

PATCH USE AND PATCH DEPLETION BY THE SPIDER AND HOWLING MONKEYS OF SANTA ROSA NATIONAL PARK, COSTA RICA

by

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(With 7 Figures)
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Introduction

Many of the models proposed to explain aspects of foraging behaviour, group size, or social structure assume animals use resources that occur in patches, and that through such use the patches become depleted. For instance, a number of models developed to predict group size suggest that the costs and benefits of using patches vary with group size, such that for a given resource state there is an optimal group size which tends to maximize foraging efficiency (S. ALTMANN, 1974; BRADBURY & VEHCAMP, 1976a, b, 1977; CARACO & WOLF, 1975; HORN, 1968; KLEIN & KLEIN, 1975, 1977; LEIGHTON, 1982; LEIGHTON & LEIGHTON, 1982; STACEY, 1986; TERBORGH, 1983; VAN SCHAIK *et al.*, 1983; WARD & ZAHAVI, 1973). In opposition to the assumption of patch depletion, is the suggestion that the food resources used by primates are superabundant (CARPENTER, 1965; COELHO *et al.*, 1976; STRUHSAKER, 1978). If resources are superabundant, the assumption of patch depletion would likely be invalid. Thus, the application to primate species of models of foraging

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behaviour and group size, which rely on this assumption, are unlikely to accurately represent the animal's behaviour. In addition, primates may deplete only certain types of patches, or deplete patches only in specific circumstances. For instance, patches may not be depleted if food toxins, digestibility, nutrient requirements, or the actions of competitors cause a group to leave a tree prior to its depletion. Since patches may not be depleted because of reasons such as these, it is essential to determine if primates deplete the food patches they use prior to applying any of the foraging models that incorporate this assumption.

The objective of this investigation was to examine under what circumstances the spider (*Ateles geoffroyi*) and howling monkeys (*Alouatta palliata*) of Santa Rosa National Park, Costa Rica likely deplete the patches they use. Defining what constitutes a patch has proven difficult in field situations. This is partially because food resources may be aggregated on a number of spatial and temporal scales (PIELOU, 1969). Thus, an appropriate scale must be defined for each situation and species. Temporal predictability is represented as the persistence of food resources at a given location once the food resource is available (COLWELL, 1974; WARNER, 1980); however, it is difficult to determine when resources are available and if an animal has sampled its environment sufficiently to know the location of the resource. The selection of an appropriate spatial and temporal scale for a given species and situation will depend on many factors including the animal's movement capabilities, foraging strategies (including energetic and nutrient needs), digestive efficiencies, and the spatial and temporal patterning of resources in its environment. A number of theoretical or conceptual definitions of patches have been proposed (S. ALTMANN, 1974; HASSELL & SOUTHWOOD, 1978). For the purpose of this study a patch was considered as an aggregation of food items structured such that animals could use the area without interrupting their feeding activity. In operationalizing this definition a patch was assumed to be a single tree (or under rare circumstances the food trees of the same species with adjoining canopies; this usage is examined below).

It is difficult to count the individual food items remaining in a tree after a primate group has left it. Thus, for the purpose of this investigation, patch depletion was inferred from the actions of individual monkeys. Their behaviour was monitored in situations where their actions could be predicted if they were depleting the patches in which they fed. For example, if a primate group was depleting a food patch, the acquisition of food items per individual in a patch should be negatively

related to the time the group has spent in the patch. Also, the time the study group spends in a patch will be a function of the size of the patch and the number of individuals in the group (*i.e.* if depletion occurs large groups should stay in equally sized patches for less time than small groups and small patches should be left sooner than large patches). Theoretically, a patch may be considered depleted when the feeding activities of consumers have led to the disappearance of all food items (CANT & TEMERIN, 1984). However, once food items become rare within a tree, they become progressively harder to obtain, and thus a patch will be functionally depleted before all of the food items are eaten. From this perspective, patches have been considered depleted when the rate of intake of food items in a patch equals the average of the environment (CHARNOV, 1976; PYKE, 1984).

Methods

The study was carried out in Santa Rosa National Park, Costa Rica during four field seasons encompassing 24 months (July and August 1983, January to August 1984, January to July 1985, and February to August 1986). In the last season only spider monkeys were studied. Rectangular in shape and covering approximately 10,800 ha, Santa Rosa consists of a series of plateaus which start at an elevation of 300 m and drop to the ocean. The vegetation of the park is a mosaic of grassland (*Hyparrhenia rufa*), dry deciduous forest in which *Spondias mombin*, *Luehea candida*, *L. speciosa*, *Guazuma ulmifolia*, *Bursera simaruba*, and *Chlorophora tinctoria* are common, and small fragments of semi-evergreen forest containing *Hymenaea courbaril*, *Mastichodendron capiri*, *Castilla elastica*, and *Manilkara chicle* (BONOFF & JANZEN, 1980; JANZEN, 1986; CHAPMAN, unpubl. data).

The climate of the region is characterized by two distinct seasons; the dry season that extends from approximately mid December to late May, and the wet season which encompasses the remainder of the year. Rainfall in the park ranges from 900 to 2400 mm annually, almost all of which falls in the wet season. Thus, during the dry season the majority of the non-riparian trees lose their leaves.

The howling monkey study group consisted of 40 individuals; 7-8 adult males, 16-18 adult females, 1-2 large immature males, 1 large immature female, 4-6 small immatures, and 6-9 infants. An exact count of the size of the spider monkey community was not possible, because of the fission-fusion type of social organization exhibited by spider monkeys. However, a minimum estimate of the size of the community was obtained by summing the maximum counts of all age/sex classes seen in any one year. Using this method the community was estimated to consist of 42 individuals; 4 adult males, 17 adult females, 2 large immature males, 4 large immature females, 7 small immatures, and 8 infants. Counts were made repeatedly over the study period and the total group sizes presented here represent means of these counts.

Behavioural sampling.

Behavioural data were collected using a focal animal sampling regime with 10-minute sessions (J. ALTMANN, 1974). When possible the subject chosen for sampling was selected according to a fixed rotation between age and sex classes. Normally, the species chosen to be sampled was alternated each day. Also, an attempt was made to obtain a complete

record of each species' activity during a 3-week sample period so that at the end of each period an equal number of observations were made in each hour of the day. Using this sampling regime, 394 hours of focal animal data were collected on the howling monkey group and 335 hours on the spider monkeys. Whenever all food items handled by an individual could easily be seen, counts were made of the rate of ingestion. The Diameter at Breast HEIGHT (DBH) of the trees used by the monkeys was estimated visually (error in estimation of DBH was + 1.6 cm, $n = 46$, mean DBH of trees used was 43.1 cm for spiders and 62.6 cm for howling monkeys). Simultaneous to the taking of focal animal data, a continuous record of the group's activity was collected (*e.g.* the number of animals feeding in a tree, the first animal to arrive in a patch, the time the last animal left the patch). These observations allowed the calculation of interpatch movement times and the estimation of the average time spent feeding in a patch.

Both the spider and howling monkey groups frequently formed subgroups. The members of a subgroup tended to coordinate their activities, maintain relatively close spatial contact, and be spatially discrete from other subgroups. This type of association was similar to that typically described for spider monkeys, but was a radical departure from the relatively stable cohesive social groups typically described for howling monkeys (CHIVERS, 1969; ESTRADA, 1984; GLANDER, 1980; MILTON, 1980; SMITH, 1977). The howling monkey study group frequently fragmented into 2 or more subgroups that were spatially separated by up to 2 km, for periods that lasted as long as 4 weeks. The howling monkeys were in subgroups, rather than in a single group, for 84% of the time. The group tended to split into two approximately equally sized subgroups. Occasionally, one of these subgroups would also fission (mean subgroup size 19.3 individuals, $n = 324$ sightings). The composition of the subgroups changed frequently as animals moved between them. Adult males were the most mobile age/sex class; recognizable males were often seen moving between subgroups (solitary animals when moving between subgroups were not considered in the calculation of mean subgroup size). When subgroups united, agonistic behaviours were rarely seen. Similarly fragmentation of howling monkey social groups have been observed on Barro Colorado Island, Panama (K. MILTON, pers. comm.). To determine the size and composition of howling monkey subgroups, counts were normally made once each time a subgroup was observed and the composition was assumed to be stable over the period of observation. Since the location and size of all howling monkey subgroups were usually known, a count of any single subgroup was thought to be accurate since the sum of all subgroups closely approximated the total group size. In an effort to obtain an accurate estimate of the size of spider monkey subgroups, whenever a subgroup was sighted the immediate area was searched for unseen animals. Also, only subgroups that were followed for more than 30 minutes were used in the following analyses. Inactive and unseen individuals would likely have been seen prior to the end of that time. The spider monkey subgroups changed composition approximately every 2.0 hours.

Ecological sampling.

To determine the size and distribution of the food resources eaten by each species, the most commonly used plant species were determined from the preceding 3 weeks of behavioural observations, and 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 10 m by 10 m in size. Corners of the cells were marked with steel posts. An adult tree was considered as any individual tree with a DBH greater than the smallest individual seen to bear fruit. 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 both of these species precluded the counting of food items, so patch size was represented by DBH. Several previous studies have demonstrated that DBH accurately predicts the reproductive capacity of fruiting individuals for a number of tropical tree

species (LEIGHTON, 1982; LEIGHTON & LEIGHTON, 1982; McDIARMID *et al.*, 1977). The phenological information recorded involved assessing the stage of leaf development and noting the presence or absence of fruit and flowers. In 1984, phenological data were recorded on the major plant species used by either of the monkey species during the preceding 3 weeks of behavioural sampling. In 1985 and 1986, the phenological status of all individuals of all major plant species used by either the howlers or spiders any time during the study were assessed. When a plant species was used that had not been eaten in the past, phenological data were recorded for it in all subsequent ecological sampling periods.

A 3-week sampling period was chosen because within this period an adequate sample of each species' behaviour could be obtained and the phenological cycles of the majority of the food plants used by the monkeys bore food items for over 3 weeks; thus individual trees possessing food items at the beginning of a 3-week period usually possessed them at the end of the sample period. Individuals of the few species of plants that were exceptions to this rule (*e.g.* flowering *Tabebuia ochracea*) could be identified by looking for food items that had fallen to the ground. Thus, food resources were not so ephemeral that they could not be accurately sampled in a 3-week period or that the two primate species could not respond to the changes.

The distributions of all variables used were examined for normality, and when values were not normally distributed an appropriate transformation was applied. The reverse transformations were corrected for bias (see BEAUCHAMP & OLSON, 1973; MILLAR, 1984).

Results

Does a tree equal a patch?

To determine if the resources used by these primates can be considered to occur in patches and whether or not it is a typical situation for one tree to represent a patch, the time spent moving between food trees (excluding rest stops) was determined for each instance where a subgroup was followed from one tree to another. This sampling procedure tended to bias the sample in favour of short movements because subgroups were more likely to be lost or abandoned during long movements. For spider monkeys the average time spent moving from one food tree to another was 703 seconds (range = 5 to 3660 seconds, in 172 movements). Fewer than 15% of these movements were less than 1 minute in duration and of these short travel bouts 76% involved foraging bouts occurring in one area with a number of *Muntingia calabura* trees growing close together. In 90 observed movements of howlers, the average time spent moving between food trees was 402 seconds (range from 10 to 1421 seconds). Fewer than 13% of these movements involved travel bouts of less than 1 minute. Spider monkeys spent significantly more time moving between food patches than did howlers ($t = 3.5$, $P = 0.032$). Relative to the time spent moving between trees, both species tended to have movements of short duration within a tree (94% of the movements made by howlers

within a tree were of shorter duration than 30 seconds, 97% of the spider movements within a tree were less than 30 seconds).

To further examine this assumption, the grid location of all individuals of the major food plant species was determined in all of the sample periods for both of the monkey species. Many of the resources used by both species (*e.g.*, *Ficus* spp., *Swartzia cubensis*, *Mastichodendron capiri*) occurred at low densities. Resources occurring at low density tended to be spatially separated, and thus an individual tree was likely to represent a patch. The average density of the food plants that were used by the howling monkeys for greater than 1% of their feeding time was low (7.96 trees/ha) and 63% of these plant species occurred at a density of less than 1 individual per hectare. Similarly, food plants constituting greater than 1% of the spider monkey's feeding time were found at an average density of 4.76 individuals per hectare and 52.9% of these species occurred at a density of less than 1 individual per hectare. For both species it was common for only 1 individual food bearing tree of a particular species (*e.g.*, *Ficus* spp., *Swartzia cubensis*) to occur in the 12 ha gridded area.

Foraging behaviour as related to patch use.

The howling monkeys studied in Santa Rosa spent 49.0% of their feeding time eating leaves, compared to 28.5% and 22.5% of their feeding time eating fruit or flowers, respectively. In contrast, spider monkeys spent 77.7% of their feeding time eating fruit, and patches containing fruit represented 88.0% of the total number of patches visited. Feeding on flowers and leaves constituted 9.0% and 11.9% of the spider's feeding time, respectively.

On average, spider monkeys spent 810 seconds feeding in a patch they visited (range = 10-5021 seconds, $n = 147$). The time spent feeding in a patch did not differ between the types of patches being used. Spiders on average used flower patches for 729 seconds ($n = 13$), and used patches containing fruit ($n = 121$) or leaves ($n = 13$) for 814 seconds and 853 seconds, respectively ($F = 0.058$, $P = 0.943$). The time spent feeding in a patch was related to the season; spiders spent significantly less time in each patch visited in the dry season (mean = 643 seconds, $n = 78$) than in the wet season (mean = 999 seconds, $n = 69$, $t = 2.17$, $P = 0.032$). Howling monkeys spent an average of 1275 seconds feeding in a patch ($n = 78$), which tended to be a longer period than that of spider monkeys ($t = 1.87$, $P = 0.068$). The time that howlers spent feeding in a patch did not differ between the types of patches they were using (fruit

1638 seconds $n = 44$, flower 684 seconds $n = 24$, leaves 906 seconds $n = 20$, $F = 1.397$, $P = 0.262$). The howlers spent longer in patches in the dry season (mean = 30.1 minutes) than in the wet season (mean = 12.9 minutes, $t = 7.927$, $P < 0.001$).

The average DBH of the food trees used by spider monkeys was 43.1 cm with a range of 7 cm to 185 cm. The patches used to obtain flowers had on average the largest DBH (mean DBH = 56.6 cm, $n = 13$), followed by fruit patches (mean DBH = 37.8 cm, $n = 121$), and leaf patches (mean DBH = 33 cm, $n = 13$), but these differences were not significant ($F = 0.651$, $P = 0.438$). Although time spent feeding in patches showed seasonal variability, patch size showed no significant change with season (mean patch size, dry season 39.2 cm DBH $n = 79$, wet season 47.0 cm DBH $n = 69$, $t = 1.39$, $P = 0.167$). The howling monkey group used patches with an average DBH of 62.6 cm, which was significantly larger than the size of the patches used by the spider monkeys ($t = 3.39$, $P < 0.001$). The average sizes of the different types of food patches used by the howlers were similar (fruit, mean DBH = 63.8, $n = 44$; flowers, 63.9 $n = 24$; leaves, 59.0 $n = 20$). Unlike spiders, the size of the patches used in the wet season by the howlers (mean DBH = 79.4 cm, $n = 34$) was significantly larger than the size of those used in the dry season (mean DBH = 44.9 cm, $n = 54$, $t = 22.4$, $P < 0.001$).

Do these primates deplete the patches they use?

One line of evidence suggesting that both spiders and howlers generally deplete the trees they use in a single visit is that they were frequently observed to feed in a number of individual trees of the same species in direct succession. This occurred even if the individual trees were far apart. For instance, spider monkeys on average spent 821 seconds moving between different individual *Sloanea terniflora* trees, and it was not uncommon for them to visit four or five different trees in direct succession. One explanation for these observations is that the monkeys were feeding in a tree and depleted its food resources to a level where it was more profitable for the animals to travel to a new tree where presumably the rate of intake of food items would be higher than if they remained feeding in the original tree. Other explanations for the observed pattern, such as a need to travel in order to adequately defend territorial boundaries, cannot be ruled out by these observations.

A second line of evidence of patch depletion is that for most tree species the rate of intake of food items during a feeding bout in a single patch

was higher at the start of the feeding bout than later in the same feeding session (paired t-test howlers $t = 5.51$, $P = 0.005$, spiders $t = 4.32$, $P < 0.001$, average length of feeding session for spiders was 810 seconds and for howlers 1275 seconds). One possible interpretation of this result is that food items are easier to find when a subgroup first enters a tree than after they have been feeding in it for some time. An alternative explanation for the decrease in the number of food items obtained over the duration of the feeding bout is that the animals are becoming satiated. If this explanation were true one might expect a decrease in the rate of acquiring food items obtained with all types of plants. However, that was not the case. For instance, the rate of intake of leaves eaten by howling monkeys did not change over the length of a feeding bout ($t = 0.780$, $P = 0.717$, $n = 20$), nor did the rate of intake of fig fruit by spider monkeys decrease ($t = 0.39$, $P = 0.359$, $n = 17$), but the rate of acquiring other fruits by spiders, such as *Bursera simaruba* ($t = 11.0$, $P = 0.029$, $n = 23$), *Muntingia calabura* ($t = 9.00$, $P = 0.035$, $n = 17$), or *Dipterodendron costaricensis* ($t = 6.43$, $P = 0.012$, $n = 12$) did change over the length of the feeding bout.

An alternative method of assessing the validity of the patch depletion assumption is to assume that primates deplete patches and examine relationships that should be true if the assumption of patch depletion were correct. For instance, if patches were depleted by primate exploitation, larger groups should spend less time than smaller groups in patches of equal size, and thus individuals in a larger group should have to travel farther to obtain their daily ration. Consequently, individuals in large groups might spend more time feeding per day than individuals in small groups to compensate for the added energy expended in travel. There was a significant positive correlation between subgroup size and the time spent travelling for both howlers ($r = 0.4829$, $P < 0.001$) and spiders ($r = 0.461$, $P = 0.027$). Similarly, there was a significant positive relationship between subgroup size and the amount of time spent feeding for howlers ($r = 0.491$, $P < 0.001$) and spiders ($r = 0.565$, $P = 0.007$). An alternative explanation for this relationship is that members of large subgroups obtain fewer food items per minute, possibly associated with increased interference. For both primate species in Santa Rosa intake rate was not related to subgroup size (howler $r = 0.197$, $P = 0.250$; spiders $r = 0.054$, $P = 0.417$), so members of differently sized subgroups obtained food items at approximately the same rate.

If patches were depleted by primate use, one would expect that the time spent feeding in a patch would be a function of the size of the patch

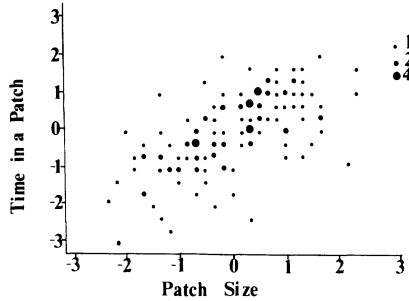


Fig. 1. A standardized partial regression plot which expresses the influence of the size of the patches used by the spider monkeys of Santa Rosa National Park, Costa Rica on the time spent in patches when the subgroup size is held constant. This analysis uses all types of trees. Dot size represents the number of observations of that value.

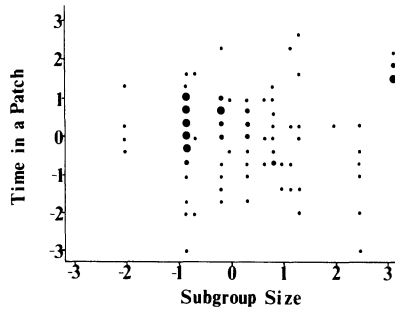


Fig. 2. A standardized partial regression plot which expresses the influence of the size of the subgroup of the spider monkeys of Santa Rosa National Park, Costa Rica on the time they spent in patches when the size of the patch is held constant. This analysis used all types of patches. Dot size represents the number of observations of that value.

and the number of animals using the patch, such that equal sized groups would spend more time in large patches than in small patches, and small groups would spend more time in a patch of a given size than would a larger group. A multiple regression to predict the time that spiders spent feeding in a patch from the size of the patch (all types of trees) and the number of individuals feeding in the patch produced a significant relationship ($R^2 = 0.421$, $P < 0.001$, $\log \text{ time in a patch} = 1.11 + 1.11 \log \text{ patch size} - 0.25 \log \text{ subgroup size}$). The relative influence of these two variables on the time that spider monkeys spent in a patch can be assessed in a number of ways. A partial correlation analysis of feeding time *versus* patch size and the number of individuals using the patch suggests that the size of the patch has a stronger influence on the time spent

in a patch than does the number of individuals using it (log transformed feeding time *versus* patch size, controlling for subgroup size, $r = 0.644$, $P < 0.001$, feeding time *versus* subgroup size, controlling for patch size, $r = 0.151$, $P = 0.028$). A more precise means to show the relative influence of the dependent variables on the time the spider monkeys spent in patches, which shows the actual data used, is to construct standardized partial regression plots (Fig. 1, 2). Comparing the scatter in Figs 1 and 2 illustrates that the influence of patch size on feeding time is stronger than the influence of subgroup size on feeding time in a patch.

For howling monkeys, using all types of patches, the size of the patch and the number of animals feeding within the patch explained little of the variation in time spent feeding in a patch ($R^2 = 0.093$, $P = 0.860$, log of time in a patch = $2.27 - 0.31 \log \text{subgroup size} + 0.55 \log \text{patch size}$).

It is possible to examine what types of patches are depleted by primate use. Although the time howlers spent feeding in all types of patches could not be predicted well by patch size and the size of the subgroup, if only fruit patches are used in this analysis, the relationship is significant ($R^2 = 0.333$, $P = 0.011$, log of time in a patch = $1.00 + 1.46 \log \text{patch size} - 0.46 \log \text{subgroup size}$). The relative influence of these variables on the time howling monkeys spent in patches was assessed in two ways. In a partial correlation analysis both the number of individuals using a fruit patch and the size of the patch were significantly related to the amount of time spent feeding in that patch (partial correlations of feeding time *versus* patch size controlling for subgroup size log transformed $r = 0.577$, $P = 0.002$; feeding time *versus* subgroup size controlling for the size of the patch, $r = 0.267$, $P = 0.050$). By plotting the standardized partial regressions, the data can be presented and the relative influence of each dependent variable on the time spent in a patch when the other dependent variable is held constant (Figs 3, 4).

In contrast to when howlers fed on fruit, when they fed on leaves, patch size and the number of individuals in the subgroup did not predict feeding time in the patch ($R^2 = 0.249$, $P = 0.366$, log of time in a patch = $4.61 - 0.69 \log \text{patch size} - 0.51 \log \text{subgroup size}$).

Different subgroups of spiders occasionally used large fruiting trees soon after they were abandoned by a previous subgroup, or one subgroup would return to a large fruiting tree repeatedly throughout the day *e.g.* *Ficus* spp.). These observations suggest that large fruiting trees may not have been depleted by the spider monkeys. A multiple regression of the time in a patch *versus* patch size and subgroup size was conducted using only trees of specific size. This relationship became non-

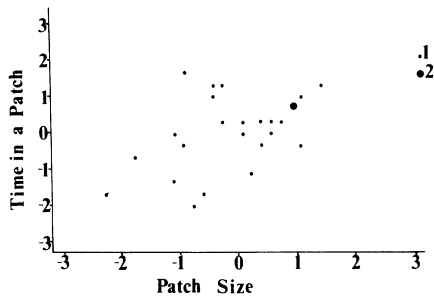


Fig. 3. A standardized partial regression plot which expresses the influence of the size of the patches used by the howling monkeys of Santa Rosa National Park, Costa Rica on the time they spent in patches when the subgroup size is held constant. This analysis used only the fruiting trees used by the howling monkeys. Dot size represents the number of observations of that value.

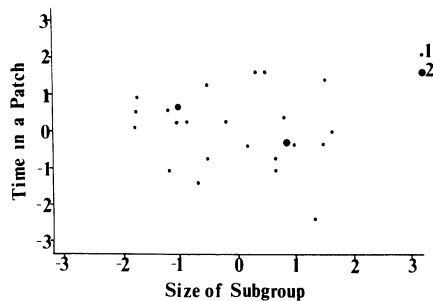


Fig. 4. A standardized partial regression plot which expresses the influence of the size of the subgroup of the howling monkeys of Santa Rosa National Park, Costa Rica on the time they spent in patches when the size of the patch is held constant. This analysis uses only the fruiting patches used by the howling monkeys. Dot size represents the number of observations of that value.

significant only when trees with a DBH greater than 60 cm were used (log transformed >60 cm $R^2 = 0.103$, $P = 0.135$, <60 cm DBH $R^2 = 0.408$, $P = 0.001$). This suggests that trees larger than 60 cm DBH were not depleted by spider monkeys. Trees with a DBH larger than 60 cm only accounted for 20.5% of the patches that spiders visited and 36.5% of these occurred in one sample period. Similar to howlers, the depletion of patches by spider monkeys was a function of the type of patch they used. When spiders fed on leaves, the time they spent in a patch could not be predicted by its size and the size of the subgroup using

it (log transformed leaves $R^2 = 0.052$, $P = 0.389$). However, when spiders fed in fruit or flower patches the multiple regressions were highly significant (flowers $R^2 = 0.705$, $P = 0.007$, log of time in a patch = $0.53 + 1.60 \log \text{ patch size} - 0.37 \log \text{ subgroup size}$, fruit $R^2 = 0.448$, $P = 0.001$, log of time in a patch = $1.08 + 1.13 \log \text{ of patch size} - 0.27 \log \text{ subgroup size}$).

The question of when patches are depleted can be asked for each tree species that the spiders used by examining if the time a subgroup spends in a patch can be predicted from the tree's size and the subgroup's size. However, since many of the trees the spiders used were found at a low density, there was little variation in the size of the patch for many tree species, and thus the number of tree species for which this multiple regression can be examined is small. The time that spiders spent in *Sloanea terniflora* ($R^2 = 0.554$, $P = 0.030$, $n = 10$), *Bursera simaruba* ($R^2 = 0.455$, $P = 0.011$, $n = 23$), and *Muntingia calabura* trees ($R^2 = 0.391$, $P = 0.020$, $n = 17$) was related to the size of the tree and subgroup size, but for *Ficus* spp. ($R^2 = 0.121$, $P = 0.216$, $n = 17$) and *Dipterodendron costaricensis* ($R^2 = 0.009$, $P = 0.480$, $n = 12$) that relationship was not significant.

Discussion

For both species, an increase in the time spent travelling associated with membership in large subgroups corresponded closely to an increase in feeding time. That suggests that animals may attempt to obtain a constant amount of energy after varying expenditures are accounted for. Large subgroups may spend more energy on travel, but ingest more over the course of the day, so that the energy gained minus the energy expended is the same regardless of subgroup size. If these primates attempt to reach a certain net energy level every day, both the amount of food in a patch and the distance between patches, could set the optimal group size to maximize feeding efficiency.

I used the multiple regression equation of feeding time in a patch versus patch size and the number of individuals using the patch, and set patch size to the average, to calculate the expected feeding time of subgroups of different sizes (for howlers only fruit patches were used). This procedure simulates the effect of repeatedly adding members to a feeding subgroup and reveals that the effect on feeding time of adding an additional member is greater for small subgroups than for large subgroups (Fig. 5). This trend could result from an exponential increase

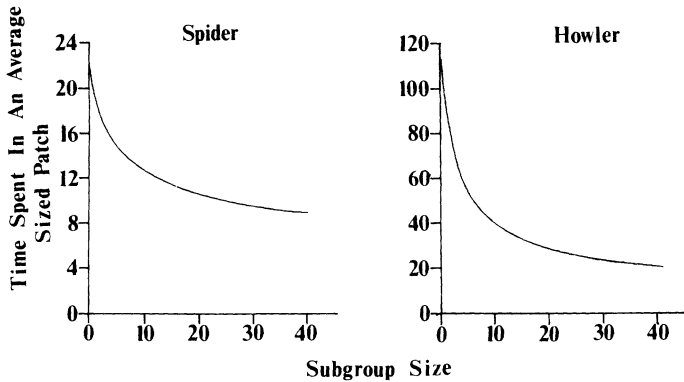


Fig. 5. For the spider and howling monkeys of Santa Rosa National Park, Costa Rica the effect on expected feeding time of adding group members to a subgroup was simulated by using a multiple regression equation of feeding time *versus* the patch size and the size of the subgroup and setting patch size to the average.

in interference as subgroup size increases. KLEIN (1972) observed that when a spider monkey subgroup fed in a tree, all members were dispersed evenly throughout the canopy, and when one member moved to a different location, the other members tended to move to maintain equal spacing. This cost of repeatedly maintaining personal space would increase dramatically in a large subgroup. Thus, in larger subgroups where interference is high, animals would not deplete the patches as rapidly as they would if there was no interference, for they repeatedly spend time avoiding conspecifics that would otherwise be spent eating. This tendency would result in the group staying in the patch longer than predicted based on the size of the patch. A number of researchers have found a relationship between the level of aggression and the size of the patch. WASER (1977) found increased aggression in small patches as the size of mangabey groups increased. Similarly, KLEIN & KLEIN (1977) found an increase in aggression when spider monkeys fed in small trees, and CHIVERS (1977) observed the same relationship with siamangs. SUSSMAN & RICHARD (1974) found that lemurs were aggressive when food occurred in limited areas. However, for the spider monkeys of Santa Rosa there was no relationship between agonistic behaviour and patch size (Spearman Rank Correlation, $r_s = 0.112$, $P = 0.210$).

By substituting the average patch size and subgroup size into the same regression equation, the average feeding time can be calculated. Subsequently, the effect of different patch sizes on the expected feeding gain

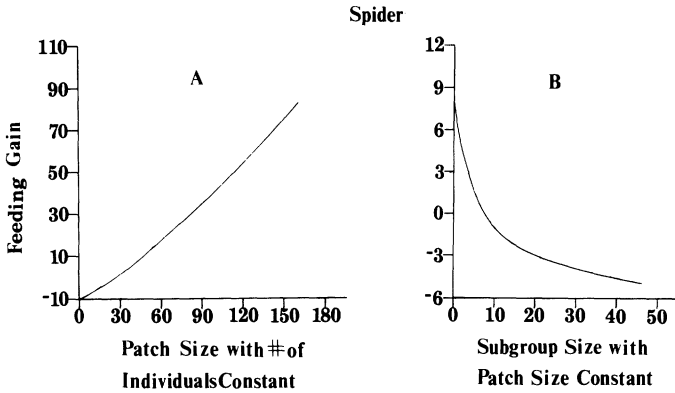


Fig. 6. For the spider monkeys of Santa Rosa National Park, Costa Rica the average feeding time was calculated first with subgroup size held constant and then with patch size held constant, from a multiple regression equation of feeding time *versus* the patch size and the size of the subgroup using the patch.

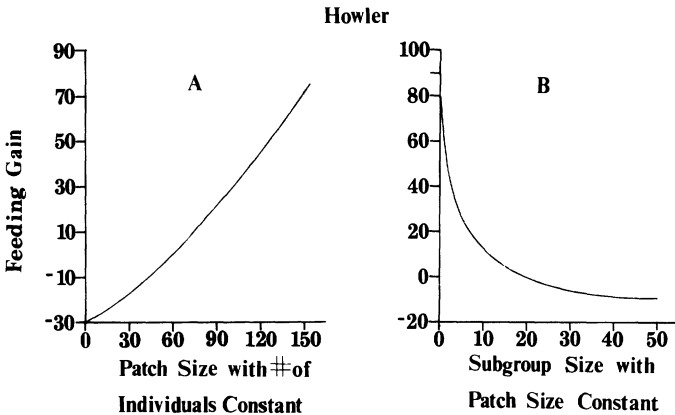


Fig. 7. For the howling monkeys of Santa Rosa National Park, Costa Rica the average feeding time was calculated first with subgroup size held constant and then with patch size held constant, from a multiple regression equation of feeding time *versus* the patch size and the size of the subgroup using the patch.

with subgroup size held constant can be calculated, and vice versa (Figs 6A, 7A). Feeding gain was calculated in this fashion to construct a relative scale, so that any values above zero represent a gain in feeding time above the average time that was normally spent in a patch, and negative values represent feeding bouts of shorter duration than the average. These calculations illustrate that the advantage of feeding

increases almost linearly with patch size for both howlers and spiders. This demonstrates one advantage of selecting large trees. In contrast, the effect of subgroup size on feeding advantage is not linear for either species. Figs 6B and 7B illustrate that for both species, there is a substantial feeding advantage to an individual if it feeds in a small group or as a solitary animal. Since most primates do not forage alone, this relationship implies that the advantages of living in a group, such as social advantages or protection from predators, are substantial.

By comparing the point at which the curve, depicted in Figs 6B and 7B, intersects the ordinate for howlers and spiders, provides some clues as to why spider monkeys have a social system so atypical for a primate. For spiders, the feeding gain of very small subgroups was relatively less than the feeding gain of small howling monkey subgroups. Thus, a spider monkey stands to gain a larger feeding advantage by being in a small subgroup than would a howling monkey. For instance, when spider monkeys are feeding in average sized patches, foraging costs, such as travelling between patches, will equal feeding benefits when 9 animals are in a subgroup. In contrast, for howling monkeys, costs will not equal benefits under these conditions until 20 animals are in a subgroup. Ignoring other possible influences on group size, this finding suggests that to forage efficiently, spider monkeys should be in smaller subgroups than howling monkeys.

This study suggests that howling and spider monkeys use resources that occur in patches and deplete many of the patches they use, particularly fruit patches. The decision of when to leave a patch should be a function of the rate at which the patch is depleted, relative to the availability of other patches (CHARNOV, 1976; PYKE, 1984; KREBS, 1979). Depletion rates will be strongly influenced by the number of co-consumers using the same patches. In tropical ecosystems a large number of species frequently use the same resources (FLEMING, 1979; ROCKWOOD & GLANDER, 1979). For instance, WILLIS (1966) observed 28 Columbian bird species using a single plant.

Since deciding when to leave a patch is a function of the animal's perception of the availability of alternative food sources, it will also be related to the species' ability to sample their environment. A number of researchers have stated that there are striking regularities in many aspects of primate ranging behaviour (CLUTTON-BROCK, 1975; NISHIDA, 1968). Regular movements may serve as a systematic means of sampling their environment. Sampling ability may be highly variable between species. The two species studied here had very different strategies of

sampling. The spider monkeys used resources that appeared relatively ephemeral in comparison to the howlers. The longer day ranges of the spiders may represent their attempt to sample the environment. Also, the sleeping trees of the spider monkeys, which were used at night by the subgroups that had been foraging separately throughout the day, may serve as "information centers" as proposed by WARD & ZAHAVI (1973) for colonial birds. Since the evidence presented suggest that these primates generally deplete the patches they use, and since the patches they use are relatively discrete and easily located, they may prove to be good subjects for the investigation of sampling behaviour.

Summary

Patch depletion is an assumption that underlies many behavioural ecological models, yet it has rarely been examined. The evidence presented here suggests that the spider and howling monkeys of Santa Rosa National Park, Costa Rica use food resources that occur in patches and generally deplete the patches they use. However, some types of patches (*e.g.* large fruiting trees for spider monkeys, and trees used as sources of leaves for howlers) are not depleted by the feeding activity of primates. An examination of which types of patches are depleted and the manner in which depletion likely occurs, allows an assessment of possible factors underlying the different types of social organizations in these species.

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