountain savanna forest with indicator species *Guettarda acreana* (114) and *Ecclinusa guianensis* (119), *pina* swamp forest with indicator species *Euterpe oleracea, Pachira insignis* (14), *Eperua falcata* (61) and *Virola surinamensis* (111), and high forest, a subtype of high forest on relatively red (ferrosiallitic) forest-soil may be distinguished, covering roughly blocks A and B, showing relatively abundant leading species, such as *Protium polybotryum* (18), *Tetragastris altissima* (19), *Tetragastris panamensis* (20) and *Capparis maroniensis* (21).

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HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

1

Anacardium giganteum
'boekasjoe'
(23)

2

Spondias mombin
'mope'
(28)

HOME RANGE OF ATELES

0 100 200 300m

3

Duguetia sp,
gele bast jar- jari'
(14)

4

Ephedranthus guianensis
man-pikapika'
(312)

5

6
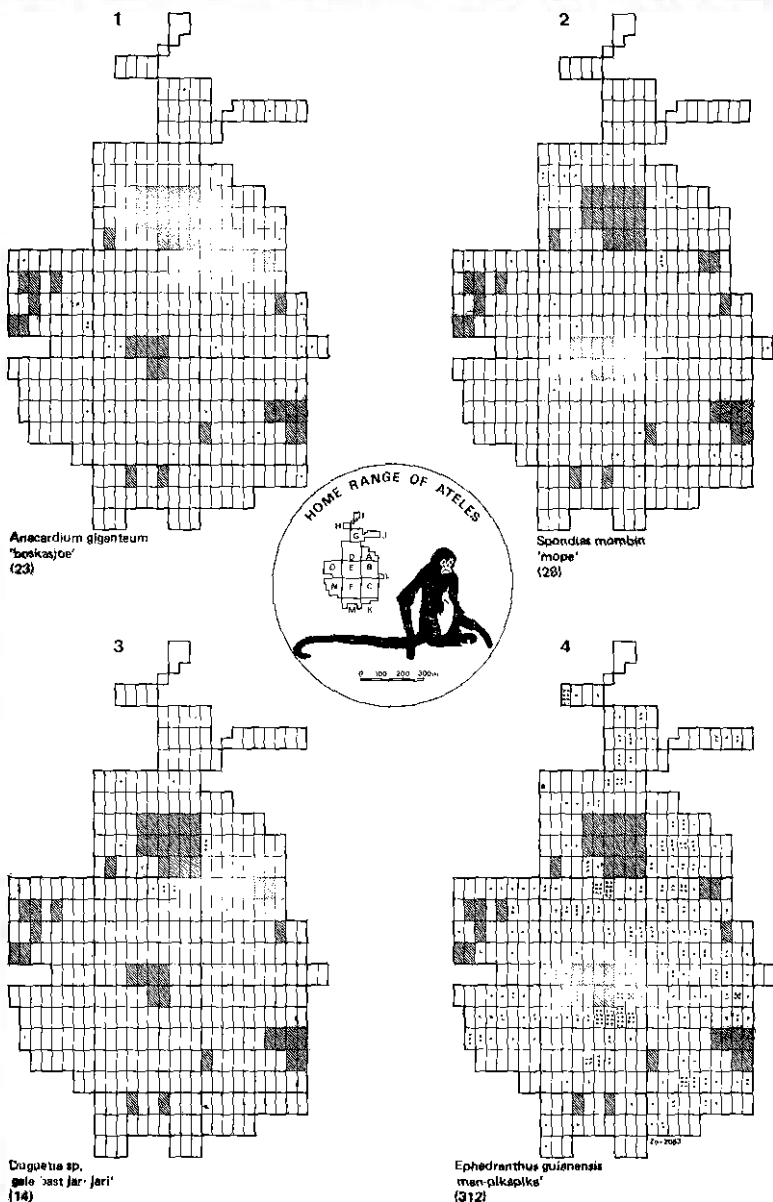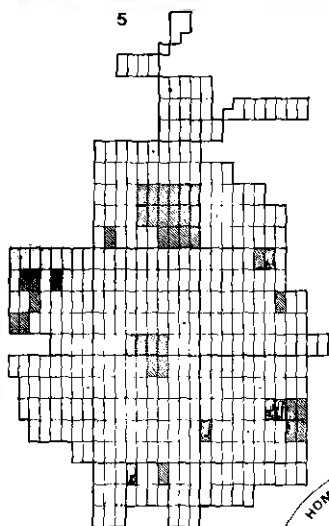
Fusaea longifolia
'langbladige jari jari'
(6)

HOME RANGE OF ATELES

Guatteria chrysopetala
(7)

7

8
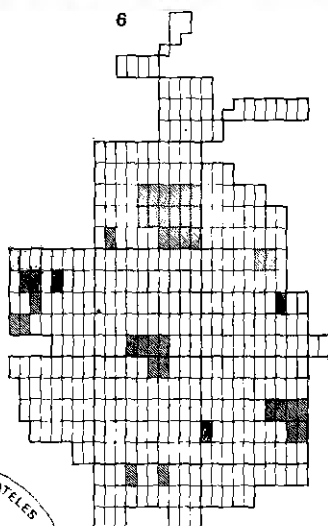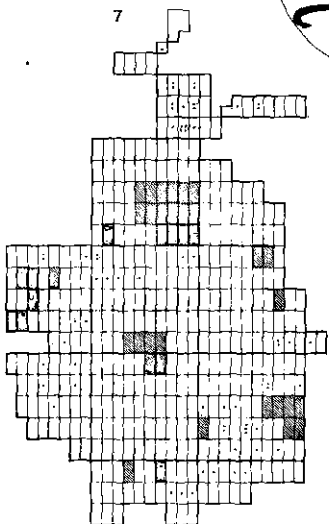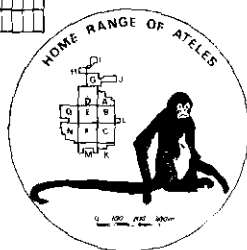
Unonopsis glaucopetala
'gewone jari jari'
(63)
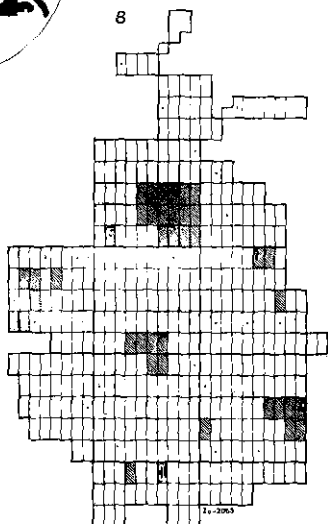
Aspidosperma excelsum
'zwart perelhout'
(21)

Van Roosmalen

9

Aspidosperma marcgravianum
'wit parelhout'
(6)

10
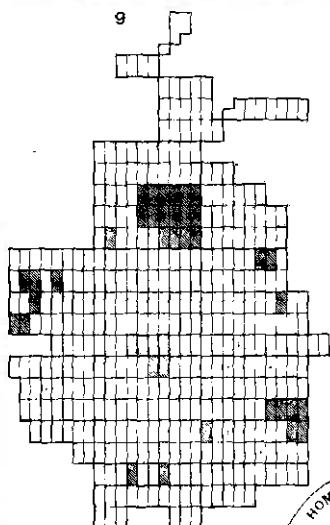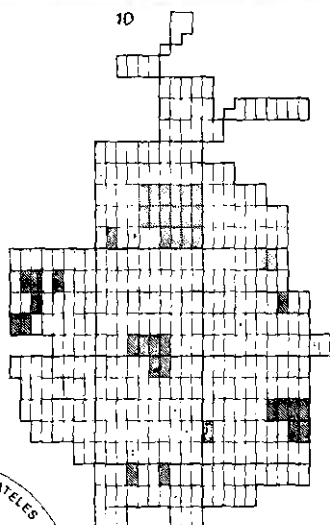
Geissospermum sericeum
'hoogland bergi-bita'
(7)

HOME RANGE OF ATELES

11
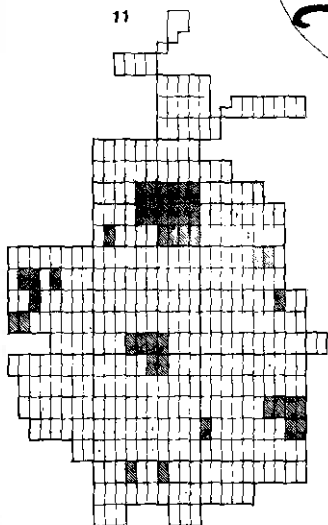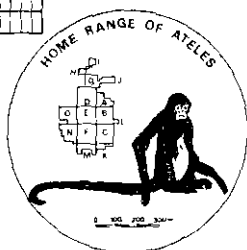
Macoubea guianensis
'sokosoko-maba'
(7)
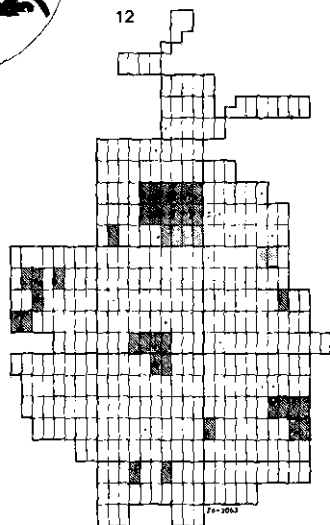
12

Tabebuia capitata
'makagdin'
(15)

13

14
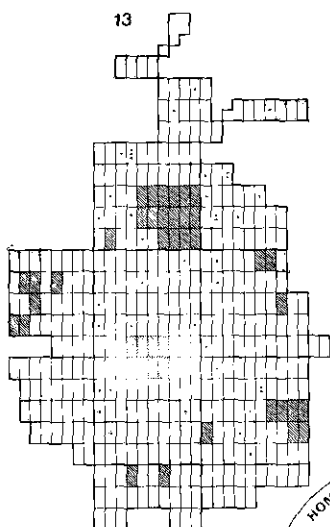
Tabebuia serratifolia
'groenhart'
(38)
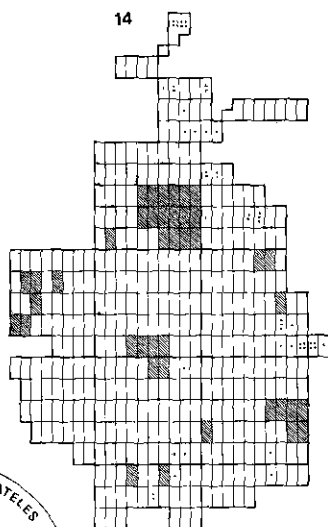
Pachira insignis
'boosi-momow'
(51)

HOME RANGE OF ATELES

0   100   200   300m

15

16
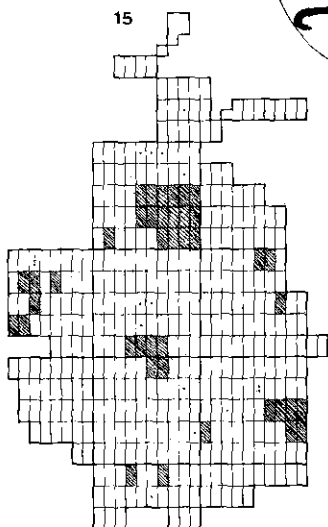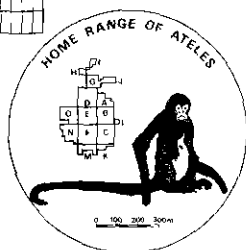
Ceiba pentandra
'kankantri'
(18)
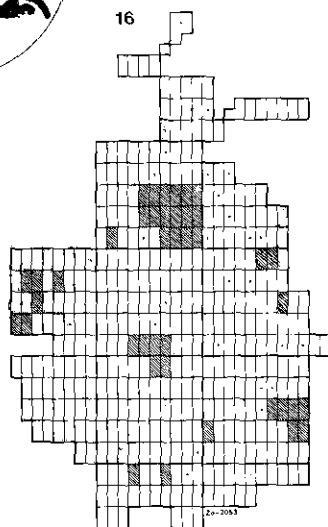
Cordia sagotii + Cordia lomatoloba
'hoogland tafrabon'
(28)
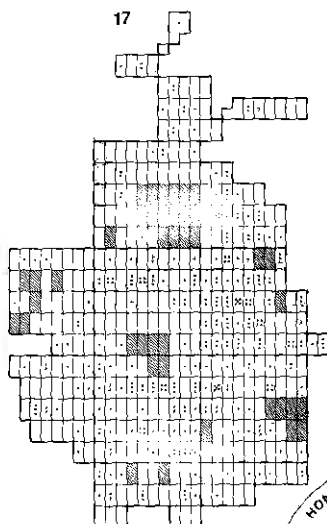
17

18

Protium neglectum
'grootbladige tingimoni'
(311)

HOME RANGE OF ATELES

0 100 200 300m

Protium polybotryum
'rode bast tingimoni'
(217)

19

20
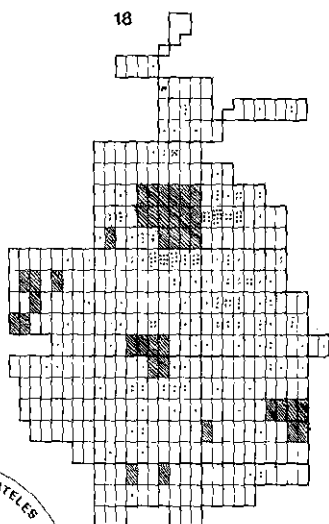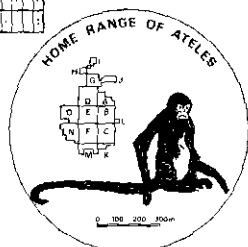
Tetragastris altissima
'rode sali'
(1531)
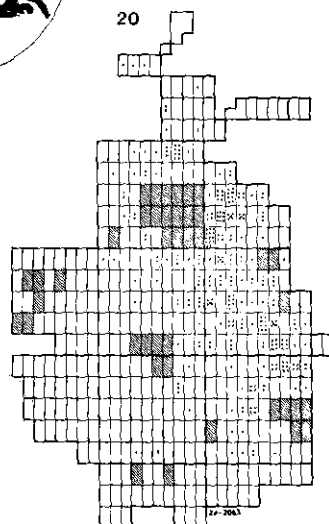
Tetragastris panamensis
'tingimoni-sali'
(280)

21

Capparis maroniensis
(304)

22

Jacaratia spinosa
'awara-oedoe'
(7)

HOME RANGE OF ATELES

0 100 200 300 m

23

Caryocar glabrum
'gladde sopo-oedoe'
(26)

24

Cheiloclinium cognatum
'liaansowtmeti-oedoe'
(20)

Zo-2053

Van Roosmalen

25

Amphizoma sp.
(2)

26

Dicranostyles guianensis
(4)

HOME RANGE OF ATELES

27

Moutabea guianensis
'llaanbosappel'
(6)

28

Maytenus sp.
'dikke bast sowtmeti-oedoe'
(3)

Habitat...

29

30
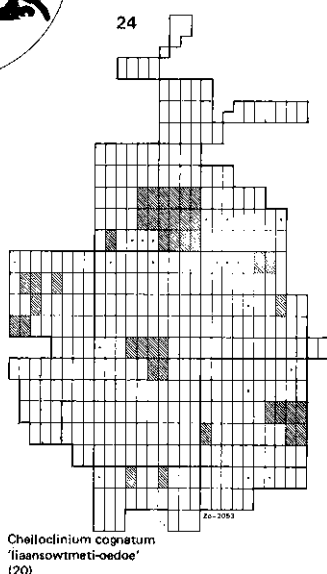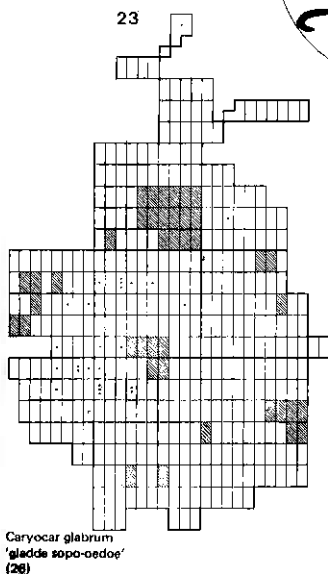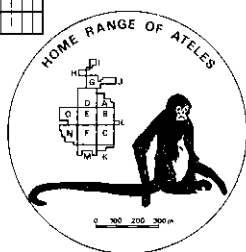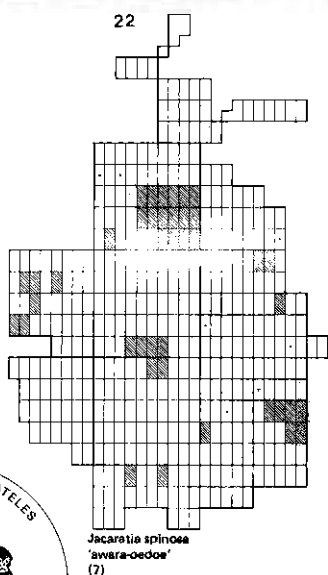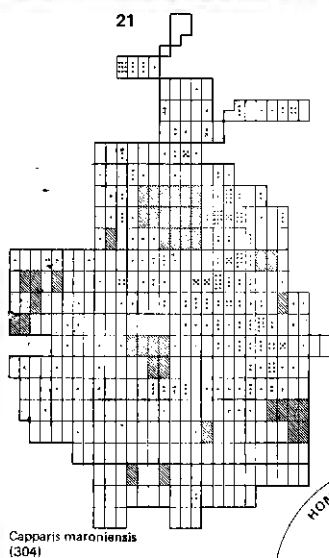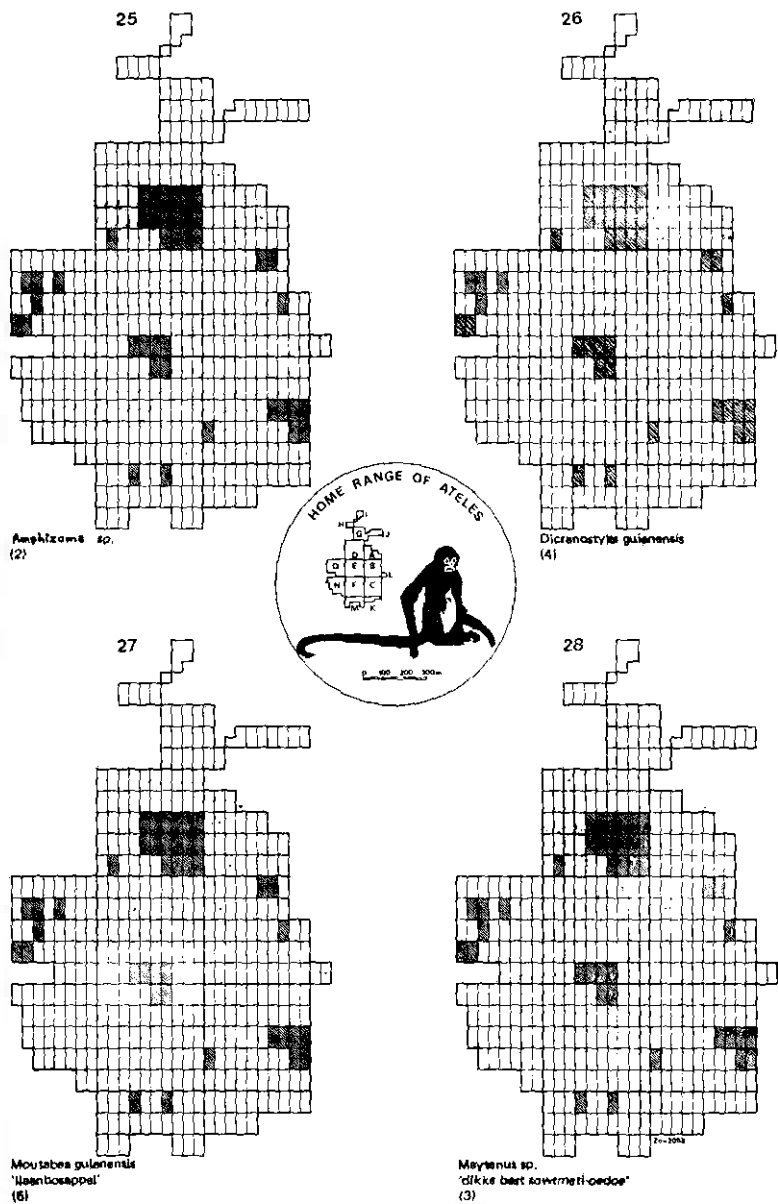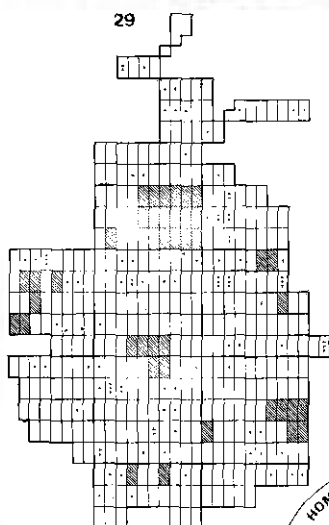
Couepia caryophylloides
'hoogland anawra'
(99)
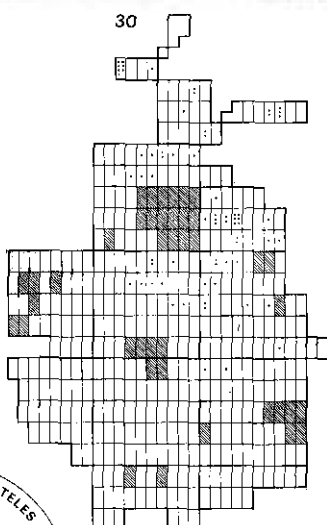
Licania majuscula
'harde bast kwepi'
(67)

31

32
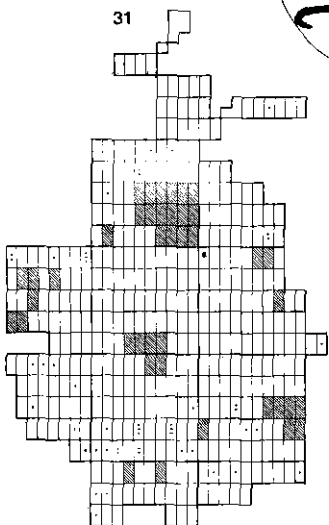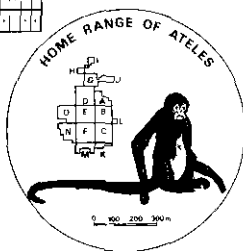
Licania micrantha
'zwarte foengoe'
(49)
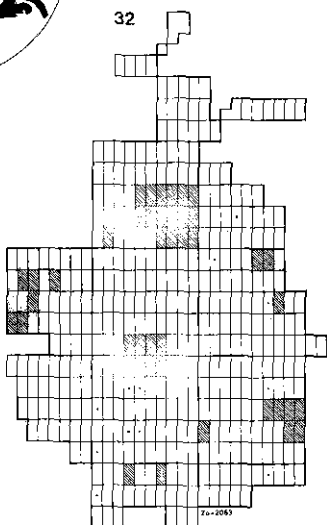
Parinari campestris
'rode foengoe'
(12)

212

Van Roosmalen

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

33

34
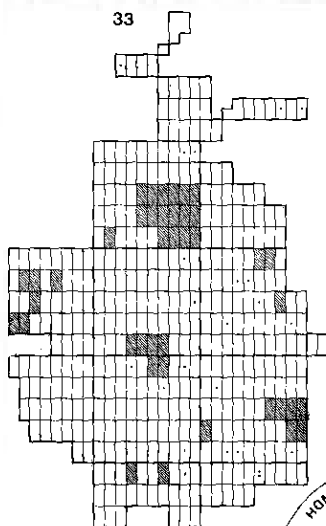
Parinari excelsa
'kleinbladige rode foengoe'
(22)
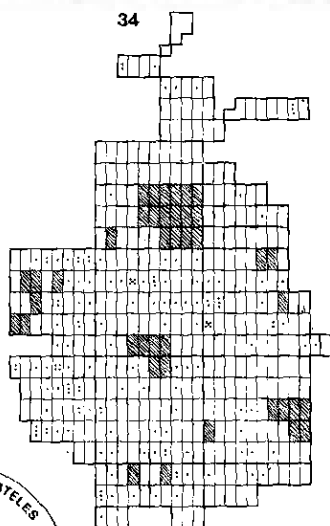
Buchenavia capitata
'djindja'-oedoe'
(160)
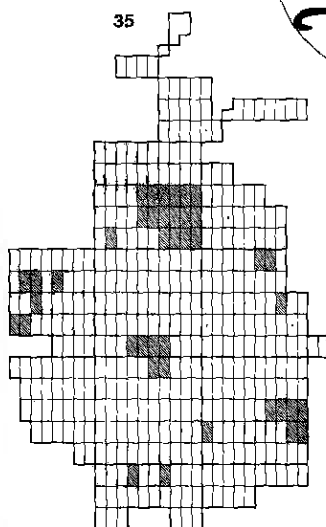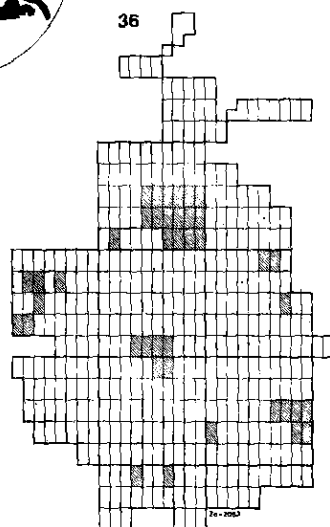
HOME RANGE OF ATELES

0 100 200 300m

35

36

Maripa scandens
(4)

Alchorneopsis floribunda
'manbebe'
(2)

37

38
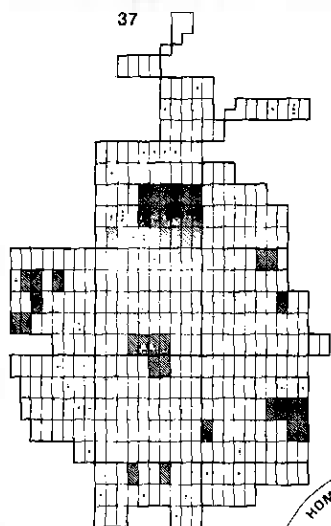
Drypetes variabilis
'witte foengoe'
(35)

Hysronima laxiflora
'ajo-ajo'
(36)

HOME RANGE OF ATELES

39

40
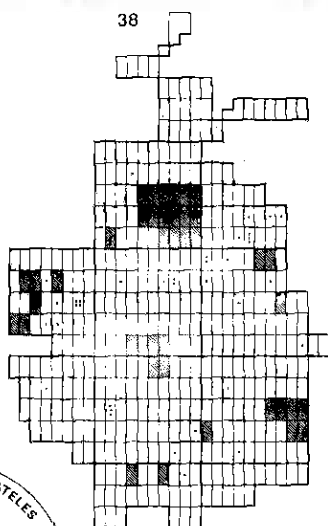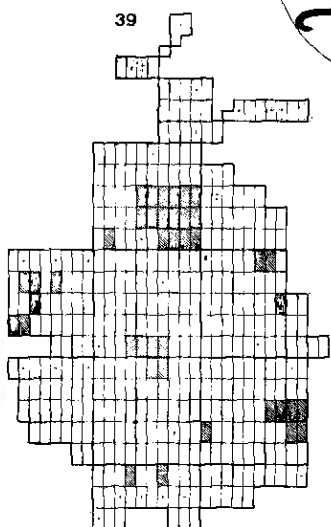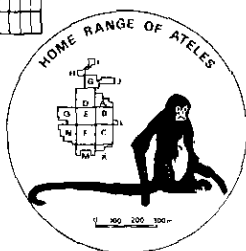
Laetia procera
'kaiman-oedoe/pintokopi'
(30)
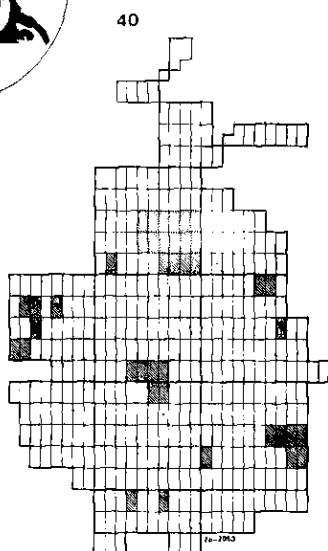
Gnetum urens
(2)

Van Roosmalen

41

Goupia glabra
'kopi'
(8)

42
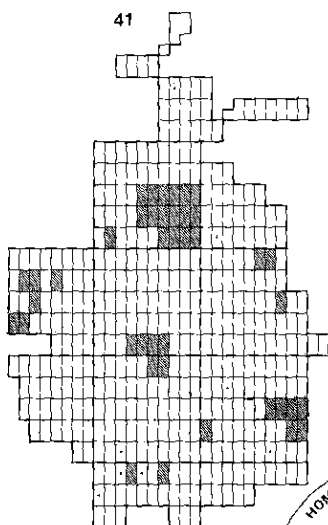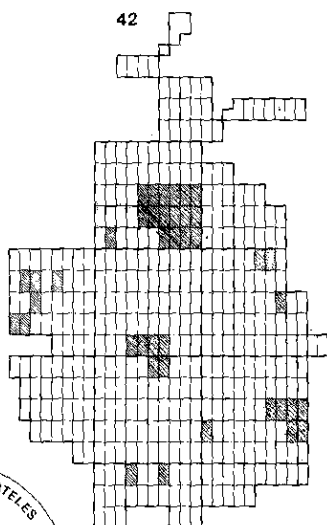
Platonia insignis
'geelhart/pakoeli'
(2)

HOME RANGE OF ATELES

0   100   200   300m

43
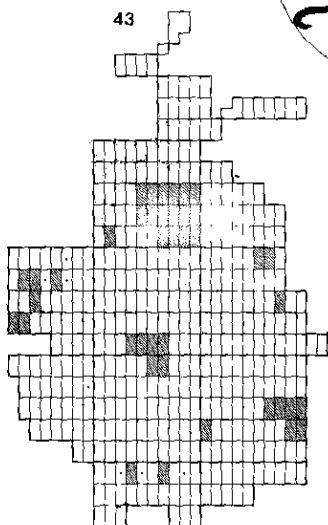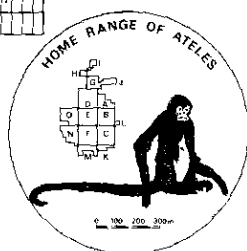
Rheedia benthamiana
'hoogland pakoeli'
(7)

44
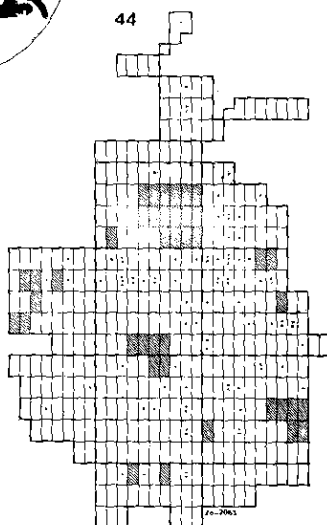
Rheedia macrophylla
'pakoeli'
(88)

45

46

47

48
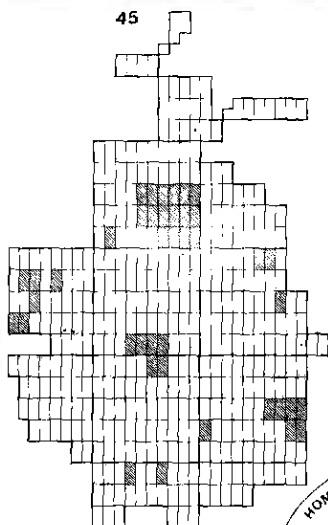
Symphonia globulifera
'matakí'
(2)
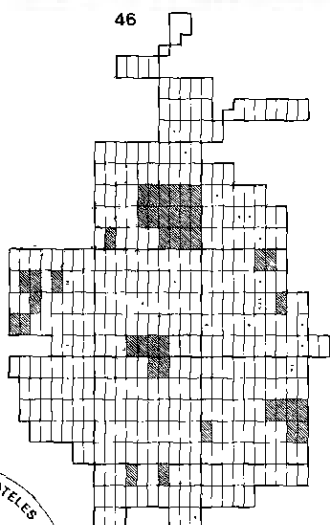
Secoglottis cydonioides
'witte bast bofroe-oedoe'
(21)
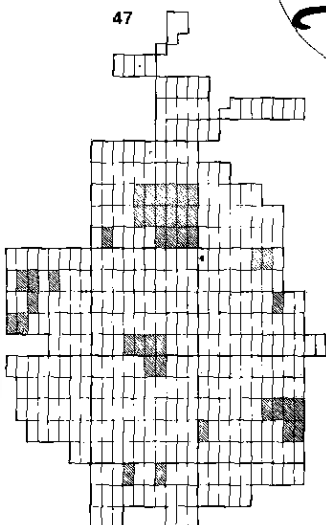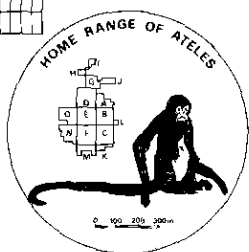
Licaria cepella
'kaneelhart'
(2)
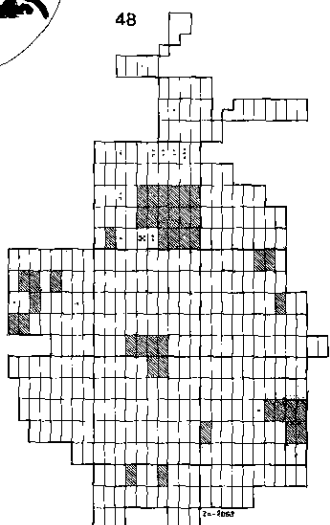
Nectandra   kunthiana
'grootbladige zwarte pisi'
(24)

HOME RANGE OF ATELES

0   100   200   300m

Van Roosmalen

49

50
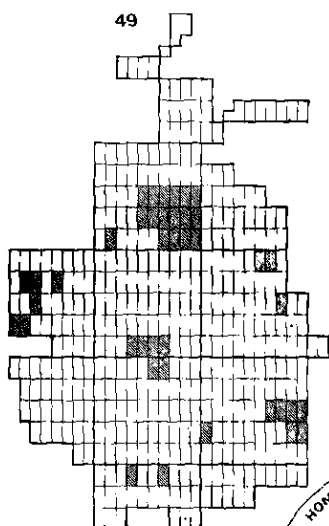
Ocotea wachenheimii
'plei'
(2)
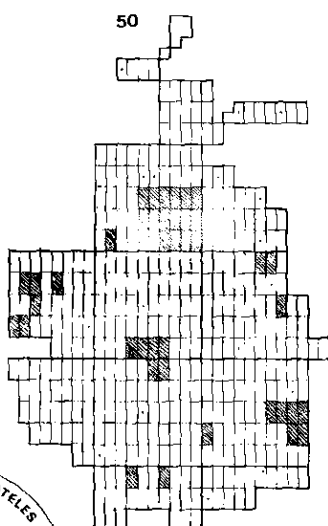
Couratari guianensis
'ingi-pipa'
(17)

HOME RANGE OF ATELES

0   100 200 300m

51

52
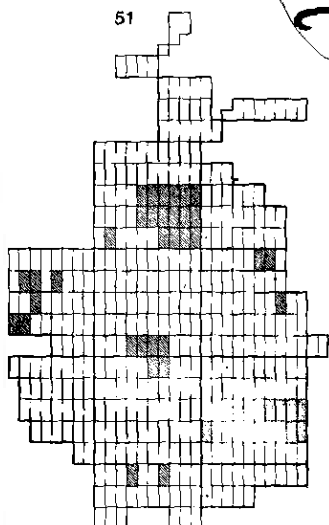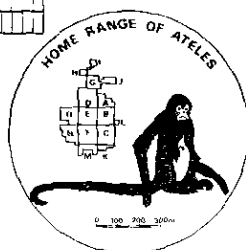
Couratari oblongifolia
'ingi-pipa'
(3)
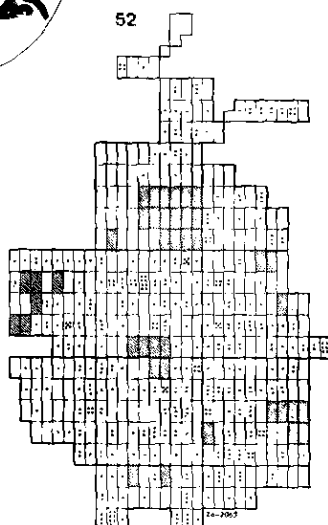
Couratari stellata
'ingi-pipa'
(403)

Habitat...   **217**

53
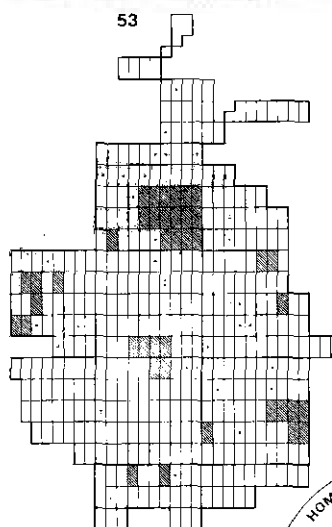
Eschweilera chartacea
'witte bast tité-oedoe'
(32)

54
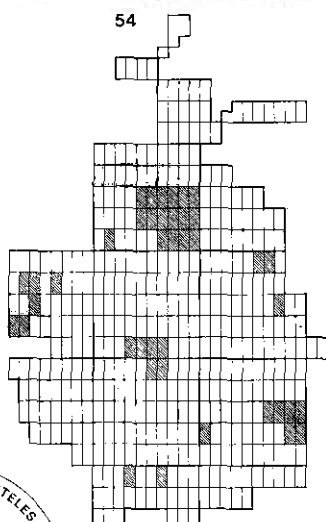
Eschweilera congestiflora
'oema-barklak'
(2)

HOME RANGE OF ATELES

0 100 200 300 m

55
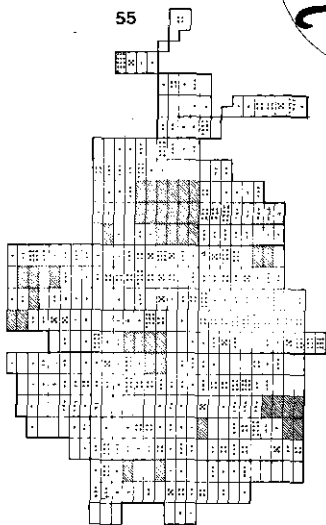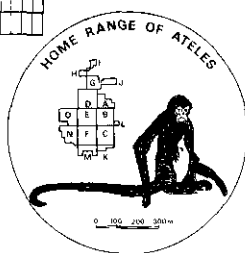
Eschweilera corrugata
'hoogland oema-barklak'
(761)

56
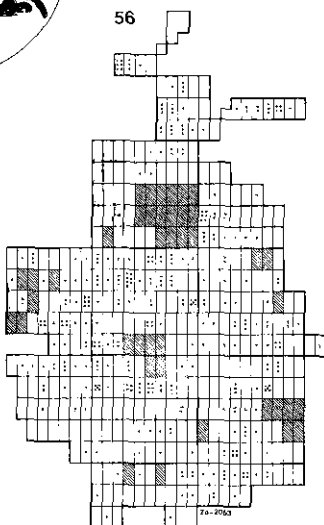
Eschweilera poiteaui
'gele bast tité-oedoe'
(336)

Van Roosmalen

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

57
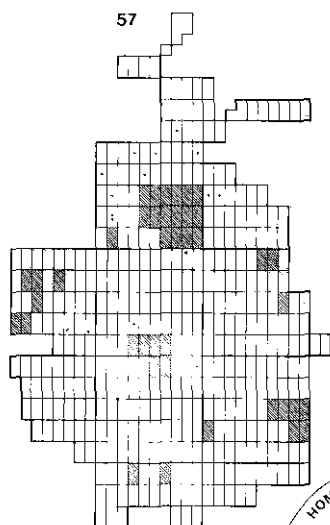
Copaifera guianensis
'hoepelhout'
(14)

58
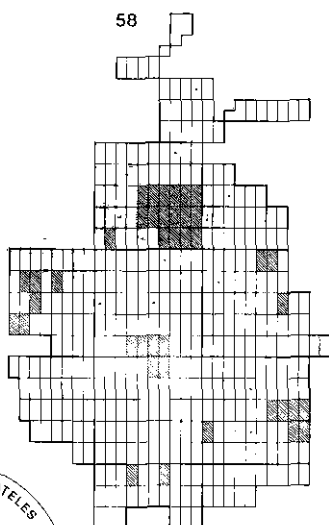
Dislium guianense
'hoogland makraka'
(13)

HOME RANGE OF ATELES

0 100 200 300m

59
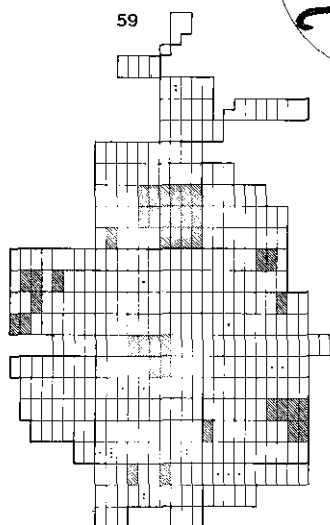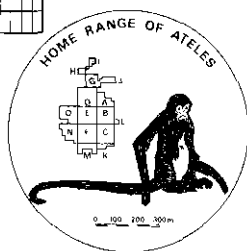
Dicorynie guianensis
'basralokus'
(19)
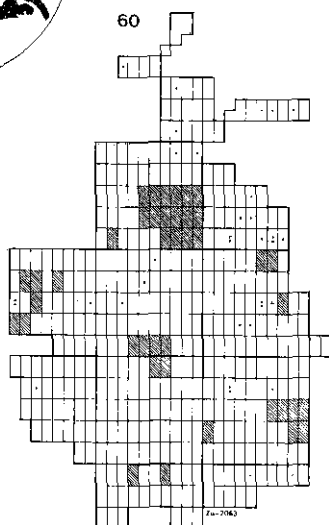
60

Dimorphandra pullei
(35)

61
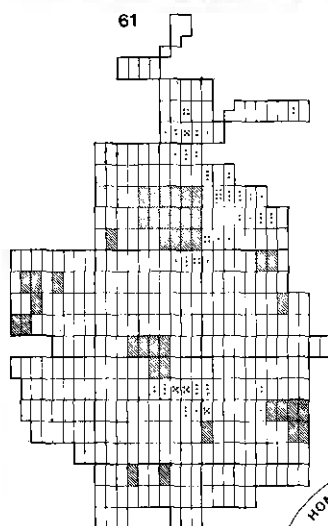
Eperua falcata
'walaba'
(102)

62
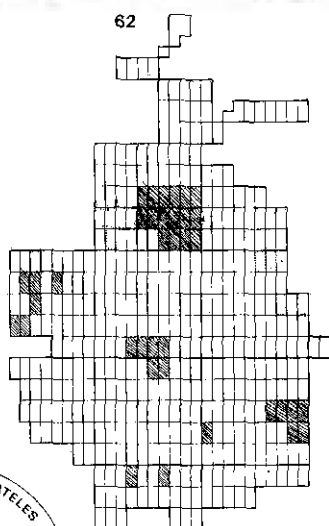
Eperua rubiginosa
'oeverwalaba'
(1)

HOME RANGE OF ATELES

0   100   200   300 m.

63
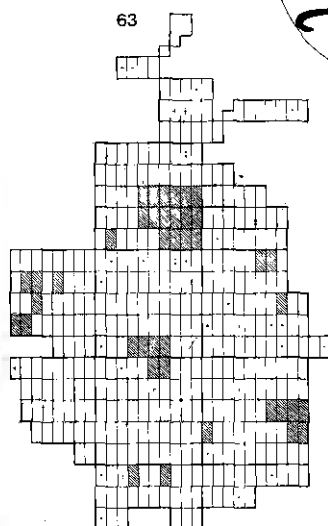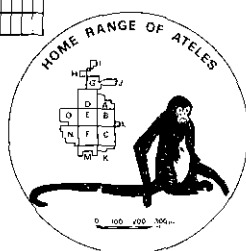
Swartzia schomburgkii
'witte boegoeboegoe'
(33)

64
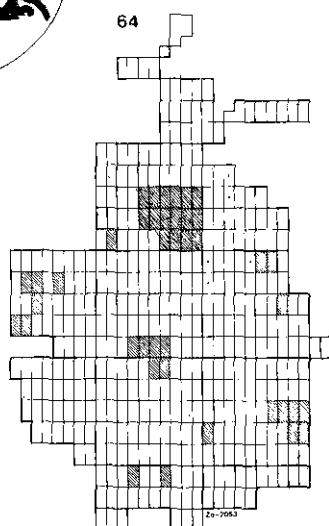
Swartzia remiger
'zwarte boegoeboegoe'
(5)

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65
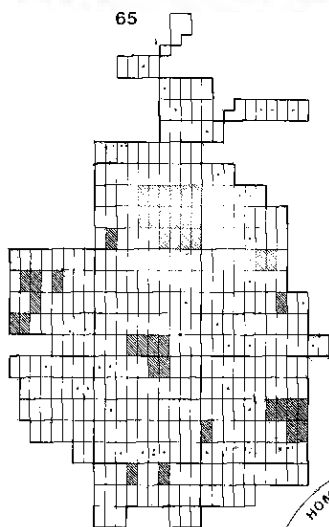
Cedralinga cateniformis
'dorncedar'
(34)

66
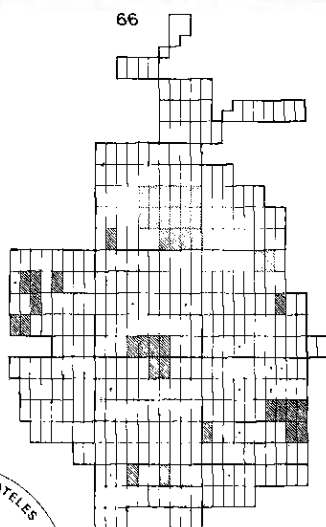
Enterolobium schomburgkii
'tamaren-prokoni'
(12)

HOME RANGE OF ATELES

0   100   200   300 m

67

Inga cinnamomea
'swit'bonki'
(5)

68
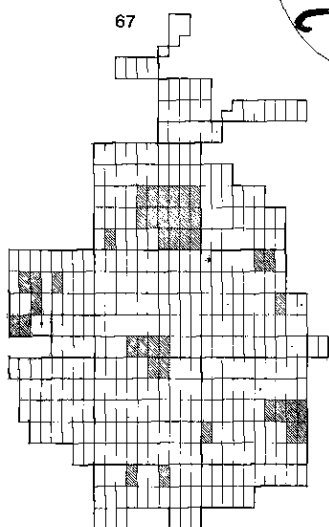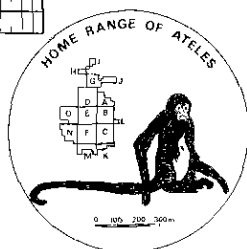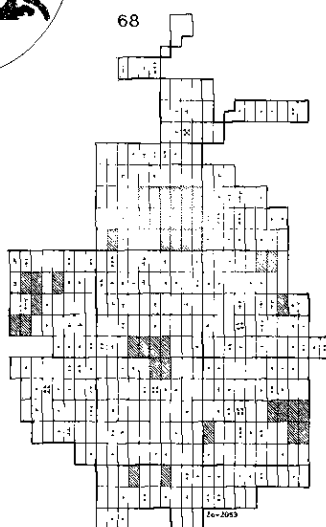
Inga alba
'rode prokoni'
(224)

69

70
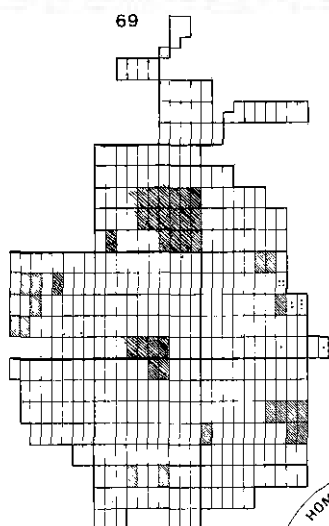
Inga bourgoni
'swit'bonki'
(11)
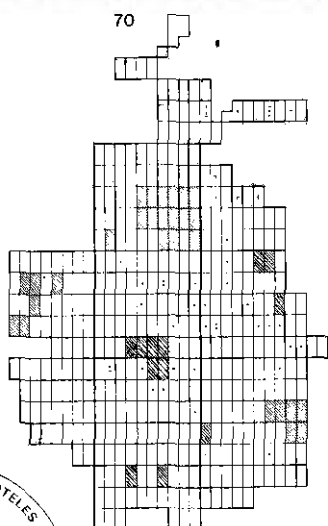
Inga cf. capitata
'swit'bonki'
(41)

71

72
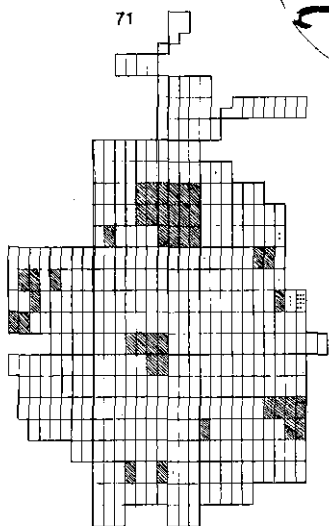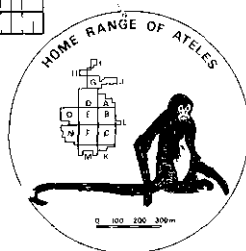
Inga edulis
'swit'bonki'
(19)
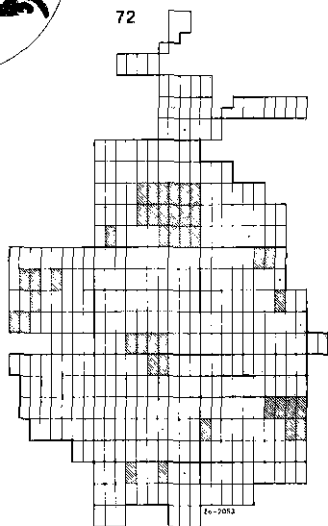
Inga leiocalycina
'swit'bonki'
(6)
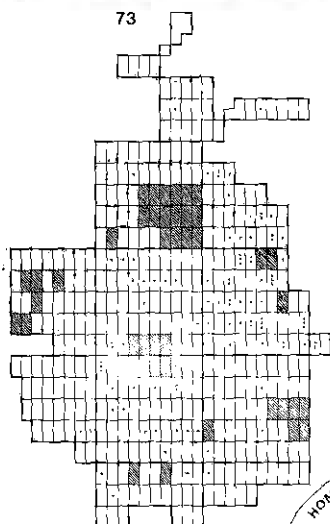
73

74

Inga acnecephala
'witte bast swit'bonki'
(96)

Piptadenia suaveolens
'pikin-mi-siki'
(45)

HOME RANGE OF ATELES

0 100 200 300 m

75

76
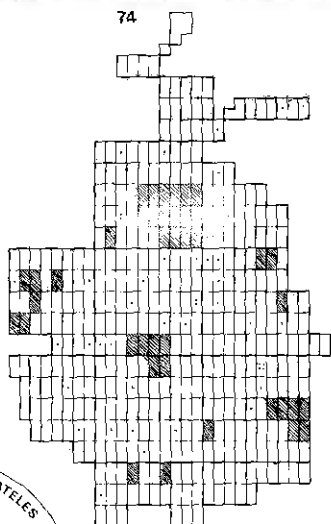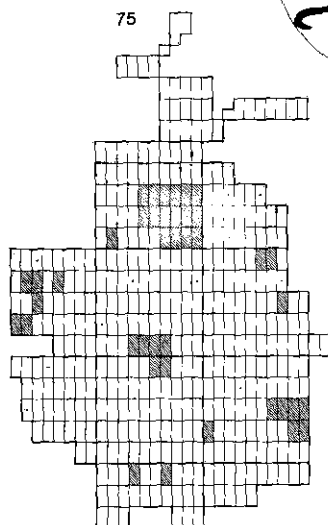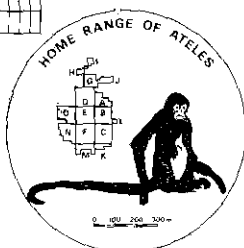
Parkia nitida
'grootbloemige agrobigi'
(11)
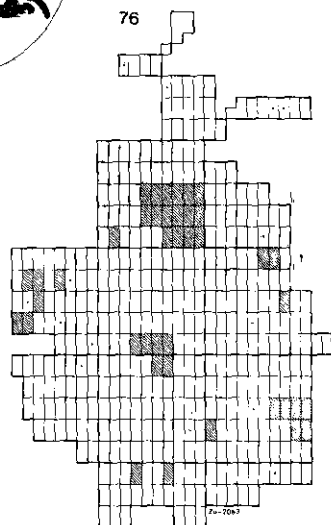
Parkia pendula
'kwatakama'
(15)

77

Pithecellobium jupunba
'fijnbladige sopo-oedoe'
(36)

78

Stryphnodendron polystachyum
'hoogland laksiri'
(15)

HOME RANGE OF ATELES

79

Dipteryx odorata
'tonka'
(11)

80

Hymenolobium flavum
'makakabes'
(19)

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81
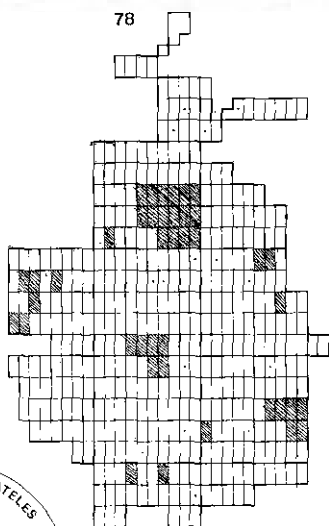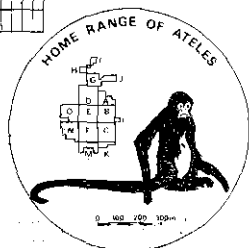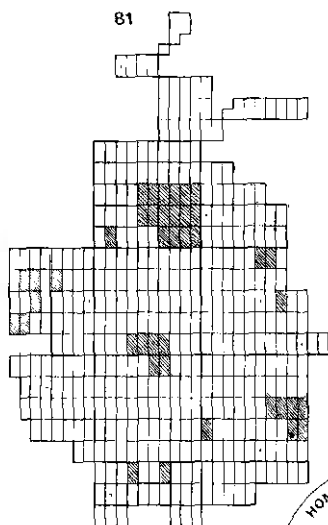
Hymenolobium petraeum
'wanakabes'
(8)

82

Platymiscium ulei
'koenatepi'
(22)

HOME RANGE OF ATELES

0   100   200   300m

83
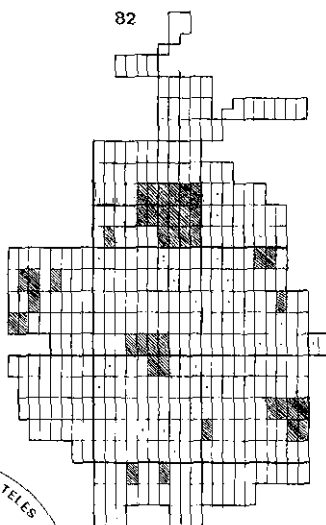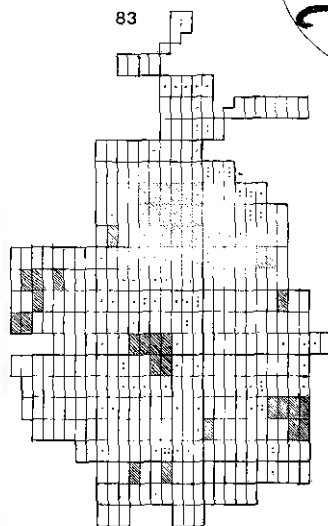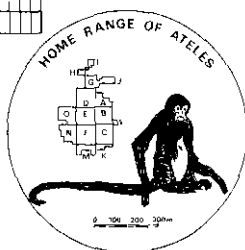
Pterocarpus officinalis
'watra-bebe'
(110)

84
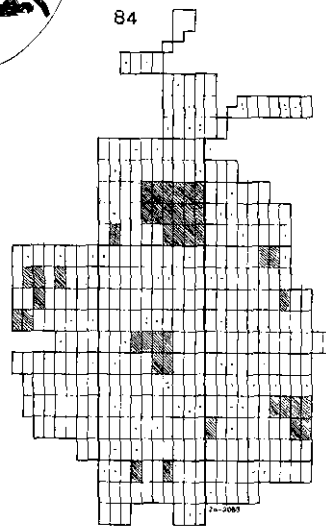
Vataireopsis speciosa
'djongokabes'
(70)

85
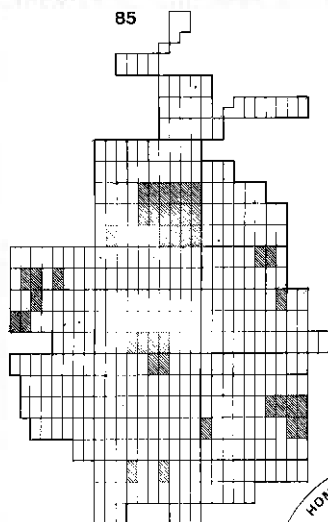
Strychnos tomentosa
'witte dobroedoewa'
(3)

86

Norantea guianensis
'rafroe-tere'
(8)

87
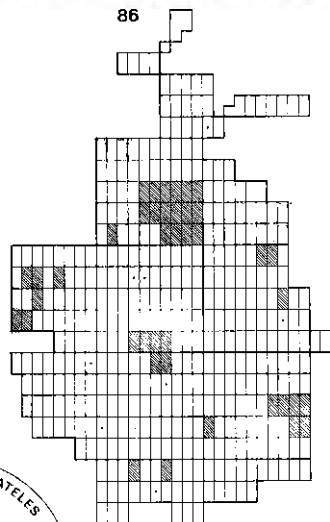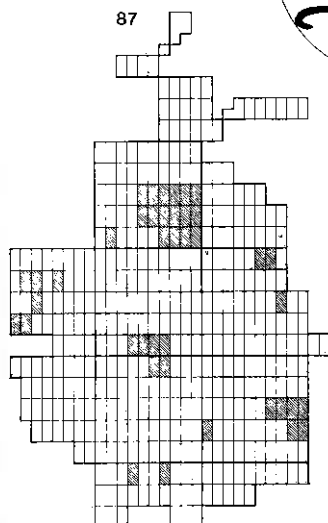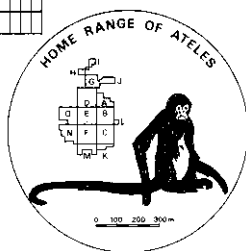
Ballucia grossularioides
'eetbare mispel'
(2)

88
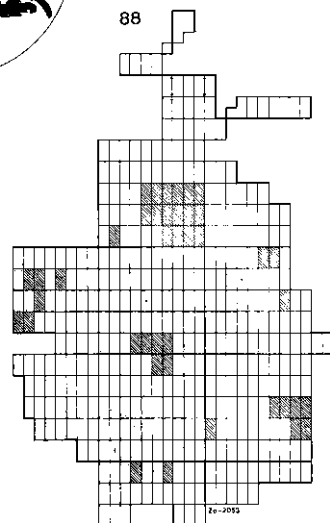
Mouriri sp.
'hoogbos spikri-oedoe'
(3)

HOME RANGE OF ATELES

0 100 200 300 m

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89
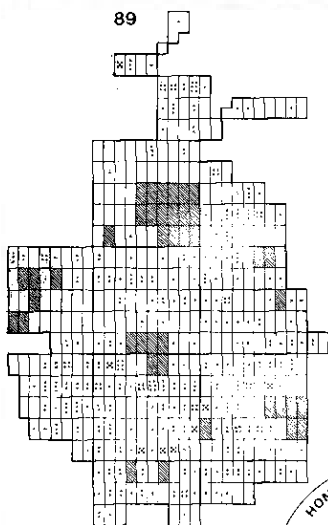
Carapa procera
'witte krapa'
(417)

90
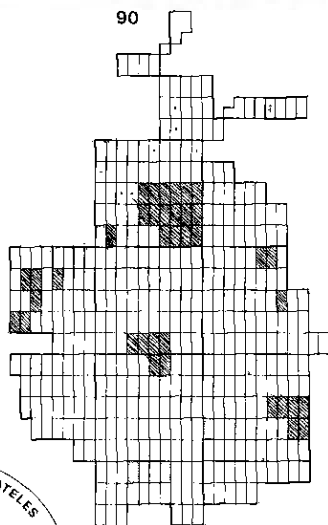
Cedrela odorata
'ceder'
(9)

HOME RANGE OF ATELES

0   100   200   300m

91
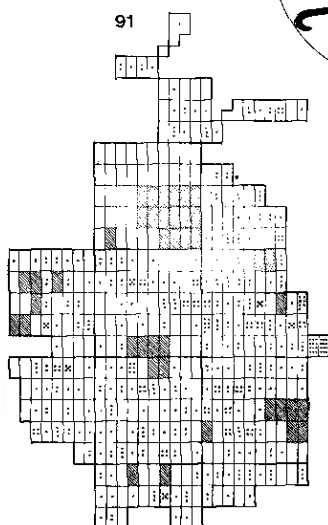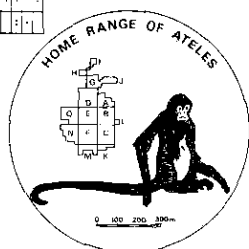
Guarea grandifolia
'doifisiri'
(449)

92
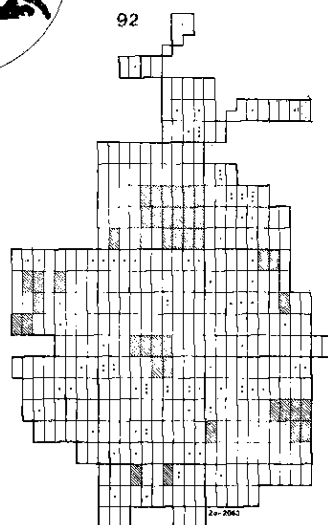
Guarea kunthiana
'zwarte doifisiri'
(88)

93

Trichilia martiana
(1)

94

Trichilia quadrijuga
'sorosali'
(102)

95

Abuta grandifolia
'bofroe-siri'
(4)

96

Bagassa guianensis
'kaw-oedoe'
(36)

97

98
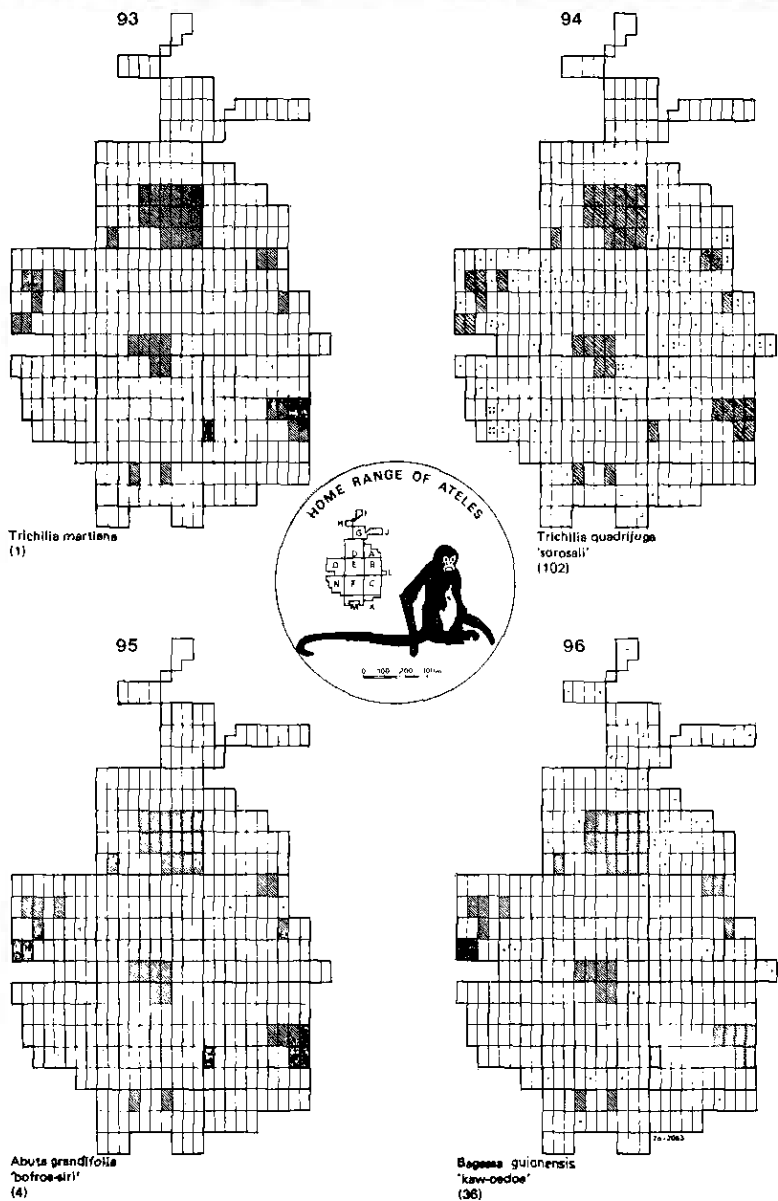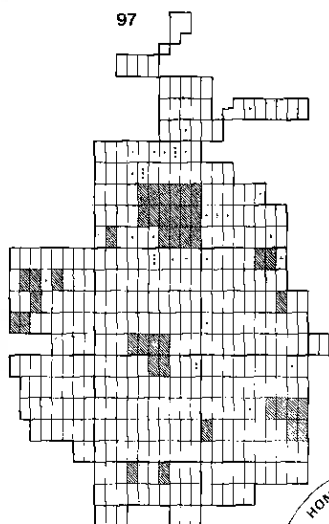
Brosimum lactescens
'kleinbladige doekali'
(32)
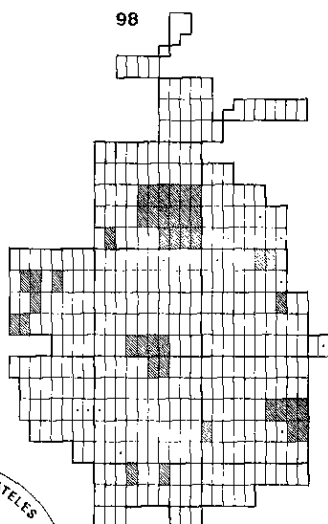
Brosimum parinarioides
'doekali'
(12)

HOME RANGE OF ATELES

99

100
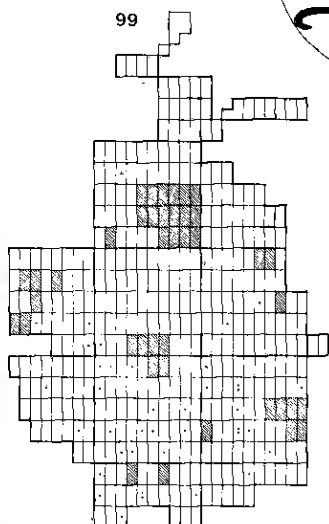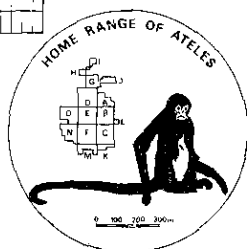
Cecropia sciadophylla
'man-bospapaja'
(40)

Cecropia latiloba
'bospapaja'
(39)

101
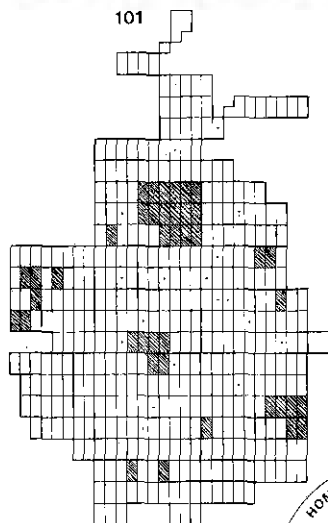
Clarisia racemosa
'rode bast doekali'
(19)

102
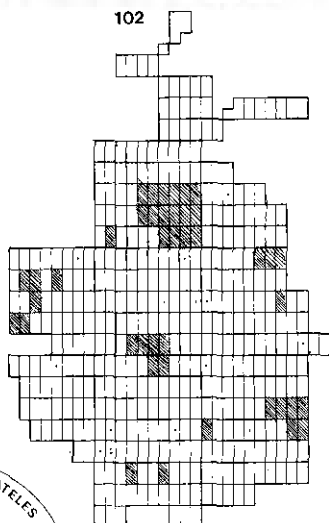
Coussapoa angustifolia
'bruinnarf-coussapoa'
(15)

HOME RANGE OF ATELES

0   100   200   300m

103
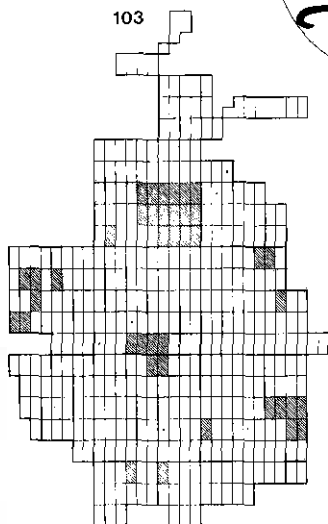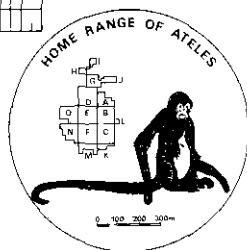
Coussapoa asperifolia
'ruwbladige coussapoa'
(5)

104
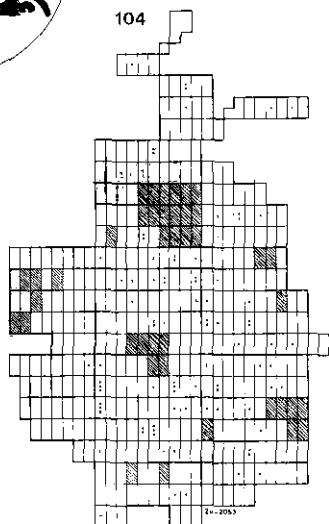
Coussapoa latifolia
'gladbladige coussapoa'
(86)

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105

106
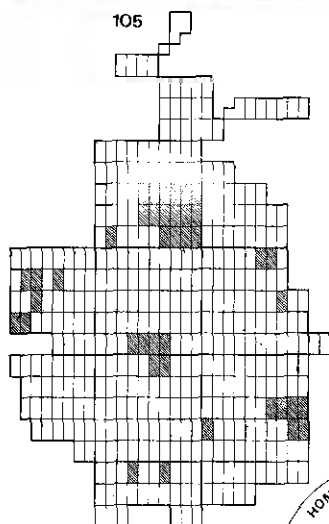
Helicostylis pedunculata
'letterhout'
(1)
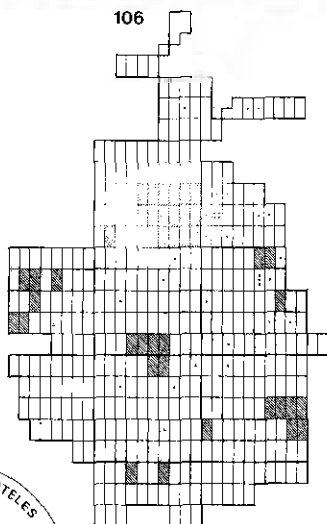
Helicostylis tomentosa
'kleinbladige manletter'
(31)

107

108
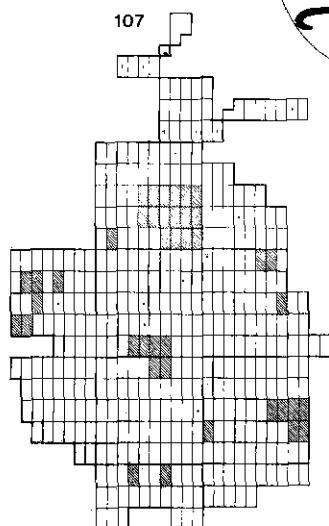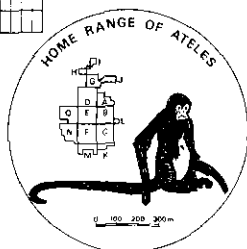
Maquira guianensis
'gewone manletter'
(12)
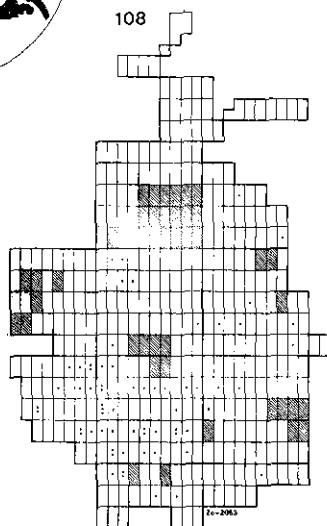
Pourouma minor
'granboesi-papaja'
(64)

109

110

111

112
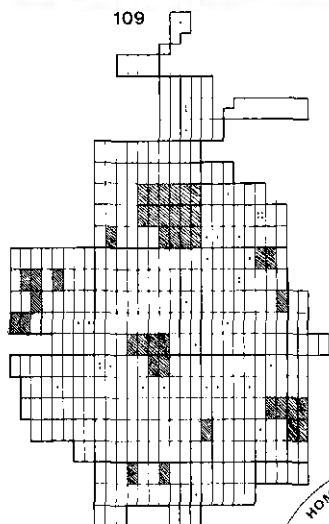
Pourouma mollis
'granboesi-papaja'
(33)
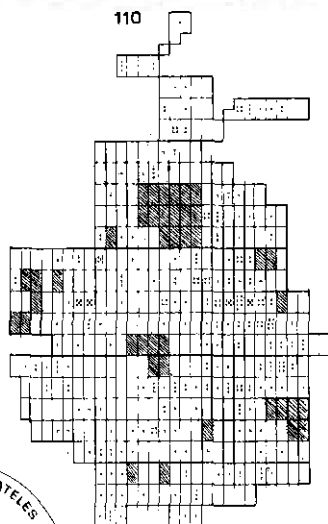
Virola melinonii
'hoogland baboen'
(313)
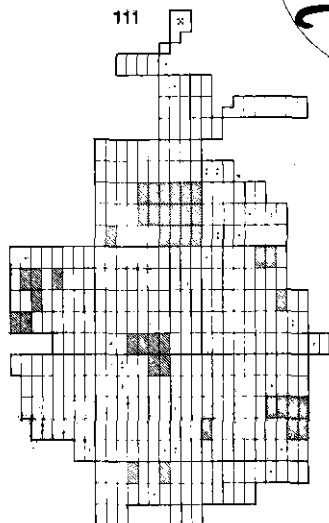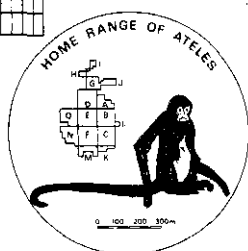
Virola surinamensis
'laagland baboen'
(32)
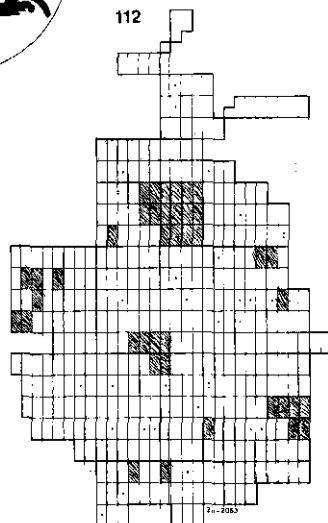
Minquartia guianensis
'slate-oedoe'
(30)

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113
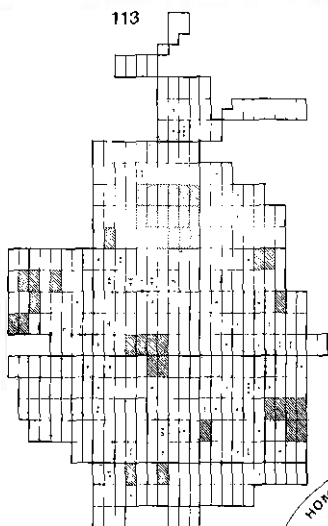
Oenocarpus bacaba
'koemboe'
(67)

114

Guettarda acreana
'bergkoffie'
(53)

HOME RANGE OF ATELES

0 100 200 300m

115
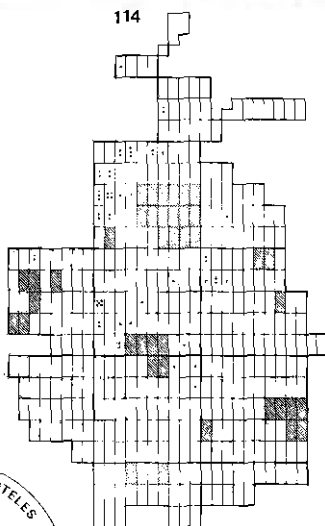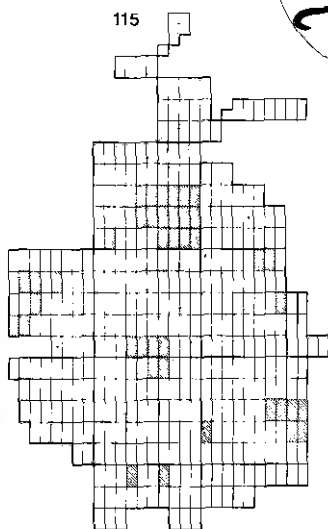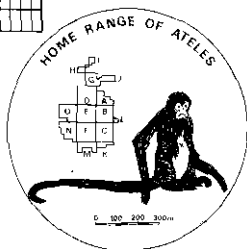
Paullinia spicata
'fefi-finga'
(3)

116
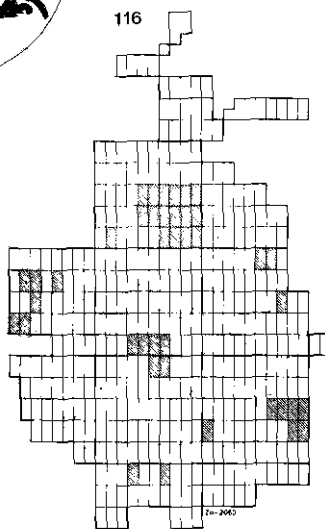
Paullinia tricornis
(2)

HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS

117

118
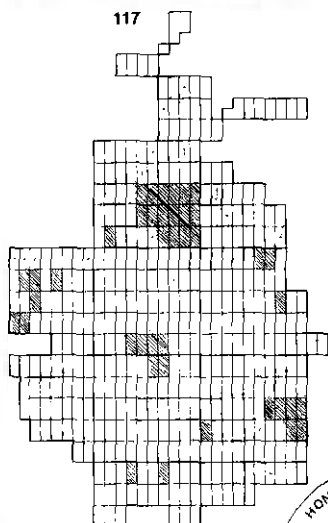
Achrouteria pomifera
'hoogland kimboto'
(19)

Prieurella cuneifolia
'kwatabobi'
(7)

HOME RANGE OF ATELES

119

120
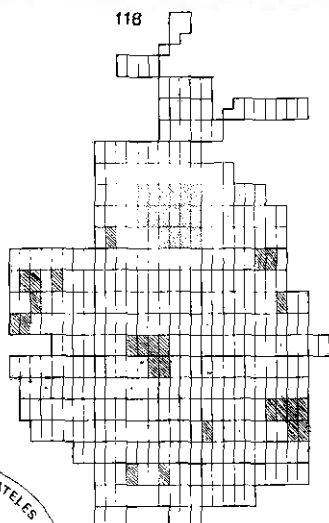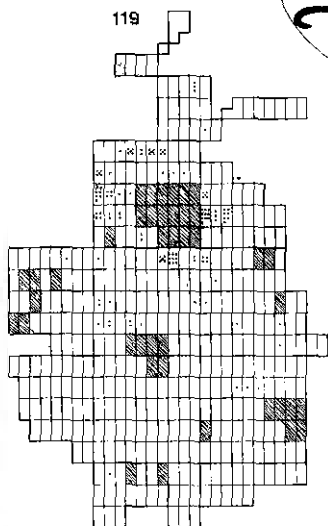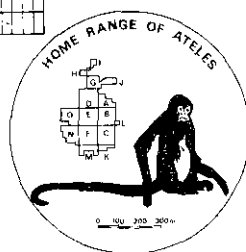
Ecclinusa guianensis
'batamballi'
(121)
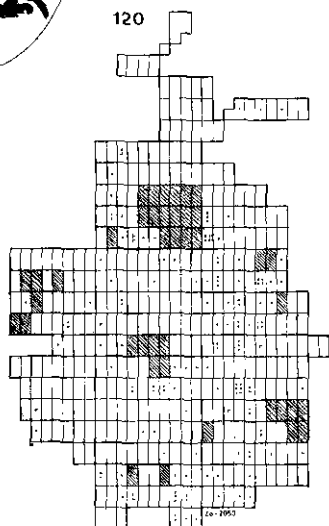
Prieurella sp.
'hoogland kimboto'
(138)

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121

122
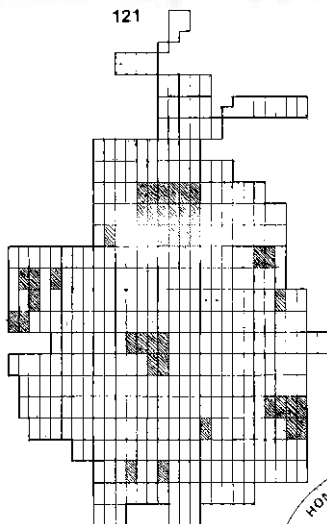
Ragala sanguinolenta
'swit'anini'
(4)
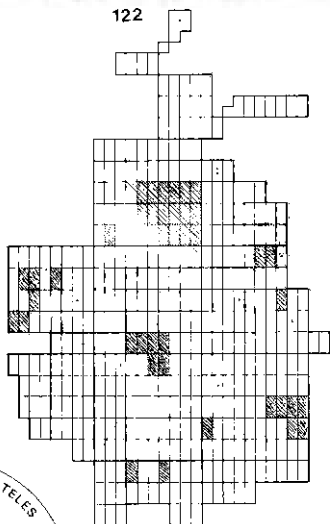
Pouteria guianensis
'jensnijder/rode jamboka'
(9)

HOME RANGE OF ATELES

0   100 200 300m

123

124
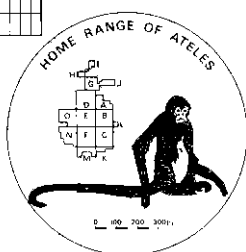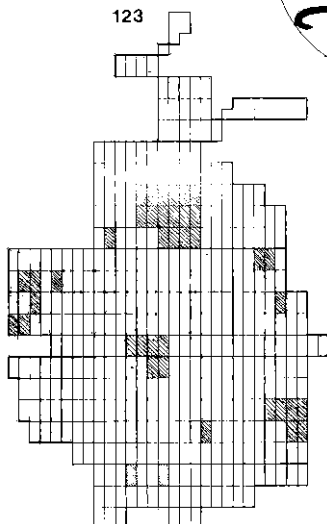
Eramoluma sagotiana
'apra-oedoe'
(1)
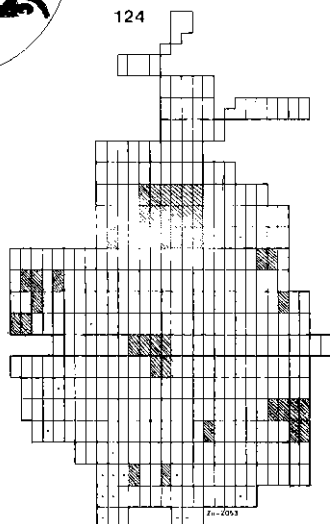
Pouteria sp.
(15)

Habitat...   235

125
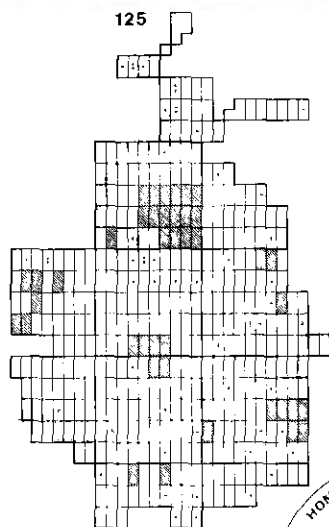
Quassia simarouba
'soemaroeba'
(53)

126
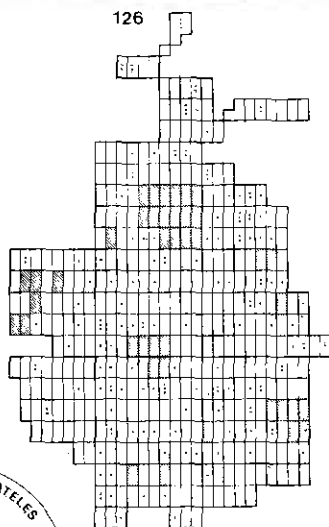
Sterculia excelsa
'okro-oedoe'
(155)

127
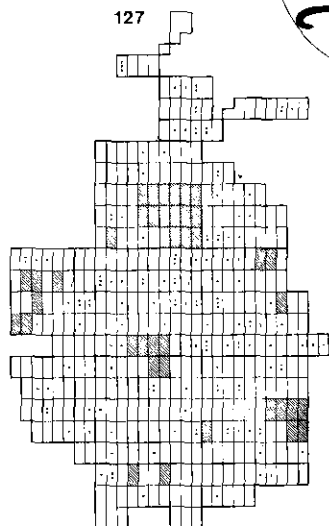
Apeiba echinata
'kankan-oedoe'
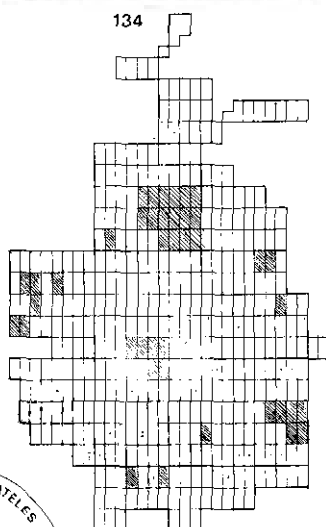(145)

128
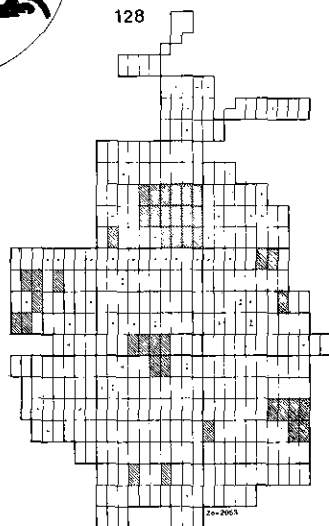
Apeiba glabra
'kankan-oedoe'
(54)

HOME RANGE OF ATELES

Van Roosmalen

129

130

Apeiba schomburgkii
'kankan-oedoe'
(4)

Apeiba tibourbou
'fokofoko-oedoe'
(8)

HOME RANGE OF ATELES

0   100   200   300m

131

132

Ampelocera edentula
'kwas'kwas'oedoe'
(19)

Vitex stahelii
'kalebashout'
(72)

Zu-2063

Habitat...   237

133

134
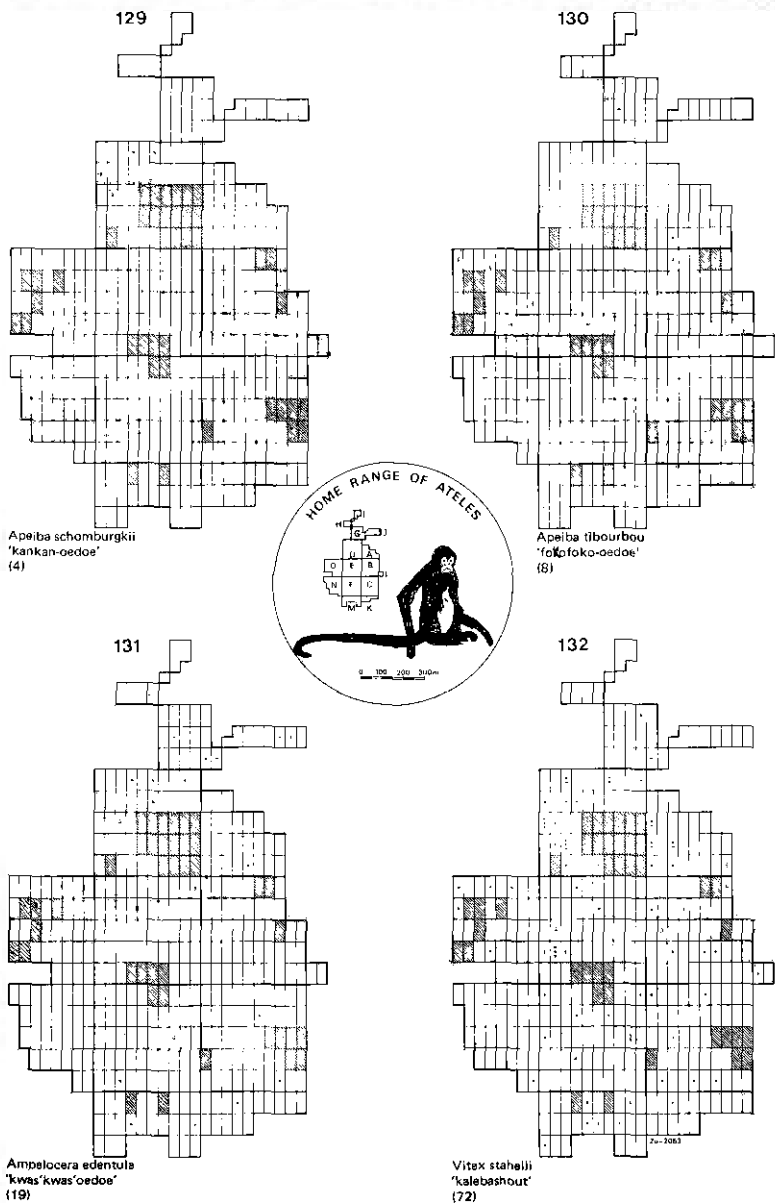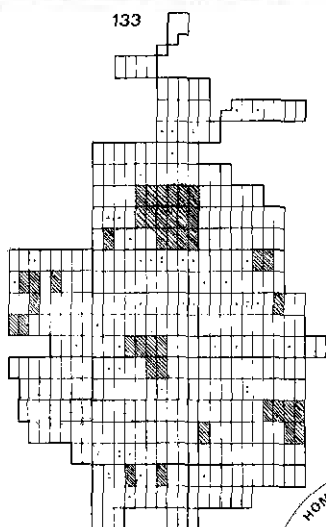
Qualea dinizii
'goejaba-kwari'
(50)

HOME RANGE OF ATELES

Vochysia tomentosa
'wane-kwari'
(20)

135

Styrax aff. fanshawei et micrasterus
(2)

Van Roosmalen