

## Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites

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**Summary.** Central place foraging models assume that animals return to a single central place such as a nest, burrow, or sleeping site. Many animals, however choose between one of a limited number of central places. Such animals can be considered Multiple Central Place Foragers (MCPF), and such a strategy could reduce overall travel costs, if the forager selected a sleeping site close to current feeding areas. We examined the selection of sleeping sites (central places) by a community of spider monkeys (*Ateles geoffroyi*) in Santa Rosa National Park, Costa Rica in relation to the location of their feeding areas. Spider monkeys repeatedly used 11 sleeping trees, and they tended to choose the sleeping site closest to their current feeding area. A comparison of the observed travel distances with distances predicted for a MCPF strategy, a single central place strategy, and a strategy of randomly selecting sleeping sites demonstrated (1) that the MCPF strategy entailed the lowest travel costs, and (2) that the observed travel distance was best predicted by the MCPF strategy. Deviations between the observed distance travelled and the values predicted by the MCPF model increased after a feeding site had been used for several days. This appears to result from animals sampling their home range to locate new feeding sites.

**Key words:** Multiple central place foragers – *Ateles* – Sleeping sites

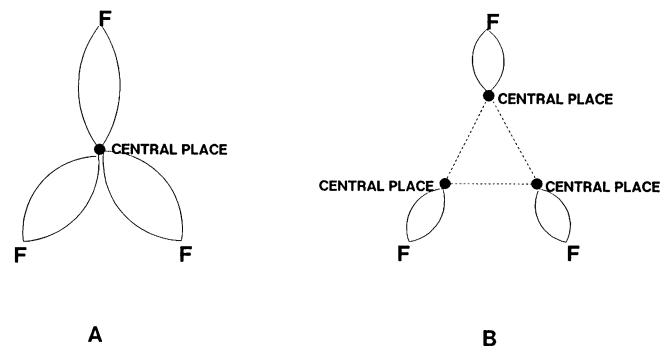
The foraging behaviour of animals which return periodically to their nest or sleeping site has often been investigated within the framework of central place foraging (CPF) (Orrians and Pearson 1979; Andersson 1978, 1981; Schoener 1979) or refuging (Hamilton and Watt 1979). These models assume that the animal returns to a single, fixed central place, such as a nest, burrow, or sleeping site. This constraint of returning to a central place has clear implications for predictions regarding prey selection, the choice of feeding sites, extent of patch depletion, and travel and feeding itineraries (Stephens and Krebs 1987). These predictions have received much qualitative and quantitative support (e.g. Kramer and Nowell 1980; Brooke 1981; Tinbergen 1981; Giraldeau and Kramer 1982; Carlson and Moreno 1982; Kacelnick 1984; Stephens and Krebs 1987).

Many animals however are not restricted to a single central place, but choose between one of a limited number of central places (e.g. *Papio hamadryas* Sigg and Stolba 1981,

*Macaca nemestrina* Caldecott 1986, *Sternus vulgaris* Caccamise and Morrison 1986). We call such animals “Multiple Central Place Foragers” (MCPF, see McLaughlin and Montgomery 1989). MCPF differs from central place foraging in that the animal’s travel costs entail both (1) travel between the central place and feeding sites, plus (2) travel between the different central places. Hence, analyses of MCPF will focus on the choice of central places, rather than the consequences of foraging around these sites.

To date, the energetic consequences of using several central places has received little theoretical treatment. Covich (1976), however, suggested that animals with multiple burrows could use a larger foraging area under a fixed level of predation. To examine the travel consequences more generally, consider an animal that regularly returns to a central place but which requires a minimum area to meet its foraging needs. If the animal used one central place, it would spend much time and energy travelling to and from the patches located far from its central place (Fig. 1 A). Alternatively, if the animal used several central places, it could potentially reduce overall travel costs, while still gaining access to a large foraging area, by switching central places (Fig. 1 B).

To compare these two strategies, let  $D_c$  be the average round trip travel cost for a forager with a single central place located near the center of its home range. The daily travel cost ( $T_c$ ) for such a forager (assuming 1 trip per day) is equal to its round trip travel cost ( $T_c = D_c$ ). For a MCPF, let  $D_m$  be the total round trip cost,  $D_b$  be the average dis-



**Fig. 1 A, B.** Diagrammatic representation of the central place foraging strategy (A) and the multiple central place foraging strategy (B). The curved lines represent the length of a foraging trip (made one or more times) to a feeding site (F), and the dashed lines represent the travel distance between central places in a MCPF strategy

tance between the alternate central places, and  $n$  be the number of consecutive days a central place is used. The total daily travel cost ( $T_m$ ) is:

$$T_m = \frac{D_b + nD_m}{n}$$

For MCPF to have lower daily travel costs on average than central place foraging ( $T_m < T_c$ ),

$$D_c > \frac{D_b + nD_m}{n}$$

$$\Delta D_f > D_b/n$$

where  $\Delta D_f$  is the difference in round trip travel cost between the two strategies ( $D_c - D_m$ ). Hence, it is energetically better to use a MCPF strategy when (1) the reduction in the round trip travel cost is larger or (2) when the cost of moving between sleeping sites ( $D_b$ ) multiplied by the frequency at which it is paid is small.

In this paper we examine the selection of sleeping sites relative to feeding sites, by a community of spider monkeys (*Ateles geoffroyi*). During the last 5 years we have documented that the spider monkeys of Santa Rosa National Park, Costa Rica exhibit a flexible social organization in which a community of approximately 42 amiably interacting individuals fission into small subgroups (mean = 4.94 individuals, range = 1–35 SD = 4.18). Subgroup composition is labile, but animals in a subgroup coordinate their activities and maintain close spatial contact (Klein 1972; Klein and Klein 1977; Chapman 1988). These subgroups forage in small, localized areas of the community's home range throughout the day, and may congregate at one of a number of regularly used sleeping sites in the evening. Although the adaptive significance of congregating at sleeping sites is not known, we assume that attending sleeping sites provides individuals with some advantages. Congregating at these sites may potentially decrease the risk of nocturnal predation, but these sites may also serve other functions, such as strengthening social bonds. The necessity of returning to specific sleeping sites may constrain the range use patterns of the spider monkeys, influencing how they can most efficiently use the available feeding sites. These feeding sites are often large fruiting trees (e.g. *Ficus* spp.) which individuals use repeatedly over several days before switching to a new feeding site.

In this paper, we first demonstrate that spider monkeys regularly use a small number of sleeping sites, and describe their foraging behaviour with respect to these sites. Second, we compare the observed travel distance with (a) the predicted travel costs for a MCPF strategy, (b) predicted values for a single central place strategy, and (c) the predicted values for a strategy of randomly choosing a sleeping site from the set of regularly used sites.

## Methods

The ecology and behaviour of the free-ranging spider monkeys of Santa Rosa National Park, Costa Rica have been studied since 1983, involving 36 months of field observations. The study area is located in the tropical dry forest of northwestern Costa Rica, a region which experiences long

severe dry seasons (see Chapman 1988 for the exact dates of the study and Janzen 1986 for a description of the study area). During the dry season, the majority of the non-riparian trees lose their leaves which facilitates behavioural observations and the visual tracking of known individual monkeys.

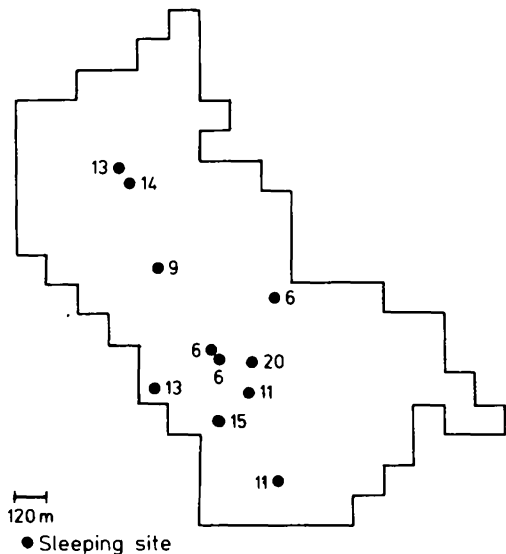
To obtain information on range use and feeding patterns, subgroups containing specific recognizable individuals were located in the morning or early afternoon. Typically, the subgroup was followed until it entered a sleeping site in the evening. Individual recognition was possible following the darting and tagging of animals, either as a result of the collars or anklets placed on the animals ( $n=13$ ) or by their scars and pelage patterns ( $n=22$ ).

Behavioural data were collected using a focal animal sampling regime with 10-minute sessions (Altmann 1974). When possible the subject chosen for observation within the subgroup was selected according to a fixed rotation between individuals and/or age and sex classes. Whenever the focal animal was feeding, the food item and the plant species were noted and the size (diameter at breast height (DBH)) of the tree was visually estimated. The average error in visually estimating the DBH was 3.7% ( $n=46$ , mean DBH of the trees used was 43.1 cm). Whenever all food items handled by an individual could be easily seen, counts were made of the rate of ingestion. Behavioural observations were recorded during a 3-week sampling period so that at the end of each period approximately an equal number of observations were made in each hour of the day and on each individual in the community. Over the entire study, 26 sampling periods were completed.

At the end of each 3-week period of behavioural observation, 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. 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 fruiting trees (Peters et al. 1988). Thus, as an index of food abundance for a 3-week behavioural sampling period, we use the density of trees that the spider monkeys were using during that period, weighted by the DBH of the trees (the sum of the DBH for all sampling grids).

The location of the subgroup being followed was continuously recorded as a coordinate on a grid consisting of cells 120 m by 120 m in size, superimposed on an aerial photograph of the study area. Since known individual trees could often be identified on the photograph, we estimated that the error was rarely greater than 50 m.

Subgroups were observed at sleeping sites on 152 occasions, and on 42% of these occasions the same subgroup was watched the next morning. In these instances, no subgroup was ever believed to join or leave the sleeping tree between the time when the observers left the sleeping tree and when they returned. Thus, the data from all 152 observations were used in subsequent analyses.



**Fig. 2.** The home range and the location of repeatedly used sleeping sites for the spider monkeys of Santa Rosa National Park, during the 1987–1988 field season. The number of times that the sleeping site was used is presented by its location

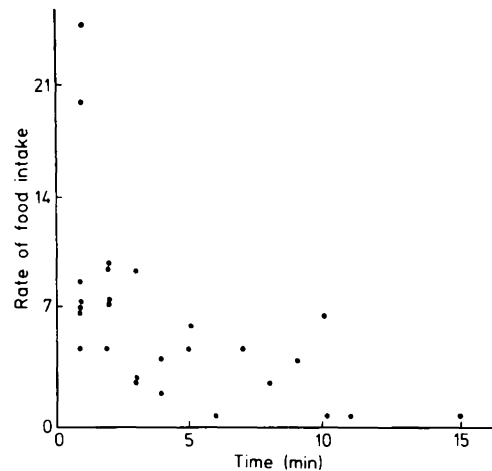
## Results

### *Description of range use and selection of sleeping sites*

There appeared to be two distinct classes of trees which spider monkeys used as sleeping sites: repeatedly used sites and sites used only once. On 81.6% of the evenings that spider monkeys were followed to a sleeping site, they chose a tree which was repeatedly used. These sites were observed being used between 6 and 20 times (Fig. 2). On the remaining 18.4% of the evenings, the spider monkeys selected sleeping trees which were never used before or after that night. Repeatedly used sleeping trees also had large piles of dung and seeds below them indicating that they were used as sleeping sites more frequently than the following of subgroups would suggest. The mean number of individuals observed in non-repeatedly used sleeping trees was significantly smaller than the number seen at repeatedly used trees (non-repeatedly used trees – mean size = 2.9 animals,  $n = 28$ ; repeatedly used sites – mean subgroup size = 6.0 animals, range 1–27,  $n = 124$ ;  $t = 7.07$ ,  $P < 0.001$ ).

Spider monkeys are fast moving primates with large home ranges, so it is difficult to locate and follow a specific individual day after day. Consequently, it is difficult to determine the number of consecutive nights that a particular individual used a specific sleeping site. However, on 9 occasions we collected data for a single individual on a number of consecutive days. On average, the target animal used a specific sleeping site for 4.3 consecutive nights before selecting a new sleeping tree (range 2–7,  $n = 9$ ).

The animals typically left the sleeping sites soon after dawn (mean = 12.2 minutes, range 0–37 min,  $n = 64$ , dawn was considered the time when observation of animals was possible) and travelled out to a feeding site. On average, spider monkeys travelled 1297 m daily. The subgroups typically followed a roughly circular route, usually returning at the end of the day to the sleeping site which they started from in the morning. On an average day individual monkeys spent 32.6% of their time travelling, 33.5% feeding, and 24.1% resting. They visited a number of patches in a day,



**Fig. 3.** The food intake rate (items per min) vs the length of time the food patch was used by subgroups of spider monkeys (all types of patches)

spending an average of 13.5 min in each patch visited (range 10 s – 84 min,  $n = 147$ ). A patch was normally a single tree containing food items, or rarely when more than one individual tree of the same species were found with adjoining canopies, all of the individuals were considered to compose the patch. The average time spent travelling between successive patches was 11.7 min (range 5 s to 61 min,  $n = 172$  patch changes). Fewer than 15% of these movements were less than 1 min in duration (Chapman 1988).

The foraging behaviour of the spider monkey suggests that they deplete local food resources (Chapman 1988). Considering all tree species, as the time that spider monkey subgroups spent feeding in a tree increased, the rate at which an individual could obtain food items declined at a decreasing rate (Fig. 3). To verify the curvilinearity of this relationship a second degree polynomial was fit to the data using a least squares regression. This regression was significant ( $r^2 = 0.468$ ,  $P < 0.001$ ; squared term  $t = 3.72$ ,  $P < 0.001$ ). Patch depletion may account for this relationship. If spider monkeys deplete the food resources in a tree, this would result in a decline in the number of food items an individual could accumulate as it spends more time in the tree. Evidence suggests that the declining nature of the intake function may have affected the fashion in which animals use a patch in relation to the distance it was from the central place. When all types of patches were considered, the time spent feeding in a patch increased the further the animal was from the central place ( $r = 0.212$ ,  $P < 0.001$ ).

### *Multiple central place foraging versus alternative strategies*

Brachiation is a costly form of locomotion (Parson and Taylor 1977). Thus, spider monkeys may attempt to minimize travel costs, and we assume that individual spider monkeys should try to minimize their daily travel costs while still meeting their daily food requirements. Based on single central place models (Orians and Pearson 1979), we expected that the sleeping sites used by the monkeys would be located in the “center of gravity” for the food distribution (Horn 1968). While most of the repeatedly used sleeping trees were in the center of the community’s home range, there were some sleeping trees located near the edge of their home range (Fig. 2). Since spider monkeys were not con-

**Table 1.** The difference between the different strategies in terms of the distance travelled (MCPF = multiple central place foragers, CP = single Central Place Forager). The strategies were compared with an ANOVA and Scheffe *a posteriori* comparisons ( $F = 14.2$ ,  $P < 0.001$ ,  $n = 68$ )

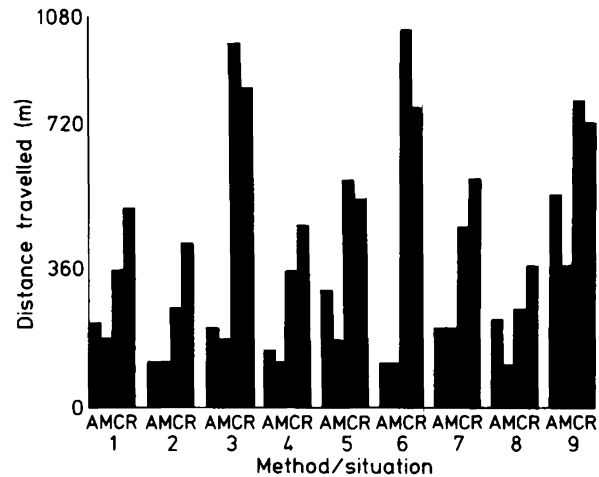
Prediction	Difference		Scheffe probability
	$\bar{x}$ difference	SE	
Observed-MCPF	193 m	61.7	$P > 0.05$
Observed-CP	330 m	100.4	$P < 0.05$
Observed-Random	366 m	83.7	$P < 0.05$
MCPF-CP	526 m	85.3	$P < 0.05$
MCPF-Random	560 m	88.4	$P < 0.05$

strained to return to a single central sleeping tree (e.g. because of dependent young, or a food cache), they were free to reduce travel costs by choosing the sleeping tree closest to the feeding area that was being used, and to change sleeping sites once local resources had been exhausted.

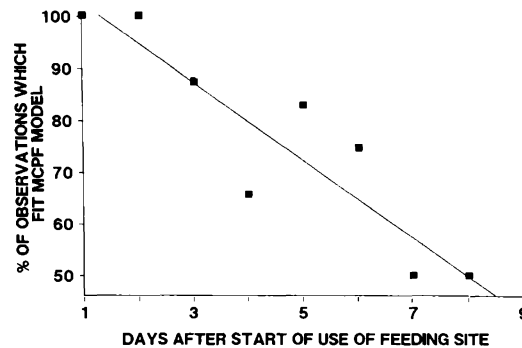
To evaluate the travel consequences of having several repeatedly used sleeping trees, we compared a MCPF strategy, to a central place strategy of returning to a single fixed central place, and a strategy of randomly choosing a sleeping site from the 11 repeatedly used sleeping trees (the mean of 100 random selections). With the MCPF strategy we expected the monkeys would choose the sleeping tree closest to the feeding area being used on that given day. For this analysis, we used only those occasions in the 1987–1988 field season when a subgroup was followed from early afternoon or earlier in the day to the sleeping site. We determined the observed distance travelled from the major feeding area to the sleeping site chosen ( $n = 68$  days). The actual observed behaviour of the spider monkey did not differ from that calculated from the multiple central place foraging strategy, but did differ from the central place and random models ( $F = 14.2$ ,  $P < 0.001$ , Scheffe 0.05, Table 1). Thus, this analysis suggests that a MCPF model describes the actual behaviour of the spider monkeys, whereas the other models do not.

As a second comparison of observed travel distances and predictions from the three different strategies, we examined sleeping site selection for those occasions where individual spider monkeys fed almost exclusively on a single large fruiting tree (e.g. large *Ficus* spp.) for a period of more than 4 consecutive days. The sample size for these episodes was small, as the original sampling procedure was not designed to watch specific individuals day after day. However, nine episodes are available (mean number of consecutive days = 5.6). The observed distance travelled by the spider monkeys was not related to the travel distance predicted by the central place strategy ( $r = 0.225$ ,  $P = 0.561$ ), or that based on the random selection of sleeping sites ( $r = 0.207$ ,  $P = 0.592$ ). However, the observed values were related to the multiple central place model ( $r = 0.791$ ,  $P = 0.011$ ). In 8 out of the 9 situations, the multiple central place model more closely represented the actual distance travelled than the other models (Fig. 4). In the case which is the exception, the density of food resources in the environment was higher than any other period. Thus, if an animal travelled further than the most economic route, it may have been relatively easy for it to recover the extra energy spent in travel.

On 6 of the 9 occasions just analysed we have informa-



**Fig. 4.** The distance travelled from 9 repeatedly used feeding sites to a sleeping site calculated using a MCPF strategy (*M*), a central place foraging strategy (*C*), a random strategy (*R*, 100 random selections of one of the repeatedly-used sites), and the actual distance travelled (*A*)



**Fig. 5.** The percentage deviation between observed and predicted daily travel distances (MCPF model) vs. the number of consecutive days spent using the feeding site

tion on which sleeping site was used after the feeding site was abandoned. Thus, the distance travelled between sleeping sites once a particular feeding site was abandoned can be incorporated as a cost into the MCPF model. When this distance was incorporated into the multiple central place foraging model, the predicted values were related to the observed values ( $r = 0.87$ ,  $P < 0.01$ ,  $n = 6$ ) and a larger proportion of the variance could be explained than when the costs of travelling between sleeping sites was not incorporated.

While the MCPF strategy provided the best fit to the observed travel distance, there was a systematic deviation from its predictions related to the time that a feeding area had been used. We found a negative relationship between the number of days following initial use of a feeding site and the percentage of the observations which corresponded to the predictions of the MCPF model (i.e. used the sleeping sites nearest the feeding site,  $r = 0.941$ ,  $P < 0.001$ , Fig. 5). We suggest that this occurred because resources in the vicinity of the sleeping site were depressed over time, and monkeys therefore needed to sample more distant areas for new feeding sites (Morrison 1978). Such sampling would then take the monkeys within the vicinity of other sleeping trees.

## Discussion

Based on their selection of sleeping sites, the spider monkeys of Santa Rosa are best described as multiple central place foragers. This strategy reduces the average distance travelled per day because the monkeys select sleeping trees which are located close to the feeding area currently being used. Further, since the monkeys have many repeatedly used sleeping trees which were used for several days consecutively, MCPF allows them to efficiently use a relatively large home range, while still gaining the advantages of using a sleeping site where conspecifics congregate. Deviations of the observed travel distance from that predicted by the MCPF model appear to reflect the animals sampling their environment to locate new feeding sites.

One would expect this strategy to be advantageous when the efficient use of food resources was at a premium and food abundance was low. With the spider monkeys of Santa Rosa we found a positive relationship between number of animals seen at the central sleeping sites and the abundance of food resources ( $r=0.630$ ,  $P<0.01$ ,  $n=8$ , only observations made in 1987–1988 were appropriate for consideration). Thus, we suggest that when resources are abundant, and there is an advantage to using a central place, animals should become single central place foragers. The added costs of travel associated with this pattern can easily be recovered. In contrast, if the resources are low, an animal may find it difficult to recover the increased costs of travel associated with single central place foraging, and a multiple central place foraging strategy may be more advantageous. Or, at the far extreme, if the available resources are very low, an animal may forego the benefits of using central place or multiple central place foraging strategies because the travel costs are too high and may choose to sleep at the nearest suitable site to the feeding area.

There are many animal species which may potentially use a MCPF strategy. Considering primates, there are a number of descriptions of species which regularly use a few sleeping sites (12 sleeping sites *Papio cynocephalus* Rasmussen 1979, 11 sleeping sites *Callicebus torquatus* Kinzey et al. 1977, 14 sleeping sites *Saguinus oedipus* Neyman 1978, 9 sleeping sites *Macaca nemestrina* Caldecott 1986). Fleming (1982) describes that bachelor male and immature female *Artibeus jamaicensis*, a tropical frugivorous bat species, roost in small groups in the forest canopy during the day. These foliage roosts change location frequently and are found closer to their food trees than the roosts of adults. Many species of ground-dwelling squirrels have a number of different burrows from which they forage (Armitage 1988). Hobson (1972) describes the use of shelter by Hawaiian reef fish. After foraging, a number of reef fish species return to crevices to rest and seek shelter from predators. Observations suggests that individual fish have specific sites that they use, but that this selection may change over time. Caccamise and Morrison (1986) describe the foraging activities of the starling (*Sternus vulgaris*). These birds switch between roosting in their own feeding area or using a colonial roost. For species such as these it may prove profitable to examine their behaviour in terms of a MCPF model.

Current foraging theory has focused on problems of diet choice and patch use, while other foraging decisions, such as the choice of foraging itinerary, have received far less attention. In this study we recognize that many foragers may have more than one central place from which they

radiate their activities, and demonstrate that having more than one central place can reduce overall travel costs. Future studies should consider additional questions such as: what is the optimal number of central places?, or what is the optimal location for central places?

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