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ORIGINAL ARTICLE

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Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*)

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Abstract Scale invariant patterns have been found in different biological systems, in many cases resembling what physicists have found in other, nonbiological systems. Here we describe the foraging patterns of free-ranging spider monkeys (*Ateles geoffroyi*) in the forest of the Yucatan Peninsula, Mexico and find that these patterns closely resemble what physicists know as Lévy walks. First, the length of a trajectory's constituent steps, or continuous moves in the same direction, is best described by a power-law distribution in which the frequency of ever larger steps decreases as a negative power function of their length. The rate of this decrease is very close to that predicted by a previous analytical Lévy walk model to be an optimal strategy to search for scarce resources distributed at random. Second, the frequency distribution of the duration of stops or waiting times also approximates to a power-law function. Finally, the mean square displacement during the monkeys' first foraging trip increases more rapidly than would be expected from a random walk with constant step length, but within the range predicted for Lévy walks. In view of these results, we analyze the different exponents characterizing the trajectories described by females and males, and by monkeys on their own and when part of a subgroup. We discuss the origin of these patterns and their implications for the foraging ecology of spider monkeys.

Keywords Animal movement · Spider monkeys · Lévy walks · Scale invariance · Foraging

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Introduction

Understanding how pattern and variability change with the scale of analysis is one of the main goals of ecological research (Levin 1992). Ideally, one would like to extrapolate findings in one scale of analysis to another. This may be achieved by simplifying the problem at one scale, finding an expression that describes its main features without unnecessary detail, and then using this expression to extrapolate to larger scales. Thus, modeling animal movements by diffusion equations, where individuals are assumed to move at random as if they were Brownian particles, has been successful in predicting large-scale features of populations, such as their rate of spatial dispersal (Turchin 1998).

Fractal geometric patterns show statistical similarity over several orders of magnitude in the scale of observation (Mandelbrot 1983). In biology, scaling relationships which describe the same pattern at different scales have been found in many different systems, from the geometry of vascular networks to the natural fragmentation of landscapes (reviewed in Gisiger 2001). Fractal geometry has been successful in predicting optimal strategies for foraging on resources that occur in patches of varying size and distribution (Ritchie 1998) and the different scaling relationships existing between body size and home range in different species (Haskell et al. 2002).

Here we describe the movement patterns of individual spider monkeys (*Ateles geoffroyi*) in the wild and find that they resemble what physicists have long recognized as Lévy walks. As opposed to Brownian random walks, in which the length of steps is constant, Lévy walks show spatial scale invariance in the length of constituent steps and temporal scale invariance in the duration of intervals between steps (Shlesinger et al. 1993). Shlesinger and Klafter (1986) first suggested that animals could forage efficiently by performing Lévy walks (see also Klafter et al. 1990). Viswanathan et al. (1999) developed an analytical model suggesting that Lévy walks could be an optimal strategy for finding randomly distributed, scarce resources. Empirically, these movement patterns have already been found in the foraging movements of jackals (*Canis adustus*; Atkinson et al. 2002) and wandering albatrosses (*Diomedea exulans*; Viswanathan et al. 1996).

In a Lévy walk (Shlesinger et al. 1993), the length of each successive step (x) varies according to a power-law function of the form:

$$N(x) \sim x^{-a} \text{ where } 2 < a < 3$$

Thus, a Lévy walk has no intrinsic step length scale, and steps of seemingly very long length may be observed. When taking the logarithm in both sides of the equation, the power-law equation becomes a straight line, implying that there is a constant proportion of steps of different lengths at any scale.

Lévy walks have been studied experimentally in many different fields in physics (Klafter et al. 1996). For instance, in fluid dynamics, the position of tracer particles is analyzed at regular intervals under different flowing media conditions (Weeks et al. 1995). In these experiments, a particle can remain in the same location for some time before moving again. These waiting (or sticking) times also vary according to a power-law function of the form:

$$N(t) \sim t^{-b} \text{ where } b \simeq 2$$

Because some very long steps may occur, in a Lévy walk the mean-squared displacement will not be a linear function of the time t as it is in regular random walks (i.e. with constant step length). Rather, the mean-squared displacement $<R^2(t)>$ will vary as:

$$< R^2(t) > \sim t^c \text{ where } 1 < c < 2$$

This implies that the mean-squared displacement of a Lévy walker grows faster in time than that of a random walker with constant step lengths or one with a normal distribution of step lengths. In theoretical studies of Lévy walks, there is a precise prediction about the relationship that should exist between the three exponents presented above (Weeks et al. 1995; Zumofen et al. 1995):

$$\text{for } b > 2,\ c = 4 - a$$

$$\text{for } b < 2,\ c = 2 + b - a$$

Here we analyze the trajectories described by free-ranging spider monkeys in the rainforest of the northeastern Yucatan Peninsula, in Mexico. We use the trajectories that 20 different individuals followed from dawn until dusk to analyze the frequency distribution of step lengths, the frequency distribution of the waiting time durations, and the mean squared displacement at different times. We find that spider monkey foraging trajectories are surprisingly similar to the Lévy walks studied by physicists.

We then use this finding as a tool to explore the possible variations in trajectories with regard to the grouping behavior of spider monkeys. This species forms temporary aggregations that vary in size and composition throughout the day, which have been suggested to occur in response to the variation in food availability (Klein and Klein 1977; Symington 1987, 1988). The trajectories described by lone individuals could then be different to those described by individuals in a subgroup, as they probably represent different strategies for finding or exploiting known food patches. In addition, compared to females, male spider monkeys occupy larger home ranges and travel farther per day in subgroups that are larger on average (Symington 1987; Ramos-Fernández and Ayala-Orozco 2002) a difference that may reflect different space use strategies (Wrangham 2000). Therefore, we analyzed the Lévy walk parameters separately in the trajectories of lone and grouped individuals, as well as in those of females and males.

Methods

Study site and animals

Data were collected in the area of forest surrounding the Punta Laguna lake (2×0.75 km), in the Yucatan Peninsula, Mexico (20°38′ N, 87°38′ W, 14 m elevation). This region is characterized by a seasonally dry, tropical climate, with mean annual temperature of about 25°C and mean annual rainfall of around 1500 mm, 70% of which is concentrated between May and October. The main forest fragment near the lake consists of 60 ha of medium, semi-evergreen forest. This, in turn, is surrounded by secondary successional forest about 30–40 years old in an area of 5,367 ha recently declared as a protected area, the Otoch Ma'ax Yetel Kooh Sanctuary. Spider monkeys use both of these vegetation types, although they spend more than 70% of their daily time and every night in the medium forest (Ramos-Fernández and Ayala-Orozco 2002). Trails were cut throughout the fragment of medium forest and through part of the successional forest. In these trails, trees and other landmarks were used to make accurate maps of this area. Visibility conditions were very good as monkeys used the canopy at heights from 5 to 25 m. More details about the study site, including the tree composition and the density of important species of trees, can be found in Ramos-Fernández and Ayala-Orozco (2002).

Two study groups, one occupying 0.95 km^2 of forest and the other 1.66 km^2, have been studied continuously since January 1997. One group (five female and three male adults in 1999) was habituated to human presence before the study began and the other (15 female and six male adults in 1999) was habituated during 1997. All monkeys were identified by facial marks and other unique features. Adults were defined by their size and darker faces and, in the case of males, for their fully descended testes. All monkeys could be reliably identified by the end of 1997. More details about the study groups can be found in Ramos-Fernández et al. (2003).

Data collection

Data reported here were collected between September through December 1999. On 20 days during that period, a different known adult was chosen as the focal subject and followed by at least two observers from dusk until dawn, taking an instantaneous sample of its location, activity, and subgroup size and composition every 5 min. The location was estimated visually by two observers to the nearest 5 m with respect to landmark trees or paths.

Data analysis

Trajectories were analyzed according to the methods outlined by Turchin (1998). The trajectory of each focal monkey consisted of a sequence of paired coordinates, one pair for each 5 min interval where an instantaneous sample had been recorded. A step was defined as an interval in which any or both of the coordinates in two consecutive samples differed. The length of each step was the linear distance separating the position at two consecutive samples. In some cases, observers lost sight of the focal animal for a number of sample intervals. Steps were not calculated for those intervals but only for those in which the position was known for two consecutive 5-min samples. The frequency distribution of step lengths was analyzed using a bin size of 10 m. In order to explore the possibility of scale invariance in this frequency distribution, data were log-log transformed and the best fit was evaluated using a least-square method. In this way, the value of the slope of the line in the log-log transformed frequency distribution could be calculated easily.

Waiting times were calculated from the number of samples in which the focal animal did not change position. The frequency distribution of waiting times was analyzed using a bin size of one interval (5 min). The log-log transform of this distribution was used to calculate the relationship producing the best fit using a least-square method.

In order to calculate the mean squared displacement of the trajectories, the following procedure was used: first, the length of a line joining the first recorded location of each individual with its location at different times thereafter was measured. Then, all individual squared displacements were averaged for each time of day, yielding the mean squared displacement. From this mean squared displacement a maximum was obtained around 1030 hours, which then decreased as monkeys consistently began approaching their starting point, in some cases returning to it at noon and in most cases returning to it at dusk (see Fig. 4). The mean squared displacement from 0630 to 1030 was then taken to be a period in which most of the individuals moved away from their starting point. For this period only, a log-log plot was produced and a line adjusted by the least-square method.

Turning angles were calculated by subtracting the absolute angle (with respect to the east-west axis and in a counterclockwise direction) of each step from the absolute angle of the previous step. A frequency distribution of turning angles was thus produced, using a bin size of 10°.

The regression slopes for the Lévy walk distribution of trajectories of lone versus grouped individuals and females versus males were compared using an *F* test for regression slopes (Sokal and Rohlf 1994).

Results

The observed daily trajectories of spider monkeys are made up of steps of variable length. Three examples of these trajectories are shown in Fig. 1a–c. One important property of Lévy walks is that they show self-similarity across different spatial scales. When we close in on a

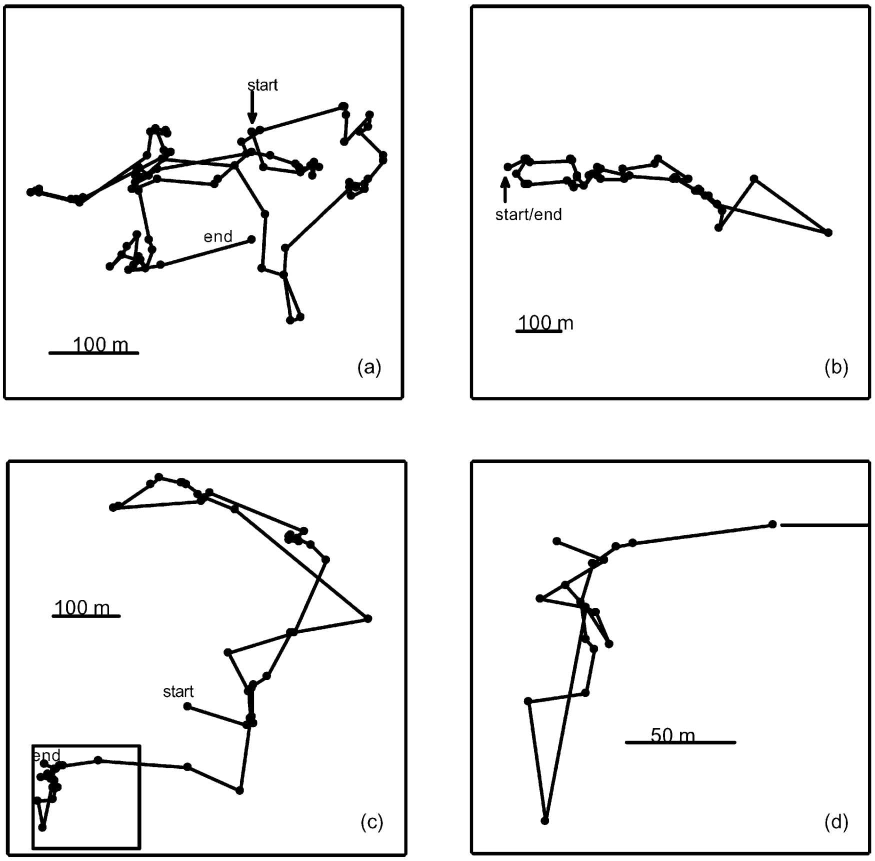

Fig. 1a–d Daily trajectories of spider monkeys. **a, b** Adult females. **c** Adult male, with the section of the trajectory within the lower-left square amplified in **d**. Note that some individuals, like the adult female in **b**, returned to sleep close to where they started their daily travel

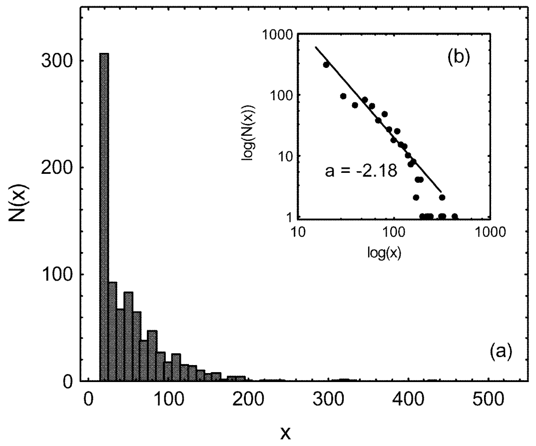

Fig. 2 a Distribution of the number of 5-min intervals $N(x)$ during which spider monkeys traveled a distance of x m. A total of 841 5-min intervals from 20 adult individuals are included. The *inset* (**b**) shows the log-log plot of the same data. A power-law relationship fits the data with r^2=0.89. The estimated value of the exponent is −2.18. The same data fitted an exponential function with r^2=0.79

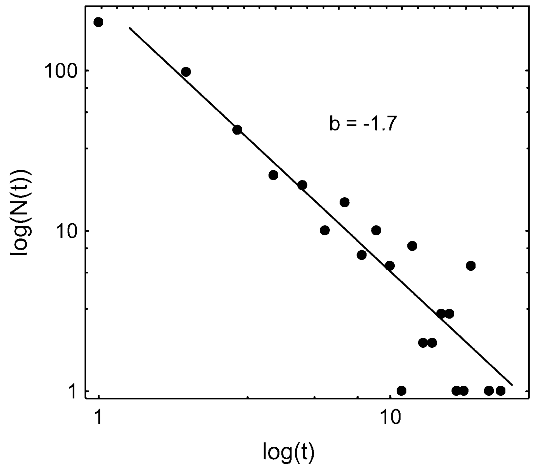

Fig. 3 Distribution of waiting times in the trajectories of spider monkeys. The figure shows the log-log plot of the number of intervals $N(t)$ with duration t. The relationship is fit by a power-law function with an estimated value of the exponent of −1.7 (r^2=0.86)

region of one of these trajectories, a qualitatively similar pattern as in the large scale appears (Fig. 1d).

The frequency distribution of step lengths of all trajectories together shows a wide range of variation (Fig. 2a). The data can be fitted better to a power-law function (Fig. 2b; r^2=0.89) than to an exponential one (r^2=0.79). The value of the exponent in the negative power-law equation fitted to the data is a=2.18.

The frequency distribution of waiting times of all trajectories together also shows a wide degree of variation. Before traveling again, spider monkeys may stop for as little as 10 min or for as much as 2 h (Fig. 3). The log-log plot of the data is fitted well by a negative power-law function with an exponent b=1.7 (r^2=0.86).

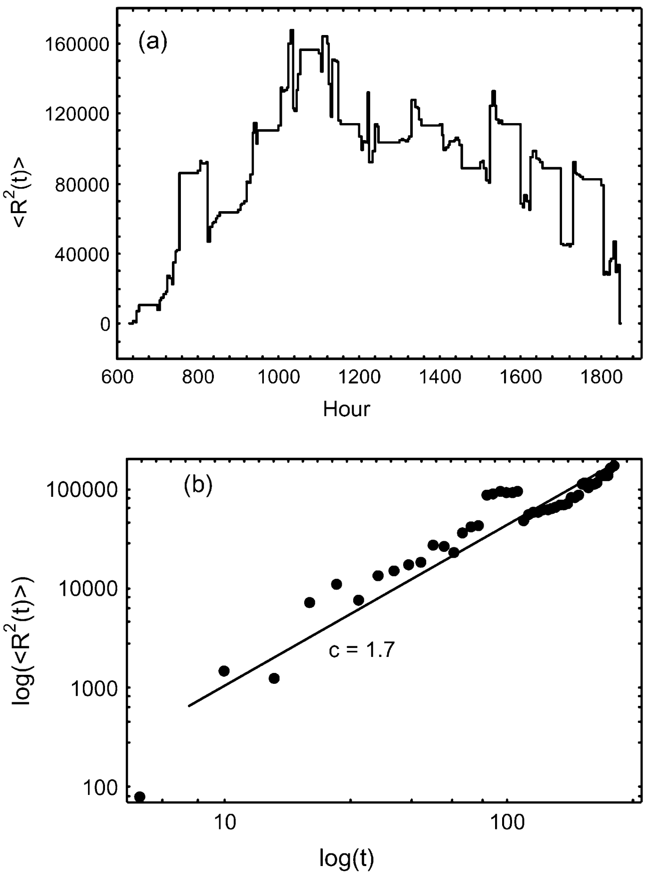

Fig. 4a, b Squared displacement in the trajectories of spider monkeys. **a** The mean squared displacement across all individual trajectories at different times of day. Note that there is a maximum at 1030 hours. **b** Log-log transformation of the mean squared displacement observed from 0630 to 1030 hours. The relationship is well fit by a power-law function with an estimated value for the exponent of 1.7 (r^2=0.87)

The squared displacement in many of the individuals analyzed shows a common pattern: monkeys tend to get away from their sleeping site for a few hours in the morning, before coming back to the origin at noon or staying in the vicinity, normally returning to the same sleeping site shortly before sunset. Some individuals, especially males, did not return to the same sleeping site at the end of the day. Close inspection of the mean squared displacement of all individuals shows a maximum at around 1030 hours (Fig. 4a). A log-log plot of the data for the period between 0630 and 1030 only, when all individuals were getting away from the origin, adjusts to a line with a slope of 1.7 (r^2=0.87), as would be expected in a Lévy walk (Fig. 4b).

The fact that spider monkeys travel back to their sleeping sites, as well as the fact that they sometimes use the same routes for going away from and returning to their sleeping site (for example, see Fig. 1b), implies that some persistence should exist in the direction of consecutive steps. Figure 5 shows the distribution of turning angles between successive steps. This distribution is far

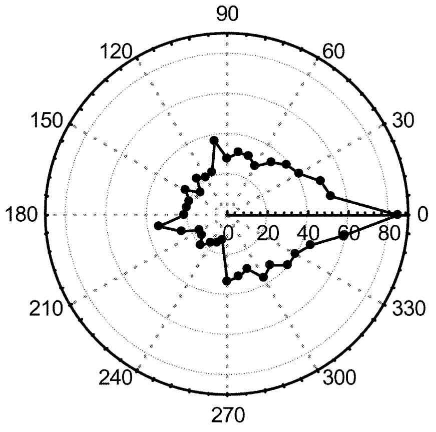

Fig. 5 Circular distribution plot of the turning angle between consecutive steps. Shown is the number of times that two consecutive steps in the trajectories differed by the degrees shown. Note that the distribution peaks around zero

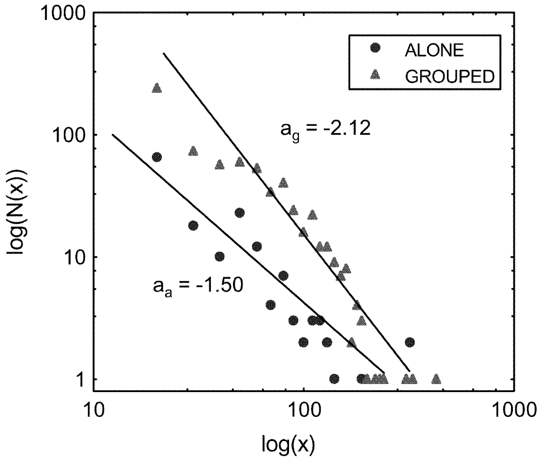

Fig. 6 Distance traveled by spider monkeys when alone and in groups. Shown is a log-log plot of the number $N(x)$ of 5-min intervals in which a lone adult spider monkey traveled a distance x. For monkeys traveling alone, a total of 156 5-min intervals is included. A power-law relationship fits the data with r^2=0.8. The estimated value of the exponent is −1.50. For monkeys traveling in a group, a total of 685 5-min intervals is included. A power-law relationship fits the data with r^2=0.89. The estimated value of the exponent is −2.12

from being uniform, being centered around zero. However, at a large enough time scale, this persistence is not expected to affect the scaling relations between the mean-squared displacement and time.

Spider monkeys change subgroup several times during a day, so the trajectory described by one individual in one complete day includes some steps traveled on its own and others as part of a subgroup. When analyzing the distribution of lengths for these steps separately, the value of the exponent is different: a_a=1.50 (r^2=0.80) for solitary individuals; and a_g=2.12 (r^2=0.89) for individuals in groups (Fig. 6). An *F* test comparing the two regression slopes shows a significant difference (F=5.72, P<0.05). Considering the fact that the number of samples in each category is different, monkeys travel a higher proportion of long trajectories when on their own than when part of a subgroup (Fig. 6).

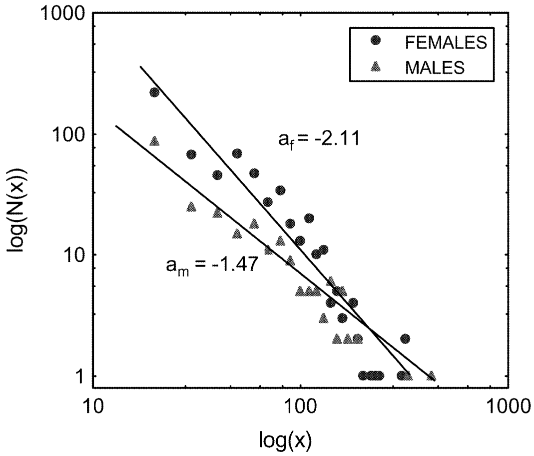

Fig. 7 Distance traveled by female and male spider monkeys. Shown is a log-log plot of the number $N(x)$ of continuous trajectories traveled by adult spider monkeys without stopping, for a distance of x m. For 14 females, a total of 604 5-min intervals were analyzed. A power-law relationship fits the data with r^2=0.9. The estimated value of the exponent is −2.11. For seven males, a total of 237 5-min intervals were analyzed. A power-law relationship fits the data with r^2=0.93. The estimated value of the exponent is −1.47

We also analyzed the distribution of travel lengths separately for females and males. Figure 7 shows that both describe Lévy walks with values of a_f=–2.11 for females and a_m=–1.47 for males. It is males who travel a higher proportion of long trajectories than females.

Discussion

We have presented evidence showing that the daily movements of spider monkeys resemble what physicists know as Lévy walks, i.e., random walks with power-law scaling in the length of their constituent steps. Waiting times, or the duration of intervals without movement, also show power-law scaling. As expected from theoretical studies of Lévy walks, the mean-squared displacement increases faster than in other random walks such as a Brownian random walk (Shlesinger et al. 1993).

In support of this interpretation, there is an agreement between all three exponents, as would be predicted from theoretical studies of Lévy walks (Weeks et al. 1995; Zumofen et al. 1995):

for $b < 2,\ c = 2 + b - a$

which, substituting the observed values of each exponent, yields the following prediction for the value of c:

for $b = 1.7 < 2c = 2 + 1.7 - 2.18 = 1.52$

a value that is quite close to the observed value of 1.7. In other words, there is an agreement between different properties of the observed trajectories, such that they can accurately be described as Lévy walks.

Lévy walks differ in fundamental ways from other types of random walks, such as Brownian random walks, which have been used in most models of animal foraging (rev. in Turchin 1998). For one thing, the mean-squared displacement after a time *t* is larger for Lévy walks than for other random walks (Weeks et al. 1995). In the period between 0630 and 1030 hours, when spider monkeys normally spend 2 or 3 h foraging away from their sleeping sites (Ramos-Fernández, personal observations), the squared displacement increases faster than in a Brownian random walk.

However, there are certain regularities in the trajectories analyzed here that would not allow us to label them as purely random Lévy walks. After 1030 hours, spider monkeys tend to stop traveling away from their sleeping sites and on most occasions return to them before sunset. The travel consequences of spider monkey sleeping site location, and in particular the effect of using multiple sleeping sites, has been discussed by Chapman et al. (1989).

Also, the shape of their home range, which circles a lake (e.g., see Fig. 1c), implies that sometimes a monkey will use the same route to go in one direction and return in the opposite direction. The idea that monkeys are actually following a route of some sort is supported by the fact that two consecutive steps tend to be given in a similar direction, as shown in the distribution of turning directions, which is centered around zero.

Interpretation of these results hinges on the crucial question of the cues that spider monkeys use for finding food sources. Feeding on the fruit from 50–150 species of trees (van Roosmalen and Klein 1987; Ramos-Fernández and Ayala-Orozco 2002), each with its own phenological pattern, spider monkeys clearly face the problem of exploiting an extremely variable resource. During certain times of year in our study site, spider monkeys may spend more than half of their daily foraging time feeding on the fruits of *Brosimum alicastrum*, a species that occurs at densities of 288 trees/ha (Ramos-Fernández and Ayala-Orozco 2002). At other times of the year, however, monkeys may divide their daily foraging time equally among several different species, each occurring at densities of 3–27 trees/ha. In addition, most of these trees show a spatial distribution pattern that is far from uniform (Ramos-Fernández, unpublished data). This spatial and temporal variability implies that, depending on the time of year and the species consumed, monkeys may need to travel anywhere from a few meters to several hundred meters between food sources.

Lévy walks could represent a foraging search strategy, in which the movements of spider monkeys are guided by the odor and visual cues they detect from the existing ripe fruit in fruiting trees, whenever these are within their detection space. Alternatively, the patterns reported here could be the result of the knowledge, based on memory, that spider monkeys could have about the location of fruiting trees.

If spider monkeys have little knowledge of the location of fruiting trees, it is possible that they travel in Lévy walks in order to exploit these unknown sources of food more efficiently. This is how Atkinson et al. (2002) interpreted their data on the Lévy patterns of foraging jackals (*C. adustus*). Viswanathan et al. (1999) have shown that a Lévy walker visiting a number of randomly distributed foraging sites will visit more new sites and revisit less previously visited sites than a Brownian random walker traveling the same total distance. This is because the long steps in a Lévy walk quickly take the forager to more distant sites, making it less likely that it will walk on its own steps again. In this study, the value for the exponent *a* in the distribution of step lengths is remarkably close to the optimum of $a=2$ predicted by Viswanathan et al. (1999) for foragers searching for randomly and sparsely distributed food sources. The possibility that Lévy walks could represent random searches should prompt a reevaluation of null models of random search, which normally assume a constant step length (e.g., Janson 1998).

Sophisticated knowledge of the location of food sources has been demonstrated in several animal species (e.g., in birds by Kamil and Balda 1985; in insects by Dyer 1994; reviewed by Kamil 1994). However, little is known about the spatial abilities of primates (Garber 2000). Observations of foraging baboon troops (*Papio hamadryas*) using the same pathways between food sources and splitting and joining back at scarce water holes suggested that these primates could be using some sort of spatial representation of their environment (Sigg and Stolba 1981; reviewed by Byrne 2000). Experimental evidence suggests that wild capuchin monkeys (*Cebus apella*) visit the closest food sources more often than would be expected on the basis of random search null models (Janson 1998). Also, they appear to use straighter lines than would be expected if they were only searching with no memory of where they had found food in the past. If spider monkeys have a similar kind of spatial knowledge about the past location of food, then the patterns that we report here may not represent "random" searches at all, but the result of more directed travel between known food sources. In this case, Lévy walk foraging patterns could be the result of the distribution of fruiting trees themselves. Very long, infrequent steps could be those given between known patches of fruiting trees, while shorter, more common steps would be given while foraging within a patch.

It is possible that, at any given time, trees with available fruit are distributed in a scale-invariant, fractal manner. In an extensive study of several species of tropical trees in different sites around the world, Condit et al. (2000) found highly aggregated distribution patterns for most of the species, showing graphs of density of neighbors as a function of distance that look strikingly similar to those described by power-law functions. Also, Solé and Manrubia (1995) report self-similar distributions of tree gaps (and thereby sites available for establishment of many new individual trees) in a tropical forest in

Panama. Clearly, more information on the temporal and spatial distribution of the spider monkeys' food resources is required to clarify this issue.

Because spider monkeys are important seed dispersers for several tree species, in reality there could exist a bidirectional relationship between their foraging patterns and the distribution of trees. By foraging and dispersing seeds in such a pattern, spider monkeys might favor, in the long run, a self-similar distribution of the very same trees on which they feed. A similar positive feedback between foraging behavior and the distribution of resources was found by Seabloom and Reichman (2001) in a simulation model of gopher-grass interaction. By restricting their movements to their defended territories, gophers disturbed areas where more grass could grow in the following season, therefore increasing habitat patchiness, which increased the foraging efficiency of gophers in the long run. Westcott and Graham (2000) report a long-tailed distribution in the distance traveled by a tropical flycatcher (*Myonectes oleaginus*) continuously after feeding. Based on the times of digestion for the seeds of different species, the authors derive the expected shape of seed shadows for different species, which also look very similar to power laws. The same pattern has been found in the seed shadows produced by tamarin monkeys (Garber 1986).

Another consequence of foraging in a Lévy walk pattern is that previously visited food sources may be revisited only after long periods of time, favoring the ripening of more fruit before the next visit. Such "harvesting" of resources was suggested by Janson (2000) to be one of the reasons why animals foraging on scarce patches of food would not necessarily visit the closest one in the most optimal route. Perhaps the foraging pattern reported here is the result of a strategy to revisit trees after appropriately long periods of time, when they already bear more ripe fruit.

We have found that the Lévy walks of females and males are different. Males have a larger proportion of long trajectories than females. This is consistent with the fact that male spider monkeys range over wider areas and travel further per day than females (Symington 1987; Ramos-Fernández and Ayala-Orozco 2002). At the boundaries of their group's territory, males form coalitions that engage in very aggressive encounters with neighboring males (Symington 1987; Ramos-Fernández, personal observations). In view of these results, the fact that the Lévy walks of males contain more long steps than those of females is consistent with their different space use strategies.

Finally, we have found a different value of the power-law exponent for the length distribution of steps given by lone monkeys to that for steps given by monkeys when part of a subgroup. In particular, monkeys on their own seem to travel a higher proportion of long steps compared to short ones. One of the cited benefits of group foraging has been an improvement in the likelihood that the group would find food patches which an individual on its own would not find (Krebs and Davies 1993; Janson 1998). If spider monkeys do not have knowledge of the location of food sources, they could still find more fruiting trees when traveling in a subgroup than when alone. The same argument applies if spider monkeys know the location of fruiting trees: if they can share information on the known location of resources (as in baboons: Byrne 2000) it would seem logical that a subgroup would find more fruiting trees than a single individual, therefore decreasing the proportion of long steps.

The origin of the grouping pattern found in spider monkeys and chimpanzees has led to some discussion (Symington 1990; Wrangham 2000). While there seems to be convincing evidence for fissioning to be favored by a decrease in feeding competition, Lévy walks could also be favored for the same reason. In a group of *n* Lévy walkers, the probability that individuals will remain near the origin (or cross each other's path if they all start together at the same spot) is considerably less than for a group of *n* Brownian walkers (Larralde et al. 1992). Long, infrequent trajectories in Lévy walks could be the cause of more group splitting, which in turn could decrease the constraints imposed on individuals in small subgroups to travel with the rest of the group, thus favoring variation in step length. An intriguing possibility is that, in a hypothetical ancestor with stable grouping patterns, group fissioning and Lévy walk foraging patterns could have reinforced each other for the decrease in feeding competition they provided. Then, social behaviors that maintained group membership even in the absence of visual contact would have been favored, leading to the fission-fusion grouping pattern that we see today. Perhaps a modeling approach such as te Boekhorst and Hogeweg's (1994), explicitly incorporating realistic spatial heterogeneity and scale-dependent forager decisions (e.g., Ritchie 1998), could be used to explore the origin of this intriguing social system.

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