

# Ecological Constraints on Group Size in Three Species of Neotropical Primates

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**Abstract.** The foraging strategies and association patterns of 3 species of primates (*Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus*) were studied over a 5-year period. The objective of the study was to provide a quantitative test of the hypothesis that the size, density and distribution of food resources influence the size of animal groups. In examining the assumptions of this hypothesis, it was shown that these primates used resources that occurred in patches, depleted the patches through their use, and that membership in large subgroups was associated with increased travel costs. The howler and spider monkey groups formed subgroups, the size of which could be predicted from the size, density and distribution of their plant food resources. When resources were clumped and at a low density, both the howler and spider monkeys were found in small subgroups, whereas when patches were uniformly distributed and at high density they formed larger subgroups. Capuchin monkeys, in contrast, did not respond to changes in these ecological variables by forming subgroups or changing the cohesion of their group.

## Introduction

Recently, several attempts have been made to formulate principles which govern animal group size. It has been suggested that resource availability can influence group size either by limiting the number of animals an area can support or by influencing foraging efficiency. Further, the density and distribution of food resources have been suggested to limit group size by determining the foraging efficiencies of groups of different sizes [1-4].

It is easy to understand how food abundance might influence the density of ani-

mals, but it is less apparent how variables such as the density and distribution of food resources might limit the size of individual groups. Animals must forage over an area that can meet their energetic and nutritional requirements. It follows that an increase in group size will increase the area that must be covered to find adequate food supplies. Thus, over a specific period of time, individuals in a group that forage in an area that meets the needs of all group members would travel further and spend more energy than would be the case if they forage in smaller groups or alone [5]. With an increase in the

time spent traveling, some point will be reached at which energy spent in travel exceeds the energy obtained from the environment, and a smaller group size should become advantageous. In this way ecological factors can influence movement patterns and thus foraging efficiency, and thereby set biological limits on the size of the groups that can efficiently exploit available food resources. Three aspects of a depleting resource can affect movement patterns: (1) patch size; (2) the density of patches, and (3) the spatial distribution of the patches. The physical size of a patch can limit the number of animals capable of using it at the same time and the abundance of food items. The density of food patches can influence feeding efficiency by affecting interpatch travel costs. And the distribution of patches can similarly affect the distance animals must travel once they leave a patch that they have depleted.

Following this line of reasoning, patches that are rapidly depleted, or patch characteristics that incur high travel costs (low density and scattered distribution) should favor small groups. When patches are small (they are depleted rapidly), at low density and clumped (animals must move between clumps), a large group will be obliged to visit many areas. However, if group size is reduced, patches will support animals for longer periods and travel can be minimized. I therefore hypothesize that the largest groups would be expected when patches are large, uniformly distributed and at high density. The smallest groups should be found when patches are small, clumped and occur at low density. Intermediate levels of size, density and distribution of resources should correspond to intermediate group sizes.

The objective of this study was to examine the hypothesis that group size is a func-

tion of the size, density and distribution of food resources for the 3 species of primates in Santa Rosa National Park, Costa Rica (*Ateles geoffroyi*, *Cebus capucinus*, *Alouatta palliata*). I assume that selective pressures exist that favor group living in these primate species and examine only factors that limit group size.

A 'group' is considered here as the largest stable social unit in which all members usually interact in an affiliative fashion and agonistic behavior is infrequent, even when individuals that have been separated for some time reunite. A 'subgroup' is any number of animals, less than the total for the group, that are associating together, taking part in coordinated activities, and maintaining relatively close spatial contact. A 'patch' is an aggregation of food items that represent an area of high food density, the limits of which are defined by adjacent areas of low food density [1, 6]. To an animal, a food patch is perceived as an area structured such that it can use the area without interrupting its feeding activity [1]. In operationalizing this definition, a patch was assumed to be a single tree (or under rare circumstances food trees with adjoining canopies).

## Methods

### *Study Site and Study Groups*

The study was carried out in Santa Rosa National Park, Costa Rica, over 5 years totaling 36 months of field observations (July and August 1983, January to August 1984, January to July 1985, February to August 1986, April 1987 to April 1988). During the last 2 years of the project, spider monkeys were the focus of the investigation. The howler study group had on average 40 individuals. Howlers have typically been described as living in relatively stable, cohesive, multimale-multifemale social groups [7, 8]. The study group had a multimale-multifemale type of social

structure with 40 members (7–8 adult males, 16–18 adult females, 2–3 large immatures, 4–6 small immatures, 6–9 infants). However, the group was neither stable nor cohesive. The group frequently fragmented into subgroups which were spatially separated for periods that lasted up to 4 weeks. The howlers were in subgroups, rather than a single group, for 84% of the total observation time. The group tended to split into 2 approximately equally sized subgroups (mean size = 19.3 individuals). Occasionally, one of these subgroups also divided. The composition of the subgroups changed frequently as animals moved between them. When subgroups united, agonistic behaviors were rarely observed. A similar fragmentation of howler social groups has been observed on Barro Colorado Island, Panama [K. Milton, pers. commun.].

The capuchin monkey group contained on average 26 individuals (2–4 adult males, 9–10 adult females, 4–5 large immatures, 5–6 small immatures, 0–4 infants). The group always maintained a multimale-multifemale type of social organization similar to that described elsewhere [3, 9] and was never observed to fragment into subgroups. However, the degree of spatial cohesion between members varied over time. Sometimes the group was cohesive and all members were in close contact, while at other times they could be spread out over 0.5 km.

Spider monkeys are typically described as living in multimale-multifemale social groups or 'communities'. These groups consist of amiably interacting individuals that rarely come together to form a cohesive unit, but tend to be found in small subgroups of 3–5 individuals which are unstable in composition [10–12]. The community was estimated to contain 42 individuals: 4 adult males, 17 adult females, 2 large immature males, 4 large immature females, 7 small immatures and 8 infants.

#### *Behavioral Observations*

Behavioral data were collected using a focal animal sampling regime with 10-min sessions. If the subject was lost prior to the end of the session, the session was terminated and the data discarded. When possible, the animal to be sampled was chosen according to a fixed rotation between age/sex classes. For capuchin monkeys a measure of the relative spatial cohesion of the group was obtained halfway through each focal animal session, by estimating the number of animals within 10 m of the subject (the 'index of spatial cohesion'). The 10-meter cutoff level was chosen because

generally all animals within this distance could be seen regardless of the type of forest the animals were using [13].

An attempt was made to obtain a complete record of the activity of each species during a 3-week sample period so that by the end of this period an equal number of observations were made in each hour of the day. The location of the group being followed was recorded every 10 min as a coordinate on a 120 m × 120 m grid superimposed on an aerial photograph.

#### *Ecological Sampling*

Three ecological variables were considered of particular interest in predicting subgroup size: the size, density and distribution of food patches. To quantify these variables, the most commonly used food plant species were identified for each primate species from the preceding 3 weeks of behavioral observations, and the location and phenological status of all adult trees of these species were determined in three 4-ha grids. Normally, only 4 plant species were chosen to represent the ecological conditions for a 3-week period. The use of only these few 'major' plant species was justified since they always accounted for over 91% of all of the time spent feeding on plant parts. An adult tree was considered as any individual that had attained a diameter at breast height (DBH) greater than or equal to that of the smallest individual seen to bear fruit. The grids consisted of 400, 10 × 10 m, cells. Corners of the cells were marked with individually labeled steel posts. The phenological information recorded included the stage of leaf development (no leaves, leaf buds, young leaves, mature leaves) and the presence or absence of fruit and flowers. Ideally, the size of a food patch would be represented as the number of food items in the patch; however, because the large number of patches used by the monkeys prohibited the actual counting of food items, patch size was represented as DBH. For several tropical tree species, DBH has been shown to accurately reflect the reproductive capacity of fruiting individuals [14].

To analyze the relationship between patch characteristics and subgroup size, only those trees of a size that can be used by the monkeys were included in the calculation of density and distribution of food resources. Howlers rarely used small adult food trees (<20 cm DBH), whereas capuchin and spider monkeys frequently fed in such trees. This interspecific difference is probably related to differences in body size and locomotor patterns [15]. Howlers fed in large

food trees (> 20 cm DBH) more often than would be expected based on the size of the food trees available ( $\chi^2 = 115.8$ ,  $p \leq 0.001$ ). Studies of howlers on Barro Colorado Island also indicated selection for large trees [8, 16]. To decide the size of the tree to include in this analysis, a frequency distribution was made of the DBHs of all the trees that howlers were observed to use. From this distribution it was clear that howlers rarely (< 5% of the observations) used trees with a DBH less than 20 cm. In contrast, trees that were less than 20 cm constituted 25.0% of the trees used by spider monkeys and 34.6% of those used by capuchin monkeys. Thus, only trees with a DBH greater than 20 cm were used to calculate the density and distribution of food resources for howlers; for the other species all adult trees were used in the calculation.

To determine the distribution of the adult trees that were bearing food items, the 'coefficient of dispersion' (CD) was calculated [17]. As the aim of this analysis was to determine the distribution of food items, not the distribution of food trees, each food tree was weighted by its size (DBH), such that the value for a cell of the grid was the sum of the DBHs of all food trees. The density of food trees was calculated from counts of individual trees in the 3 grids and was represented as individuals per square kilometer. The density of food trees was weighted for tree size by multiplying the mean DBH of the food plant species by the number of trees in the grids and dividing the product by the area of the grid. Data used in the regression analysis to predict subgroup size were log-transformed and, since these predictions were derived from the model, one-tailed tests were used.

## Results and Discussion

### Assumptions

The hypothesis to be tested requires a number of assumptions that should be discussed and, in so far as possible, validated. First, it is assumed that these primates use resources that occur in patches. The major plant food resources of these primates tended to occur at low density (mean number of patches per hectare: 4.8 for spider monkeys; 8.0 for howlers; 6.5 for capuchin

monkeys). Often only a single individual of a preferred food species (e.g. *Ficus* spp.) occurred in a group's home range. Thus, the food resources used by these primates tended to be in discrete locations and far apart. In addition, the average time spider monkeys spent moving from one food tree to another was 702 s (range 5–3,660 s,  $n = 172$  observed movements). Similarly, in the 90 observed movements by howlers, the group spent an average of 402 s moving between trees in which they fed (range 10–1,421 s). In contrast, movements within trees were of short duration. 94% of the movements of howlers within trees were less than 30 s, and 97% of the spider monkey movements in food trees were less than 30 s. Thus, it seems reasonable to consider that the resources used by these primate species were found in discrete patches. Similar information on patch use cannot be provided for the capuchin monkeys because the group was often dispersed to the extent that members could be using a number of patches at one time.

Secondly, for subgroup size to be a response to the proposed ecological conditions, as subgroup size increases, the area that must be searched to find food for all group members should increase. This assumption can be tested for howler and spider monkeys as observations were recorded for subgroups of different sizes. A positive correlation existed between subgroup size and the time spent traveling for both howlers ( $r = 0.48$ ,  $p \leq 0.001$ ) and spider monkeys ( $r = 0.46$ ,  $p = 0.027$ ; comparisons made between the sample periods; spider monkeys,  $n = 26$ ; howlers,  $n = 14$ ).

Third, I assumed that increased time spent traveling associated with membership in large subgroups is a significant cost. For both howler and spider monkeys the positive

correlation of travel time with subgroup size corresponded with a positive relationship between subgroup size and the proportion of the total observation time spent feeding (howlers,  $r = 0.49$ ,  $p \leq 0.01$ ; spiders,  $r = 0.57$ ,  $p \leq 0.01$ ). This suggests that individuals in large subgroups may travel further than those in small subgroups to find sufficient food, and that the added travel cost is compensated for by an increase in the time spent feeding.

The assumption that the primates deplete the patches was investigated by Chapman [18] following 4 lines of evidence: (1) all species were commonly observed feeding in a number of individual trees of the same species in direct succession; (2) for most food plants the rate of intake of food items during a feeding bout was significantly higher at the start of the feeding bout than later. (For some tree species the rate of intake did not change over the duration of a bout of similar or longer length, suggesting that this relationship is not caused simply by satiation.); (3) for howlers and spider monkeys, which had variable subgroup sizes, members spent more time traveling as subgroup size increased, suggesting that large subgroups deplete patches of equal size faster than smaller subgroups; and (4) for howler and spider monkeys the amount of time spent feeding was generally a function of the size of the patch and the number of animals using the patch.

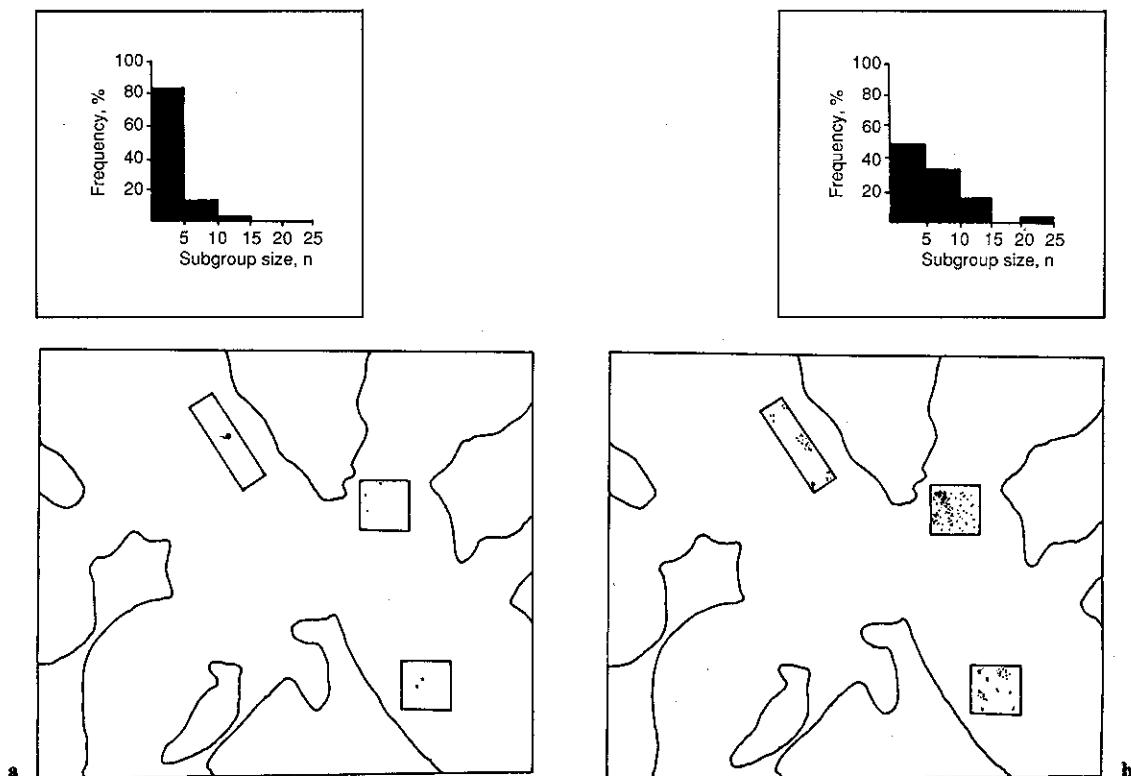
#### *Intraspecific Comparisons of Ecology and Group Size*

Based on ecological theory [2], it was predicted that subgroup size would be a function of the size, density and distribution of food patches, such that subgroups would be smallest when resources were clumped and found at low densities, and larger when re-

sources occurred at high densities and were uniformly distributed. To test this prediction, the average sizes of the subgroups observed during each 3-week sample period were compared to the ecological conditions measured at the end of these periods (for spider monkeys,  $n = 26$ ; howlers,  $n = 14$ ; capuchin monkeys,  $n = 14$ ). For spider monkeys, the average size of the subgroups seen in a 3-week sampling period varied from 2.3 to 14.4 individuals. The average size of the subgroup (excluding infants) was related to the density and distribution of food resources ( $r^2 = 0.30$ ,  $p = 0.024$ ). Partial correlations of subgroup size and resource density, controlling for distribution ( $r = 0.47$ ,  $p = 0.041$ ) and subgroup size and distribution controlling for density ( $r = 0.05$ ,  $p = 0.851$ ), suggest that the density of food resources had a stronger influence on subgroup size than did patch distribution.

Similarly, the size of howler subgroup was a function of the density and distribution of their resources, but only weakly ( $r^2 = 0.77$ ,  $p = 0.056$ ). A partial correlation on this set of variables illustrates that this relationship is primarily a function of the distribution of resources, rather than their density (subgroup size and distribution controlling for density,  $r = 0.84$ ,  $p < 0.041$ ; subgroup size and density controlling for distribution,  $r = 0.07$ ,  $p = 0.233$ ). The ecological conditions that corresponded to the sample periods when howler and spider monkeys had the largest and smallest mean subgroup sizes are depicted in figures 1 and 2.

Unlike both the howlers and spider monkeys, the capuchin monkey group did not fragment throughout the study. However, the degree of spatial cohesion of the group did change. The 'index of spatial cohesion' averaged 0.73 over all sample periods and



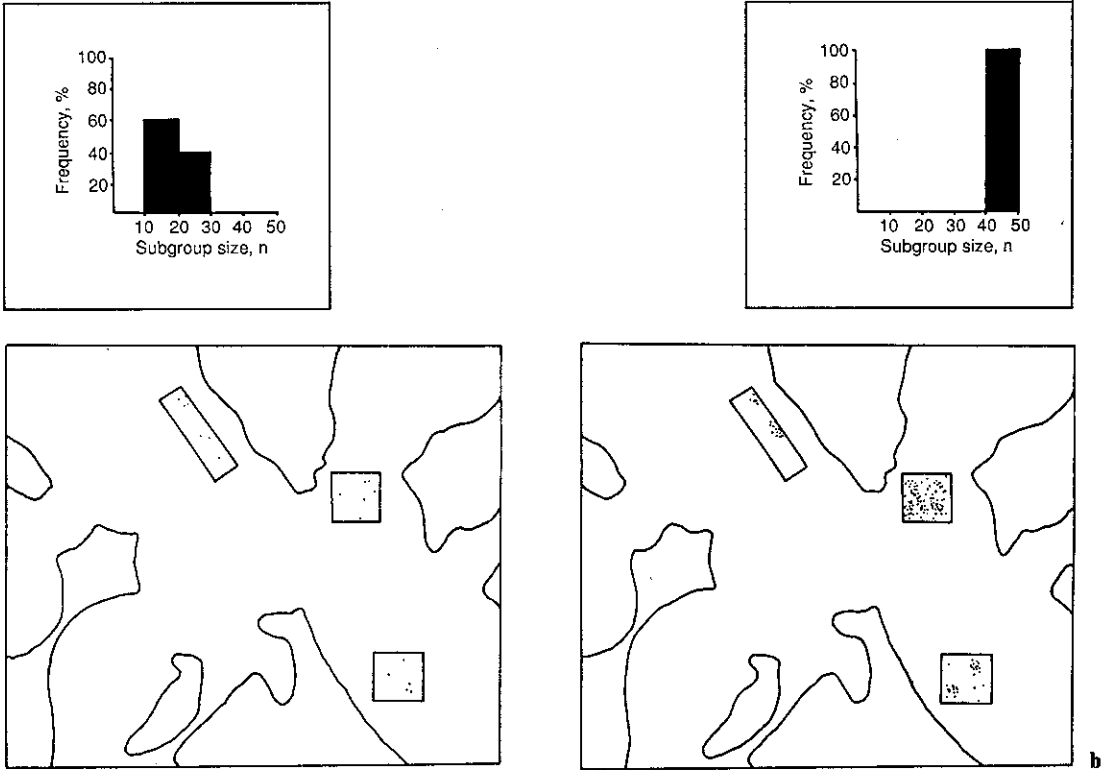
**Fig. 1. a** Ecological conditions that corresponded to the sample period when the spider monkey group was observed to occur in the smallest subgroups. The mean subgroup size at this time was 2.3 individuals. There were few food trees available, the density of trees that were bearing food items was 50 individuals/km<sup>2</sup> and they occurred in a clumped distribution ( $CD = 1.2$ ). The mean DBH at this time was 50 cm. **b** Conditions when the largest subgroups occurred. The mean subgroup size at this time was 6.4 individuals, food trees were found at high density (1,543 individuals/km<sup>2</sup>), and they were in clumps ( $CD = 1.1$ ). The DBH at this time was 66 cm. A dot represents a tree regardless of size.

ranged between 0.61 and 0.91. This variability in cohesion was not, however, related to the density and distribution of resources ( $r^2 = 0.002$ ,  $p = 0.961$ ).

#### *Interspecific Comparisons of Patch Characteristics and Group Size*

It is difficult to make quantitative interspecific comparisons of patch characteristics and group size. The most critical factor lim-

iting such comparisons is that the value of a patch will probably differ between species. Patch quality can be influenced by a variety of factors including ability to travel between patches, the size of trees that can be used, foraging strategy, body size and digestive capabilities. However, despite these limitations, it is possible to consider the traits of each species that may influence relationships between patch characteristics and social



**Fig. 2.** **a** Ecological conditions that corresponded to the sample period when the howling monkey group was observed to occur in the smallest subgroups. The mean subgroup size at this time was 13 individuals. There were few food trees available, the density of trees that were bearing food items was 158 individuals/km<sup>2</sup> and they occurred in a clumped distribution ( $CD = 1.2$ ). The mean DBH at this time was 51 cm. **b** Conditions when the largest subgroups occurred. The mean group/subgroup size at this time was 40 individuals, food trees were found at high density (1,408 individuals/km<sup>2</sup>) and they occurred in clumps ( $CD = 1.1$ ). The DBH at this time was 37.1 cm. A dot represents a tree regardless of size.

structure. Both capuchin and spider monkeys were heavily dependent on fruit. However, capuchin monkeys did not respond to changes in food resources by forming subgroups, while the spider monkeys did so readily. Unlike spider monkeys, when a patch is occupied by other animals in the group or has been depleted by their feeding, an individual capuchin monkey can still take part in profitable foraging activities by hunt-

ing for insects. When patches occurred at low density and hence a patch was more likely to be occupied or depleted, capuchin monkeys tended to spend more time eating insects (Spearman rank correlation  $r_s = -0.70$ ,  $p \leq 0.05$ ,  $n = 14$ ). Similarly, in sample periods when the capuchin monkeys were using trees that were small in size, and could hold only a few individuals at any one time, they again tended to spend more time

feeding on insects (Spearman rank correlation  $r_s = -0.46$ ,  $p < 0.05$ ).

Differences in the relationship between food patch characteristics and subgroup size in the howler and spider monkeys may be attributed to the folivorous aspects of the howler's diet. Leaf resources tend to be less temporally and spatially restricted than fruit. Howlers also have more types of food items in their diet than spider monkeys [19]. These attributes of the diet of howlers may provide individuals with foraging options if a patch is full or has been depleted by other animals.

### Summary

A 5-year study of 3 species of primates (*Ateles geoffroyi*, *Alouatta palliata*, *Cebus capucinus*) in Santa Rosa National Park, Costa Rica, was conducted to provide a quantitative test of the hypothesis that primate group size is related to the size, density and distribution of food resource. Both howlers and spider monkey groups formed subgroups, the size of which could be predicted based on measures of the size, density and distribution of their plant food resources. The capuchin monkeys did not form subgroups; instead the group was cohesive throughout the study. The capuchin monkeys may have been able to remain together, under conditions with which the other species formed subgroups, by increasing their reliance on insects, which tend to be relatively uniformly distributed.

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