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 portance 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 $\rm km^2$, or 8.2 individuals per $\rm km^2$ 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 concentrated 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 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 guality 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 dispersers may have evolved in lengthy, displaced, but broadly overlapping 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 ter-itory 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 rainforest 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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Habitat...

199

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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 ¹/₂-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.º 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).













210

Van Roosmalen





212

Van Roosmalen









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HOME RANGE SHOWING DISTRIBUTION AND DENSITY OF FOOD PLANTS



Van Roosmalen






































