



Modeling the searching behavior of social monkeys

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Received 2 November 2003

Available online 17 May 2004

Abstract

We discuss various features of the trajectories of spider monkeys looking for food in a tropical forest, as observed recently in an extensive *in situ* study. Some of the features observed can be interpreted as the result of social interactions. In addition, a simple model of deterministic walk in a random environment reproduces the observed angular correlations between successive steps, and in some cases, the emergence of Lévy distributions for the length of the steps.

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PACS: 87.23.-n; 05.40.Fb

Keywords: Biological physics; Foraging; Random walks

1. Introduction

It is often hypothesized that animals live in groups because they benefit from predator avoidance and collective food searching [1]. However, group living also imposes behavioral restrictions on individuals and may, on the other hand, facilitate the emergence of entirely new behavioral traits. Foraging (or food searching, preparation and consumption) is one of the best-known examples of behavior modulated by group. Recently, several studies on various species have shown that lone foraging animals

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follow trajectories characterized by Lévy probability density distributions for the step lengths [2–4]. In physics, Lévy flights and walks are a manifestation of anomalous diffusion (see Refs. [5,6] for reviews). It has been suggested that Lévy distributions in animals lead to an optimal search [4,7,8].

In a previous study [9], it was found that grouping has indeed an impact on the searching patterns of the social spider monkeys (*Ateles geoffroyi*). The lengths of traveled distances between two stops follow a Lévy-like distribution with a scaling exponent that is different for individuals in groups and individuals when occasionally alone. This difference in the exponent values evidences subtle differences in movement patterns over long distances. The foregoing result suggests that collective searching may be indeed a more efficient strategy, since the exponent value is close to what has been argued elsewhere to be the exponent for an optimal Lévy searching process [4]. In the following, we present probabilistic arguments to quantify group effects during foraging (Section 2). In Section 3, a simple deterministic walk model in a random environment reproduces some of the foraging patterns observed on spider monkeys.

2. Searching and effective group size

Spider monkeys forage in subgroups that change in size and composition several times during the day [10]. These subgroups remain coherent (i.e., with individuals separated by no more than 30 m from each other) for several hours, before they split or are joined by other group members [1,11]. These subgroups may contain from one to eight adults and their youngs, the majority containing two adults [12]. It has been suggested that subgroup size varies in response to the size of the food patches where spider monkeys feed, and that they may share information on the presence of newly found food patches [13,14]. The hypothesis that foraging with others reduces the length of trajectories is widely recognized among ecologists [1,15]. In a recent study [9], different food searching patterns were observed between subgroups containing one adult and those containing more than one. In particular, the difference laid in the distribution of step lengths, defined as the probability that a monkey traveled a distance l in a fixed time interval (5 min). The measured distributions for lone adults and larger subgroups, $P_s(l)$ and $P_g(l)$, respectively, can both be fitted by Lévy laws ($P_i(l) \sim l^{-\alpha_i}$, $i = s, g$), with different exponents. The data are consistent with $\alpha_s \simeq 1.5$ and $\alpha_g \simeq 2.1$, for lone and grouped individuals, respectively [9].

We develop below a possible explanation for these results. Each individual in a subgroup has a particular knowledge, developed over a long period of time, of the areas of the forest where food is located. This knowledge is not perfect nor exhaustive and may vary from one monkey to the other, since each one has its own searching history (accumulated over days or weeks of foraging alone or with different combinations of group members). In a given subgroup at a given time, this knowledge is likely to be shared. Moreover, it is often observed that, during motion, the subgroup is decomposed into a leading individual, while the others follow rather passively. The leading individual often follows a straight line between food patches, as if he knew where he was going. Yet, contrary to other species, the foraging behaviors of spider

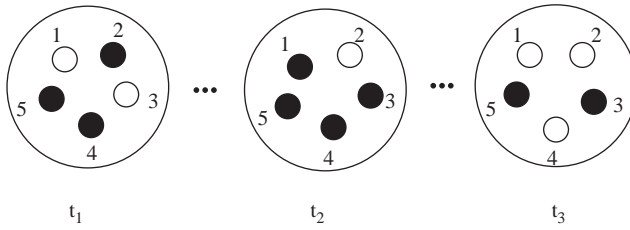


Fig. 1. A subgroup of 5 monkeys composed of active (○) and passive (●) individuals during the search process. The identities and number (n^*) of active individuals may change during the course of time.

monkeys are fairly democratic: there are no invariant leaders, and the identity of the leading monkeys continuously change over time.

We propose a simplified probabilistic argument to quantify these ideas. Assume that n animals forming a group stand together at a fixed location, before taking a decision for the next move. Among these n individuals, suppose that n^* of them ($n^* < n$) are “active”. Each active individual is susceptible to lead the group to some location where he thinks the closest food patch is. (Passive individuals are youngs, typically.) Each of these n^* “active” individual a priori has a different estimate/knowledge of the location of that close food patch. We assume that the various estimated distances are independently distributed according to the “lone” step length distribution $P_s(l) \sim l^{-\alpha_s}$. This length distribution somehow reflects the complex spatial distribution of resources that an individual monkey knows (see Section 3 and Ref. [16]). The active individuals next share their knowledge by comparing their proposed length, which suppose complex (and democratic) interactions between animals. As a result, the shortest proposed length is chosen, and the group moves coherently in the chosen direction, following the individual who proposed it and took the initiative. At the next step, the identity and number of active individual may change, as sketched in Fig. 1. The length l_g traveled by the subgroup is then given by $l_g = \text{Min}(l_1, \dots, l_{n^*})$. The trial steps being assumed independent, the distribution function P_g of l_g obeys

$$\int_{l_g}^{\infty} P_g(l) dl = \left(\int_{l_g}^{\infty} P_s(l) dl \right)^{n^*} . \tag{1}$$

If P_s is a Lévy distribution, so is P_g and its exponent is $\alpha_g = n^*(\alpha_s - 1) + 1$. Given the exponents measured experimentally ($\alpha_g \simeq 2.1$, $\alpha_s = 1.5$ [9]), this gives a value $n^* = 2.2$. (Note that n^* is an average number, it does not have to be an integer.) This rather small value is very close to the modal subgroup size of two adults per subgroup. On the other hand, lone individuals cannot profit from the cooperation of other monkeys, thereby reducing their searching efficiency, resulting in longer trajectories (i.e., $\alpha_s < \alpha_g$, as observed).

A more realistic model should explicitly take into account the random spatial distributions of resources, as well as the fusion/fission processes that frequently occur in groups.

3. A “greedy” deterministic walk model

In recent approaches of food search problems, animal movements are modeled by stochastic random walks characterized by Lévy distributions given a priori [4,7]. Here, we rather present an approach where animal trajectories are strongly coupled to (or induced by) a complex spatial distribution of resources. The aim is to understand the effects of a random spatial distribution of fixed resources on monkey trajectories. In the experimental study [9], monkeys used regular routes to travel between feeding sites, within a limited area of about 2 km^2 [17]. Many animals (bees [18], rodents [19], primates [20,21]) seem to rely on cognitive maps in order to navigate their environment. These maps may contain information on the location of different targets and the geometric relationships between them [22]. Some species of monkeys can also detect the closest target, as observed experimentally in Ref. [23]. Various animals actually keep in memory the sites that they have already visited in the recent past [18,20,22]. Models focusing on geometrical detection processes have been proposed (see Ref. [21] for an overview), but statistical analyses are still scarce.

Consider a two-dimensional space composed of point-like targets randomly distributed in space, representing the trees where monkeys can find fruits. The rules of motion are the following (see Ref. [24] for a related model): (a) a monkey located at the target number i will next move in straight line to a target j such that l_{ij} is minimal among all targets, where l_{ij} is the distance separating i and j ; (b) The monkey does not jump to an already visited target. This parameter-free “greedy” model generates random walks due to the random positions of the targets. It exhibits angular correlations between successive moves, a feature observed in real monkey trajectories. Fig. 2 shows the probability distribution $p(\theta)$ that a walker turns an angle θ with respect to its previous step, obtained from numerical solutions. With the condition (b), it is more likely that the walker encounters unvisited sites in front of him than behind

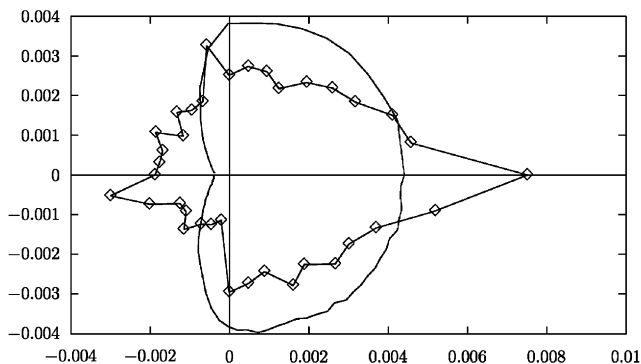


Fig. 2. Normalized polar plot of the angular distribution $p(\theta)$ of the turning angle between consecutive steps (θ in degrees), as measured in the experiments (dots), and obtained in the greedy model (solid line). Simulations are made with $N = 10^6$ targets in a square domain, averages are performed over 50 independent runs.

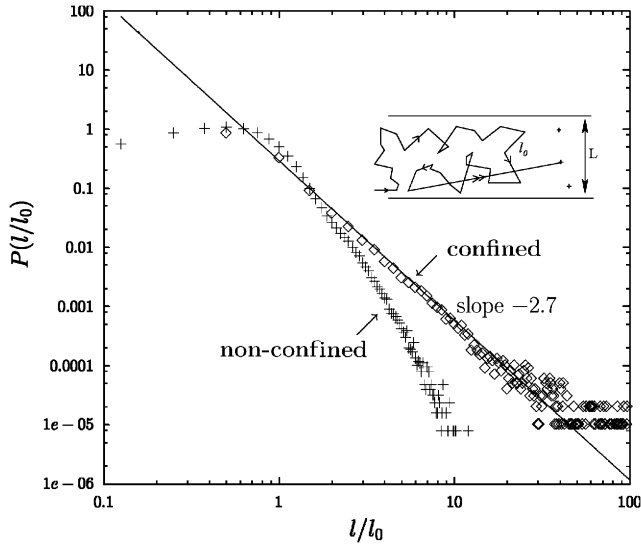


Fig. 3. Normalized step length distribution $P(l)$ of the greedy model, obtained with $N = 10^6$ targets in a domain of area 1, averaged over 10 runs (when each run stops, the number of visited sites is still $\ll N$); $l_0 = N^{-1/2}$ is the average distance between 2 nearest targets. (+): square (unbounded-like) domain; (◇): narrow domain of width $L = 10l_0$ (see inset). The solid line is a guide to the eye.

him: $p(\theta)$ peaks around zero. A qualitative agreement is obtained between the observed angle distribution and that of the model. However, the model overestimates the moves toward the sides, and under-estimates U turns ($\theta \sim 180^\circ$).

The simplest version of the model cannot account for the Lévy walks observed in the field. We hence propose the following modification. The home range of spider monkeys is actually not an infinite plane, but covers a fairly narrow and stretched area [17]. With the rules of the greedy model, we now consider targets distributed within a narrow strip, of width L and infinite in length. Fig. 3 displays the distribution of the length of the steps $P(l)$ obtained numerically for such a configuration and $L = 10l_0$ (with l_0 the typical distance between two nearest targets). The (exponential-like) distribution for the unbounded territory ($L \rightarrow \infty$) is also shown for comparison. The confined trajectories have a strikingly broad step distribution, consistent with a Lévy law of exponent close to 2.7. This can be explained qualitatively as follows: In the simulations, the walker follows a nearly 1D path (e.g. moving toward the right in average), but sometimes goes backward to eat some unvisited targets left behind. After some time, these backward paths usually end up in a region with no more fresh targets to eat, and these may be located quite far away from the most advanced point of the trajectory. To reach the following nearest site, the walker then needs to jump back at the front with a long step (see inset in Fig. 3). Surprisingly, it seems that such broad distributions are observed most easily for $L/l_0 \sim 10$. Short-range distributions are recovered as $L/l_0 \rightarrow \infty$ or $L/l_0 \rightarrow 1$.

4. Conclusion

We have discussed several aspects of foraging patterns of social monkey in a well defined territory. Foraging in small groups can modify searching patterns provided that monkeys cooperate by sharing information on the location of food patches. In addition, we have discussed a simple model based on deterministic rules of motion, emphasizing a strong coupling between the animals and the statistical distribution of resources. The results reproduce qualitatively some of the experimental data (angular correlations, and in some case, trajectories with Lévy distributions). Future improvements should incorporate the temporal variation in the location and abundance of food patches, as well as the consequences of foraging patterns for the dispersion of seeds by fruit-eating monkeys.

Acknowledgements

We are indebted to F. Leyvraz for illuminating discussions. This work was supported by CONACYT Grants G32723-E and 40867-F, DGAPA Grant IN-111000, as well as a visiting scholarship (Cátedra Tomás Brody) from the Complex Systems Department at the Physics Institute, National Autonomous University of Mexico.

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