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 *through-out 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

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 suc-
cessful every year and favoring both the specialized frugivorous ani-
mals 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 (*Chi-
ropotes 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 loose, 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).