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 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-

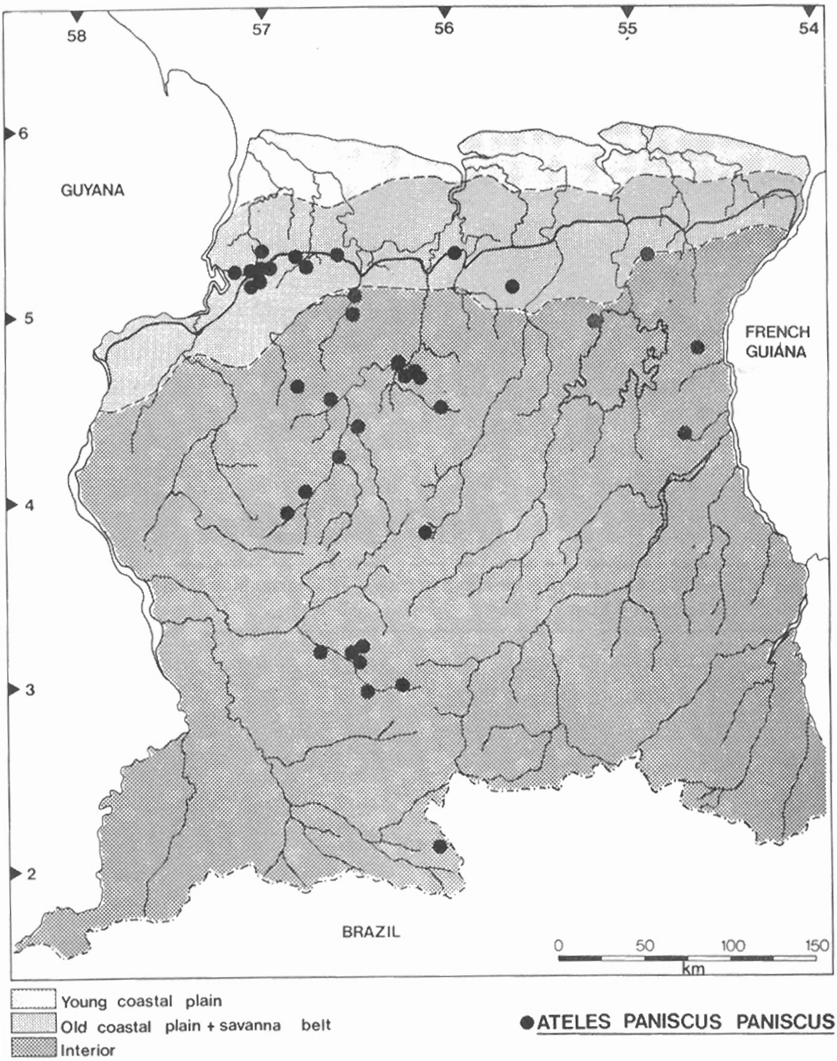

Figure 1 Distribution map for *Ateles paniscus paniscus* in Surinam. The central broken line marks the border between the coastal region and the interior. The area immediately to the north of this line is the old coastal plain, that to the south is the savanna belt. The dashed lines indicate the borders 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.

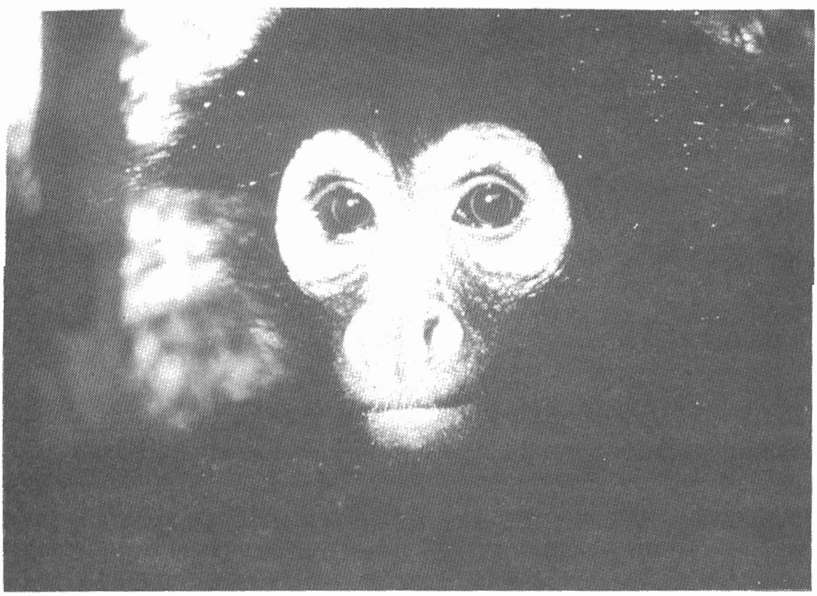

Figure 3 Adult female *Ateles p. paniscus* from Surinam (Photo by R. A. Mittermeier).

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^2in 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 weigth 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.O°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 granitodiorites 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 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-

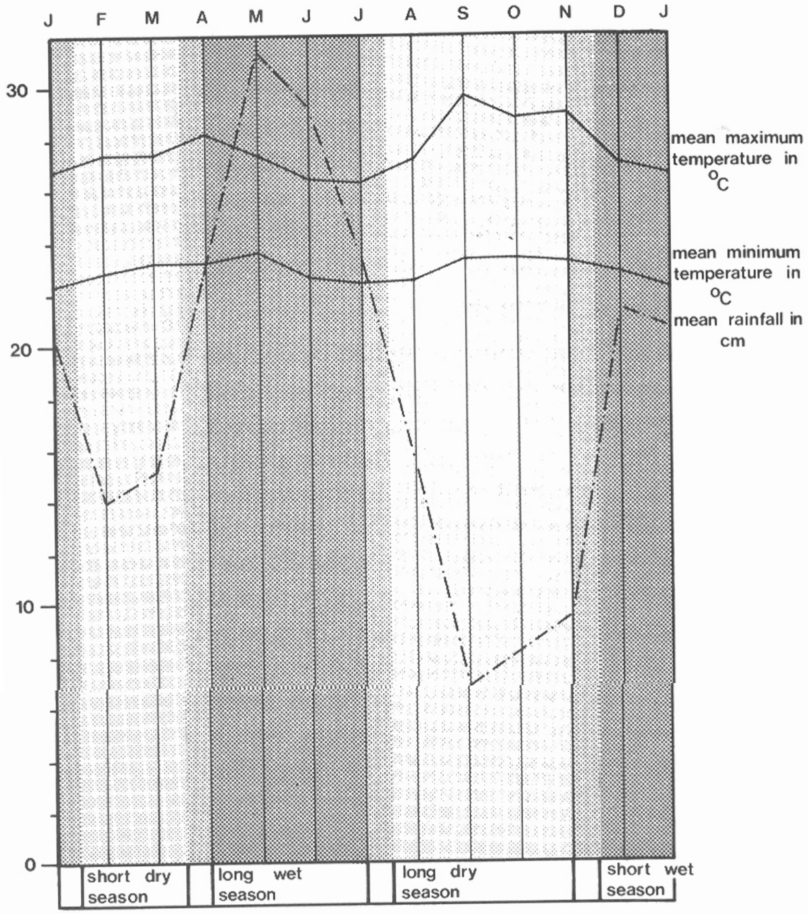

Figure 4 Climate of the Voltzberg study area during the present study, showing the monthly variations of mean maximum and minimum temperature at 1.5 m in the rain forest (full lines) and rainfall in a clearing (broken line). Data were collected from May 1976 to May 1978.

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 seasonal 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.

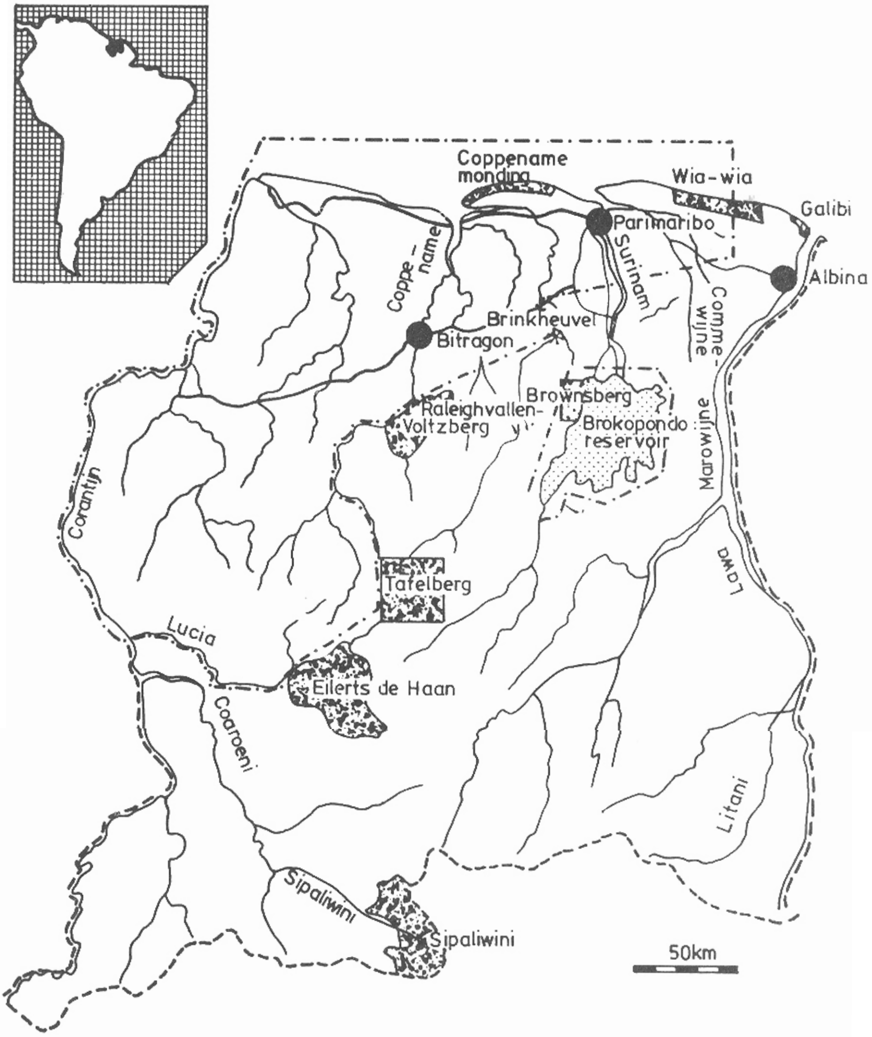

Figure 5 Map of Surinam showing the location of the Raleighvallen Voltzberg Nature Reserve and the other eight protected areas in the country.

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

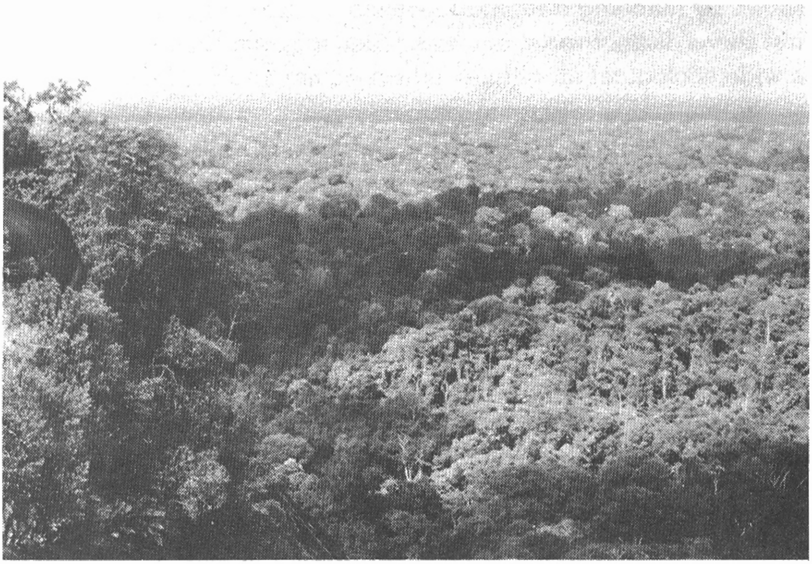

Figure 6 Scenic view looking south from the top of the Voltzberg, with part of the study area in the foreground. Note the other inselberg, the Van der Wijck top, at the horizon.

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

shown by reaching a reproductive state. The composition of the forest shows distinct variations from place to place. Some species show a wide ecological amplitude, others do not and are more local. Also the method of dispersal probably plays an important role. For example, seeds may be dispersed by wind, by water, endozoochorically, exochorically by rodents or autochorically. Figure 8 shows the distribution pattern of some species from high forest following different 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 racemosa*, 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 dispersed by scatter-hoarding rodents may show a clumped distribution 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 successfully will produce a non-random distribution pattem. This will also be the case in species which produce relatively small fruits containing many seedlets, such as berries. The seeds are mostly dormant, only germinating in a natural clearing caused by treefall. Germination is induced by strongly fluctuating soil temperature (as in *Cecropia 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 recorded for Surinam, 331 (68.1%) are found in high forest. Consequently, 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 formation.

The high forest of the Voltzberg region seems to offer a somewhat 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 *boegroemaka* palms (*Astrocaryum sciophilum*) that locally form a fairly continnuos layer at about 8 m height (fig. 7). The ground flora is very

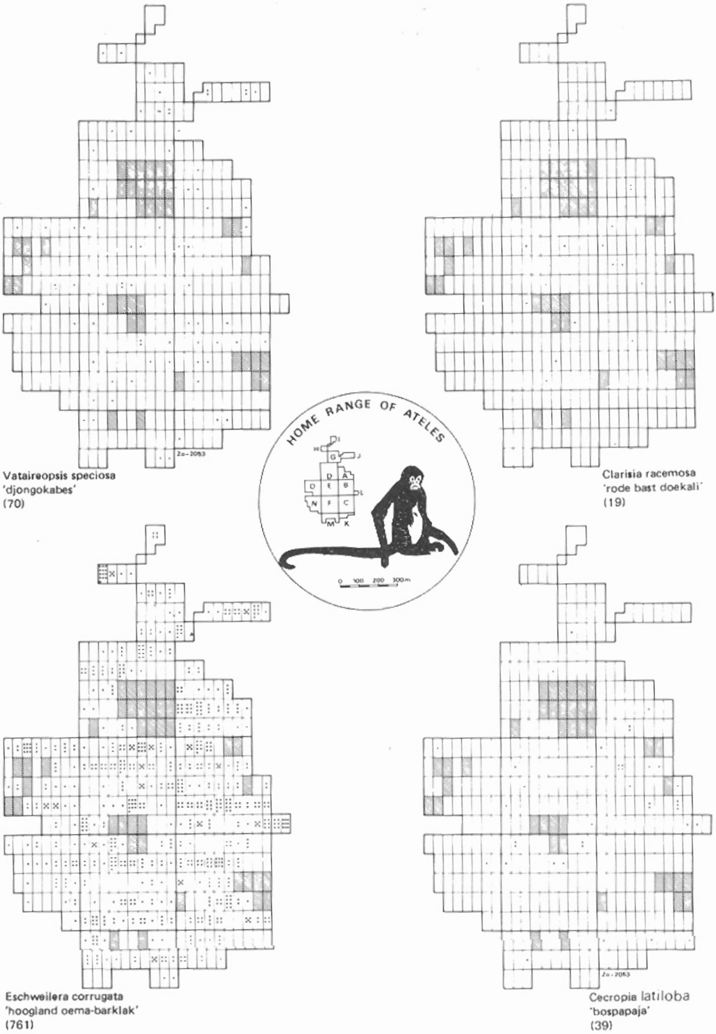

Figure 8 Distribution patterns of four tree species occurring in high forest in the Voltzberg region. The sampled area shown in the figure is part of the Voltzberg study area and is divided into ½ ha plots. The shaded areas indicate open granite and liane forest. *Vataireopsis speciosa*, an emergent 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-

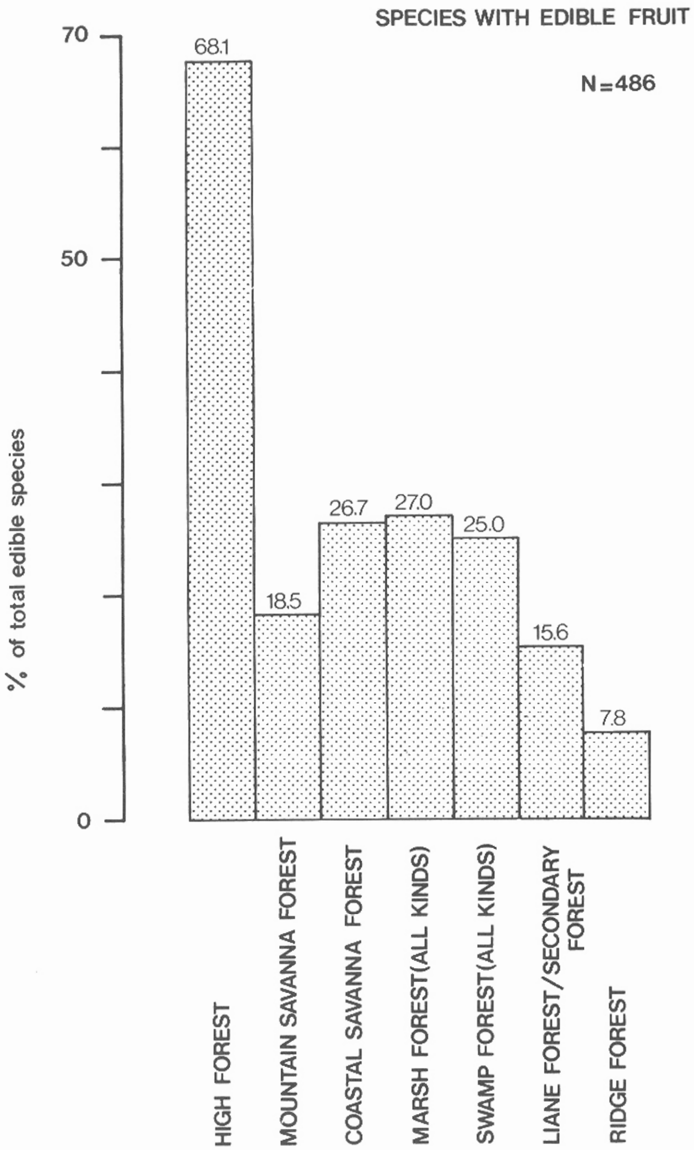

Figure 9 Woody plant species that produce fruit with an edible layer for monkeys and man and, exceed 2 m in height iin high forest and several other forest types in Surinam. Not included are the families Araceae and Palmae or those species that produce edible seeds. High forest has far more kinds of 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.

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.

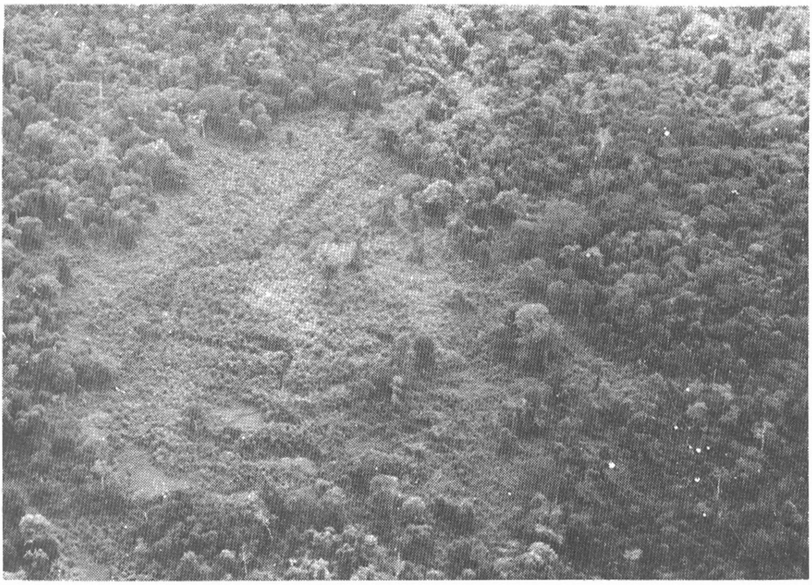

Figure 11 Aerial photograph of liane forest surrounded by high forest in the Raleighvallen - Voltzberg Nature Reserve. Note the isolated large-crowned emergents of the species *Vitex stahelii*.

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)

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.