Association patterns of spider monkeys:
the influence of ecology and sex on social organization

Colin A. Chapman

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, MA 02138, USA

Summary. In this paper I consider how the costs and benefits of group living in spider monkeys (*Ateles geoffroyi*) vary between troop members. The results suggest that ecological factors set an upper limit to the number of spider monkeys that can associate and still efficiently exploit the available resources. In addition, the needs of the individual appears to influence the type and size of the subgroup it chooses. Adult males band together, travel over a large area, and are frequently sighted near the community's boundary. In contrast, adult females spend more time solitary than males and have association patterns that are strongly influenced by the presence of a dependent infant. Females with dependent infants tend to travel in small subgroups or alone, avoid the boundaries of the community's home range, and exhibit a restricted pattern of use of their range. The results suggest that males may be attempting to locate females with which they can breed, while mothers attempt to protect their infants by avoiding conspecifics and potentially dangerous situations near territorial boundaries.

Introduction

The question of how social organizations evolve is of interest to both behavioral ecologists and evolutionary biologists. There are firm theoretical grounds to argue that certain aspects of social organizations, such as the size of groups, are adaptive responses to finding food and avoiding predation (Clark and Mangel 1986; Pulliman and Caraco 1984; van Schaik 1983; Bradbury and Vehrencamp 1976). In general, comparative studies have supported these theoretical arguments; however, they have illustrated that there is a large amount of variability that remains unexplained (Jarman 1974, 1983; Lott 1984). Much of this variability may be related to the interaction of ecological and social pressures (Wrangham 1986a). Finding mates and protecting offspring are vital components of an animal's future reproductive success and are, in the long term, of equal importance to finding food. For example, given that ecological pressures have favored a certain type of dispersion by females, males could adopt a number of different strategies that allow them to gain access to mates. Thus, ecological factors may establish constraints on the evolution of sociality, but the exact social organization that evolves will also be shaped by pressures acting on social behaviors.

In this study, I consider how the costs and benefits of group living in spider monkeys (*Ateles geoffroyi*) vary among troop members. To examine this, I first document how ecological factors influence the size of the subgroups formed. Secondly, I examine the association patterns and range use of individual spider monkeys in an effort to discover how the objectives of males, females, and females with infants differ. Finally, I discuss the generality of the finding that social organizations represent an amalgamation of individuals trying to meet their own social needs while being limited by specific ecological constraints.

Long-term studies of spider monkeys have shown that these animals live in a type of sex-segregated social system that is relatively uncommon in the primate order (Klein 1972; Klein and Klein 1977; Symington 1987, 1988a, b; Chapman 1988a, b). Adults spend their time in small subgroups that change size and composition frequently. When males are seen, they are often in all-male subgroups, which range further and travel faster than subgroups with females and young. All of the individuals associating in these subgroups are members of a single community consisting of 20–42 animals. All members are thought to use a common home range, the boundaries of which may (Symington 1987) or may not be defended (Chapman, unpublished data). Thus, unlike most primate species with cohesive social groups, male and female spider monkeys are not always in the same group, and each individual has the option of associating with subgroups of different sizes and/or compositions. This flexibility in association patterns provides the variability necessary to examine how both ecological and social factors influence this species' social organization.

Spider monkeys feed primarily on fleshy fruits (71.4% of feeding time, Chapman 1988a; 83%, Klein and Klein 1977; 76.9%, Symington 1987) that tend to be rare and located in patches that are far apart (Chapman 1988b). Previous investigations have suggested that the abundance and distribution of food resources influences spider monkey foraging efficiency by affecting travel costs and can constrain the size of the subgroups formed (Chapman 1988b; Symington 1988b). Spider monkeys tend to deplete the food resources they use, thus an increase in subgroup size results in an increase in the distance that must be travelled to find adequate food supplies (Chapman 1988b; Symington 1988b). With an increase in the time spent travelling, a point is approached where the energy spent in travel exceeds that obtained by feeding, and smaller subgroups become advantageous. Thus, the ecological conditions may strongly influence the size of the subgroup; however, it is not apparent how they influence their composition. In this study I examine the hypothesis that the composition of the subgroups is greatly influenced by social pressures.

Methods

Study site and community. A spider monkey community living in Santa Rosa National Park, Costa Rica, was studied for 36 months over a period of 6 years (1983–1989). The forest of Santa Rosa is primarily successional tropical dry forest, and during the dry season (December to May), the majority of the non-riparian trees are without leaves. This, coupled with the fact that the canopy is rarely higher than 30 m, produces conditions very favorable for the observation of arboreal primates. Chapman (1988a) and Janzen (1986) provide further description of the study site.

The study community was estimated to consist on average of 42 individuals; 4 adult males, 18 adult females, 1–2 large immature males, 3–4 large immature females, 8–5 small immatures, and 8–5 infants. Recognition of individuals was possible following the darting and tagging of animals, either as a result of the collars and anklets placed on the animals ($n = 13$) or by their scars and pelage patterns ($n = 22$). Thirty-five of the 42 individuals could be reliably recognized.

Behavioral observations. To obtain information on the association patterns and range use of individuals, subgroups containing specific recognizable individuals were located in the morning or early afternoon. Subsequently, the subgroup was followed and behavioral data were collected using a focal-animal sampling regime with 10-min sessions. When possible, the subject chosen for observation was selected according to a fixed rotation between individuals and/ or age-sex class. Whenever the focal animal was feeding, the food item and plant species were recorded, and the size (diameter at breast height, DBH) of the tree was visually estimated. The error in visually estimating DBH was 3.7% ($n = 46$; mean DBH of the trees used by the monkeys was 43.1 cm).

The behavior of the spider monkeys was monitored during 3-week sampling periods, so that at the end of each period, approximately an equal number of observations were made in each hour of the day, and all individuals of the community were sampled. Over the entire study, 26 sampling periods were completed.

The location of the subgroup being followed was recorded as a coordinate on a grid consisting of 120 m by 120 m cells, superimposed on an aerial photograph of the study area. Since known individual trees could be identified on the photograph, the error in estimating the location of the subgroup was probably small

and rarely resulted in the subgroup being recorded in the wrong cell of the grid. The home range of each individual was considered the sum of those cells that they were seen to use or would have had to pass through in order to get from the location of one sighting to that of another made on a subsequent day. Since immature animals travel with their mothers for the majority of their time, analyses of range use considered only identifiable adults. An average of 50 observations were made on each of the individuals for which home range was calculated. Each individual did not use the entire communitys home range, but rather centered their activity in particular sectors (average home range size: 53 ha). To prevent possible bias, after the first year, an attempt was made to search all areas of the community's home range. To facilitate this search, 25 km of trails were cut throughout the area. These trails were routinely searched and subgroups located by sighting the animals or by hearing calls and searching the area indicated by the call.

The composition of the subgroup being watched was monitored continuously. With small subgroups, it was relatively easy to see all individuals at one time, thus monitoring changes in composition was not difficult. However, as subgroup size increased, it became increasingly difficult to notice all departures and arrivals. Thus, when large subgroups were being followed, an observer would attempt to identify all individuals once every half hour.

At the end of the 3-week behavioral observation period, the density and distribution of the food resources eaten during the preceding 3 weeks were determined. The location, size, and phenological status of all adult trees of these species were determined in three 4-hectare grids. Each grid was 200 m by 200 m and consisted of 400 cells, each cell 10 m by 10 m in size. Corners of cells were marked with steel posts. An adult tree was considered as any individual with a DBH greater than the smallest individual observed bearing fruit. For each individual tree, the stage of leaf development and the presence or absence of fruit and flowers were determined (see Chapman 1988a and Chapman and Chapman, in press, for information of fruiting patterns). The size of a patch would ideally be represented as the number of food items it contained; however, the large number of patches used by the spider monkeys precluded the counting of food items, so patch size was represented as DBH. Previous studies have demonstrated that DBH reflects the reproductive capacity of tropical fruiting trees (Peters et al. 1988). Thus, the density of trees that the spider monkeys were using during the 3-week behavioral period that had food items, weighted by the dBH of the trees (the sum of the DBH for all grids) was used as an index of food abundance.

Definitions. A subgroup was considered as any number of individuals, less than the total community, that were associating together, taking part in coordinated activities, and maintaining relatively close spatial contact. Subgroups were categorized according to the following criteria: (1) solitary – an animal travelling alone, with no evidence of other individuals in the vicinity (including vocal exchanges); (2) one adult female with young – an adult female travelling with her dependent and/or independent young; (3) all-male – fully adult males travelling together (occasionally a large immature male would travel with the adults); (4) >1 adult female and young – two or more adult females with some dependent and/ or independent young associating together in the absence of males; (5) adult females without young; (6) mixed sex with young – females with infants or independent young travelling with males, (7) mixed sex without young – normally consisted of one adult male and one adult female (82%), but occasionally larger combinations were seen.

The dominance rank for each identifiable adult ($n = 13$) was determined from dyadic interactions involving displacements observed in the focal animal session ($n = 117$) or involving overt aggressive interactions ($n = 38$) observed either during focal animal sessions of the individual involved or at any other time. Since these overt aggressive interactions involve loud vocalizations and often chases, it is believed that all episodes that occurred while

the observer was present were recorded. For spider monkeys, dominance relationships are difficult to describe since some individuals in the community rarely if ever meet, individuals rarely meet alone, and interactions appear to be affected by the presence of others. For individuals that rarely met, dominance rank was assigned according to their interactions with individuals with which they both associated. All statistical tests involving dominance were done with non-parametric and the equivalent parametric test (Pearson's correlation, r), and if the tests agreed, the parametric results were reported (following Conover 1980). Degree of association was adjusted for unequal number of observations of each individual by calculating an index of association as $100c/(a+b+c)$, where A and B are two individuals, a = the number of subgroups observed that contained A but not B, b = the number of subgroups observed that contained B but not A, and c = the number of subgroups containing both A and B (following Nishida and Hiraiwa-Hasegawa 1986).

Results

Ecological determinants of subgroup size

Over the 5 years of the study, 1018 subgroups were observed and their composition determined. The average subgroup size was 4.94 individuals (SD = 4.18, mode = 3). However subgroups ranging in size from 1 to 35 were observed (Fig. 1). Similarly, the average subgroup size observed in each month was variable (Fig. 2).

Theory would predict that much of this variability in subgroup size would be related to changes in the density and distribution of food resources (Bradbury and Vehrencamp 1976). To examine this, I related the size of the observed subgroups to the ecological parameters that were collected every 3 weeks. The average size of the subgroups seen in a 3-week sampling period varied from 2.3 to 14.4. The average size of the subgroup (excluding infants) observed in the 3-week sampling period would be predicted, based on a multiple regression of the density and distribution of the food resources that the spider monkeys were using at that time ($r^2 = 0.30$, $P = 0.024$, $n = 26$). The regression indicated that when food resources were relatively scarce and located in patches that were far apart, the spider monkeys were found in small subgroups. The animals appeared to minimize travel costs by staying in small subgroups, which depleted patches more slowly, and localizing their activity around one or a small number of patches. In contrast, when food was abundant and relatively uniformly distributed, spider monkeys congregated in large subgroups. At this time the costs of travelling between patches were low, and the energy spent travelling could easily be recovered. Despite the significance of this general pattern, there remains a large amount of variation in the size of subgroups to be explained.

Subgroup size for different community members

There was no difference in the size of the subgroup in which identifiable adult males and females were observed ($t = 0.001$, $P = 0.995$, $n = 13$ adults). Nor was there any evidence to suggest that the average size of the sub-
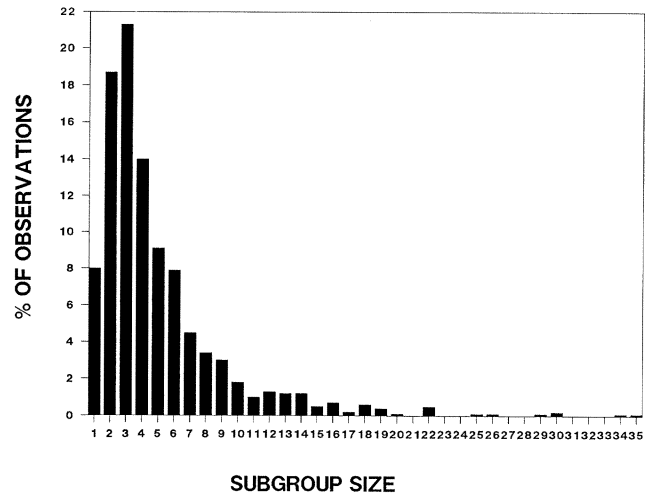

Fig. 1. A frequency histogram of the size of the spider monkey subgroups seen in Santa Rosa National Park, Costa Rica ($n = 1018$)
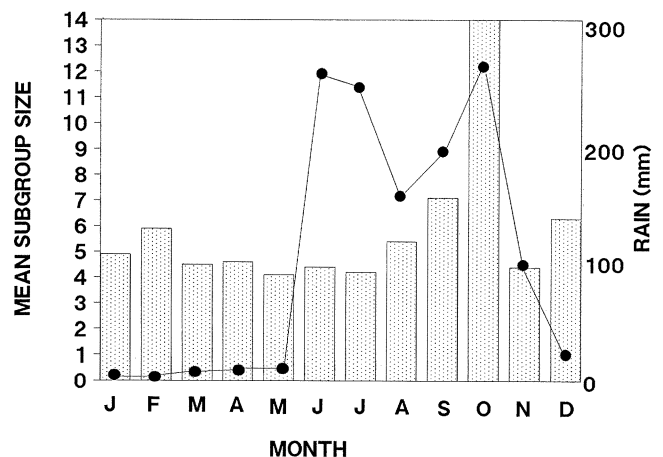

Fig. 2. The average size of the spider monkey subgroup seen in each month of the year (histograms) and the corresponding rainfall (mm, solid dots) in that month

groups in which an individual was observed was related to its dominance rank (Pearson's correlation: $r = -0.044$, $P = 0.860$, $n = 13$).

Observations at Santa Rosa suggest that aggression directed at dependent or young independent infants may be a major source of injury and may possibly result in their death. Six serious injuries have been observed among immatures, involving large cuts or the loss of part of the tail (Chapman et al. 1989). For instance, one day I was watching a subgroup feeding in a fig tree, and a young male that had moved away from his mother was attacked. Within seconds there was a ball of fighting animals attacking or defending this young male. The episode ended with the male's mother chasing another female from the tree and resulted in the infant receiving a 4 cm wound on his leg. Based on such observations, one might expect that a mother might attempt to protect her infant by avoiding conspecifics. To examine this possibility, I calculated the mean subgroup size for individu-
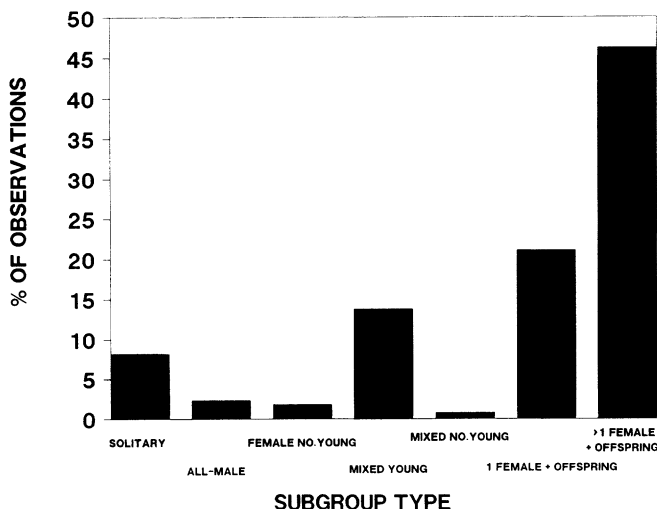
Fig. 3. A frequency histogram of the types of spider monkey subgroups (see the text for a description of the categories)
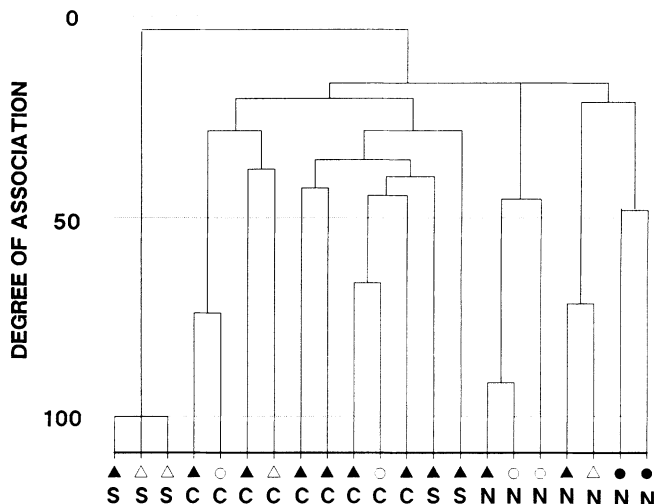

Fig. 4. A cluster analysis of the association patterns of individual recognizable spider monkeys. Degree of association was adjusted for unequal number of observations of each individual by calculating an index of association as $100c/(a+b+c)$ following Nishida and Hiraiwa-Hasegawa (1986, see "Methods" section). ● = adult males, ▲ = adult females, ○ = immature male, △ = immature female, S: indicates that the individual centered its activity to the south of the community's home range, C: indicates that the individual centered its activity to the center of the community's home range, N: indicates that the individual centered its activity to the north of the community's home range

ally recognizable females in each 3-week sample period. Females were categorized as having a dependent infant or as being without an infant. Females with dependent infants were in significantly smaller subgroups than females that did not have infants ($t = 6.12$, $P < 0.01$).

Composition of subgroups

Solitary females (a single female, or a mother with an infant) were sighted 16.2 times more than solitary males. Compensating for the female bias in the adult sex ratio, females were solitary 3.6 times more often than adult males. The amount of time a female was solitary was related to her rank ($r = 0.858$, $P < 0.001$, $n = 9$), such that low-ranking females were solitary much more often than high-ranking females. Females with infants were solitary in 31% of the subgroups in which they were observed ($n = 887$ subgroups), while females without infants were observed to be solitary only 7% of the time ($n = 718$ subgroups, $X^2 = 147.0$, $P < 0.001$).

Subgroups consisting of adult females with their young were the most frequently seen type of subgroup (47%; Fig. 3). Subgroups consisting of adult males travelling with females and young accounted for 13.8% of the sightings and ranged in size from 3 to 35 individuals. All-male subgroups accounted for only 2.3% of the observations.

Figure 4 depicts the degree of association for 21 individuals that were seen on more than 30 occasions. Clear associations are evident, the most apparent being those between mothers and small and/or large immatures (infants were not considered separate from their mothers). In addition, the two fully adult males were frequently observed together. Geographical influences on the association patterns of the spider monkeys were also evident. I categorized individuals according to where the majority of their sightings occurred: north, central, and south (Fig. 4). As one might expect, there was a tendency for individuals that centered their activity in the same region

to associate frequently; however, there were some exceptions. Thus, associations between certain members of the spider monkey community may have imposed some limitations on subgroup flexibility.

Range use

The community as a whole used an area of 1.70 km². However, no one individual used an area greater than 58% of the total area of the community's home range (mean = 30.9%, range = 18.6–57.8%). Adult males used larger areas than females (males mean = 81.4 ha, $n = 4$; females = 54.9 ha, $n = 9$; $t = 2.67$, $P = 0.026$). Dominant individuals tended to use larger areas than subordinate ones ($r = 0.623$, $P = 0.008$, $n = 13$; only females: $r = 0.663$, $P = 0.05$, $n = 9$). There was no evidence to suggest that the presence of a dependent infant reduced the area that a female used (percentage of time with a dependent infant vs range size: $r = 0.199$, $P = 0.608$, $n = 9$ adult females).

Although the size of an individual's home range may have been similar to another animal's, the pattern with which they used their home ranges could differ. Some individuals may have had a single concentrated area of use and used the remainder of their home range only rarely, while other individuals may have used their home range evenly. Spatial use within the home range was quantified using the Coefficient of Variation (CV) of the number of sightings per cell (Sokal and Rohlf 1981). The higher the CV, the more spatially clumped were the individuals sightings. Males used their home range more uniformly than females ($t = 2.56$, $P = 0.028$, CV
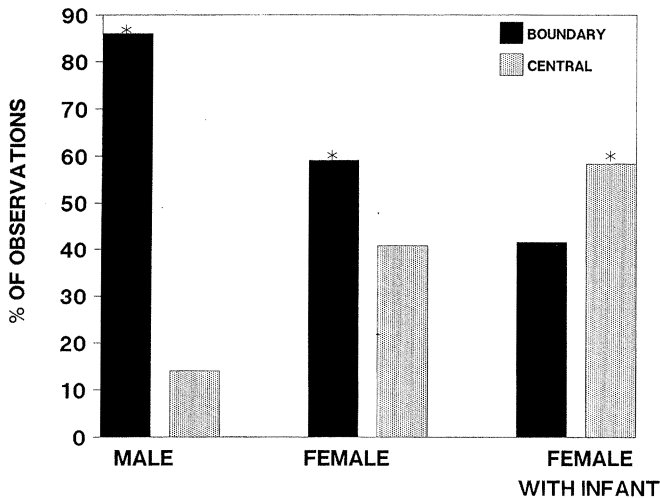
Fig. 5. The use of boundary and central areas for males, females without infants, and females with infants. Based on 1018 subgroups observed in Santa Rosa. Stars indicate significant differences between the two categories $(P<0.05)$

Table 1. Summary of the differences documented for the spider monkeys of Santa Rosa National Park, Costa Rica, in association patterns and range use

Subgroup size:	Smaller for females with infants than for other females.
Solitary sightings:	Females are more solitary than males and females with dependent infants were more solitary than females without infants.
Home range size:	Males have larger home ranges than females.
Home range pattern:	Males and females without infants use their home ranges in a uniform fashion, while females with infants have a clumped pattern of home range use.
Boundary use:	The boundary of the community's home range is used frequently by males and females without infants, but rarely by females with infants.

male = 36%, female = 69%). Females tended to restrict the use of their home range when they had infants. The percentage of time a female had a dependent infant was related to the CV of sightings $(r=0.628, P=0.05, n=9)$. The dominance of the female did not infuence the use of her home range $(r= -0.378, P=0.281, n=9)$.

Individuals could differ in their use of the boundary areas. Much of the home range of the spider monkey community was surrounded by grasslands or young regenerating forest. As a result, contact with neighboring groups could only occur along the community's northern boundary. I considered the last two rows of grid cells along the northern edge of the community's home range to be the boundary and the remainder to be central. Males and females without infants were seen in the boundary areas more than in the central areas, whereas females with infants exhibited the opposite trends (Fig. 5). Both males and females may have used the boundary areas more than would be expected, as this area was primarily nearly pristine semi-evergreen forest, while the central areas tend to be more dry semi-deciduous forest. These same trends hold if the boundary area was considered as only the last row of grid cells or as the last three rows.

Discussion

Studies that have attempted to identify the determinants of sociality have often neglected to consider variation among individuals with respect to the costs and benefits of group living (Wrangham and Rubenstein 1986). For the spider monkeys of Santa Rosa, evidence suggests that ecological factors (density and distribution of food resources) set an upper limit on the number of animals that can associate together and still efficiently exploit the available resources. However, this is only a vague upper limit; the needs of particular individuals appear to influence the size and composition of their subgroups.

Table 1 summarizes the findings of this study and suggests the strategies used by different types of individuals.

Based on the observations presented, it seems reasonable to speculate that male spider monkeys band together for potential reproductive gains. By travelling long distances and using the home range in a uniform fashion, males may be able to monitor the reproductive status of a number of females. The observation that males tend to band together and are seen frequently on the edge of the community's home range suggests that the close alliances between males may be necessary for territorial defense. The size of the defending subgroup may influence the outcome of the territorial encounter, as has been observed for chimpanzees (Nishida and Hiraiwa-Hasegawa 1986; Wrangham 1986 b). However, to date this is largely speculation since nothing that could be considered a territorial encounter has been observed at Santa Rosa (even though members of other communities have been observed to enter the home range of the study community on 31 occasions). This male strategy may frequently place males in subgroups that are larger than that appropriate for the ecological conditions. For instance, during the sampling period with the smallest overall subgroup size (mean = 2.3 individuals), males were still seen in all-male subgroups with the four members, or with females and infants (mean male subgroup size = 5.2 individuals). The fact that the adult males in the community may be related, since females disperse (Symington 1987; Chapman, unpublished data), may increase the value of any benefit accrued through male-male cooperation.

In contrast to the adult males, females were more solitary and had smaller individual ranges spread throughout the community's home range. Since spider monkeys typically deplete the fruit trees in which they feed (Chapman 1988a), by being in a small subgroup females may decrease feeding competition. Unlike a male's reproductive success, which is likely limited by the number of females with which he can mate, a fe-

male's reproductive success is likely limited by the number of infants that she'can produce and successfully raise. There is evidence for a number of animal species that suggests that if a female can decrease competition for food, she may be able to raise or care for more young (Whitten 1983; Janson 1985).

Females with dependent infants have a different pattern of association and range use than female without infants. Females with dependent infants were sighted in smaller subgroups and were more often solitary than other females, appeared to avoid the boundaries of the community's home range, and exhibited a restricted pattern of use of their own home range. Unfortunately little is known about factors influencing infant survival. However, indirect evidence suggests that spider monkey infants are commonly injured, particularly male infants (Chapman et al. 1989). By avoiding conspecifics and boundary areas, mothers may be removing their infants from situations where they could be injured by conspecifics of their own or a different community.

These suggested benefits are by no means the only possible selective advantages of the observed patterns. For instance, one factor contributing to males having larger home ranges than females could be that adult male body size is larger than females (male = 9 kg, female = 6.7 kg, Glander et al., in press). However, more strength can be placed in the suggested advantages as a number of the observed patterns all suggest the same advantage.

The evolution of spider monkey social organization is complex, but it shows many similarities to other taxa. Obviously, more data are required to ascertain the degree of influence of many of the factors discussed, such as how strategies used by mothers serve to protect infants. However, available data suggest that spider monkey social organization represents the amalgamation of individuals meeting their own needs, while being limited by the density and distribution of food resources.

References

Bradbury JW, Vehrencamp S (1976) Social organization and foraging in emballonurid bats. II. A model for the determination of group size. Behav Ecol Sociobiol 1:383–404

Chapman CA (1988a) Patterns of foraging and range use by three species of neotropical primates. Primates 29:177–194

Chapman CA (1988b) Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. Behaviour 150:99–116

Chapman CA, Chapman LJ (1990) Density and growth rate of some tropical dry forest trees: comparisons between successional forest types. Bull Torrey Bot Club (in press)

Chapman CA, Fedigan LM, Fedigan L, Chapman LJ (1989) Post-weaning resource compeittion and sex ratios in spider monkeys. Oikos 54:315–319

Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. Theor Popul Biol 30:45–75

Conover WJ (1980) Practical nonparametric statitics. Wiley, New York

Glander KE, Fedigan LM, Fedigan L, Chapman C (1990) Capture techniques for three species of monkeys in Costa Rica (in press)

Janson C (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behav Ecol Sociobiol 18:125–138

Janzen DH (1986) Guanacaste National Park. (Editorial). University of Estratal a Distancia, San Jose, Costa Rica

Jarman PJ (1974) The social oranization of antelope in relation to their ecology. Behaviour 48:215–267

Jarman PJ (1983) Mating systems and sexual dimorphism in large, terrestrial, mammalian herbivores. Biol Rev 58:485–520

Klein LL (1972) The ecology and social organization of the spider monkey *Ateles belzebuth*. Ph D Dissertation. University of California, Berkeley

Klein LL, Klein DB (1977) Feeding behaviour of the Columbian spider monkey. In: Clutton-Brock TH (ed) Primate ecology. Academic Press, London, pp 153–181

Lott D (1984) Intraspecific variation in the social systems of wild vertebrates. Behaviour 88:266–325

Nishida T, Hiraiwa-Hasegawa M (1987) Chimpanzees and Bonobos: Cooperative relationships among males. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 165–117

Peters RH, Cloutier S, Dube D, Evans A, Hastings P, Kaiser H, Kohn D, Sarwer-Foner B (1988) The ecology of the weight of fruit on trees and shrubs in Barbados. Oecologia 74:612–616

Pulliam HR, Caraco T (1984) Living in groups: is there an optimal group size? In: Krebs JR, Davis N (eds) Behavioural ecology. Sunderland, Sinauer, pp 122–147

Schaik CP van (1983) Why are diurnal primates living in groups? Behaviour 87:120–144

Sokal R, Rohlf F (1981) Biometry. Freeman, San Francisco

Symington M (1987) Ecological and social correlates of party size in the black spider monkeys, *Ateles paniscus chamek*. Ph D Disseration, Princeton University, Princeton

Symington M (1988a) Demography, ranging patterns, and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in Manu national Park, Peru. Am J Primatol 15:45–67

Symington M (1988b) Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). Behaviour 105:117–134

Whitten PL (1983) Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). Am J Primatol 5:139–159

Wrangham RW (1986a) Evolution of social structure. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 282–296

Wrangham RW (1986b) Ecology and social relationships in two species of chimpanzees. In: Rubenstein DI, Wrangham RW (eds) Ecological aspects of social evolution. Princeton University Press, Princeton, pp 352–378

Wrangham RW, Rubenstein DI (1986) Social evolution in birds and mammals. In: Rubenstein DI, Wranham RW (eds) Ecological aspects of social evolution. Princeton University Press, Princeton, pp 452–470