Lévy Flights in Dobe Ju/'hoansi Foraging Patterns

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Abstract We analyzed data on Ju/'hoansi hunter-gatherer foraging patterns and found that their movements between residence camps can be modeled as a Lévy flight. The step lengths of their movements scale as a power law with an exponent $\mu = 1.97$. Their wait times (residence times) at the camps also scale as a power law (μ =1.45). A Lévy flight with step lengths $\mu=2$ is an optimal search pattern for scarce, randomly located targets; thus, the Ju/'hoansi foraging pattern may approach an optimal search in this area of sparse plant and animal resources. These findings affect the application of optimal foraging theory to humans in anthropology and archaeology because they alter the way in which search and travel times should be quantified. These results may also carry implications for the study of other patterns of human movement, such as demic diffusion and migration.

Key words Lévy flights · hunter–gatherers · optimal foraging theory · Ju/'hoansi

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Introduction

In this paper we present evidence that human huntergatherers employ foraging movement patterns that are described by the statistics of Lévy flights rather than by conventional Gaussian statistics. Human movement across the landscape is not usually considered an anthropological problem as such. For example, Green (1987, p. 273) observed that how foragers move between resource patches has been the subject of little quantitative work. Nevertheless, movement patterns influence not only foraging itself, but also cultural diffusion, demic diffusion, gene flow, and perhaps migration into virgin territory. So the discovery of Lévy flights in foraging patterns carries implications for various theories in anthropology, including optimal foraging theory as applied to hunter-gatherers and by extension for archaeological models of human subsistence settlement systems in prehistory. Moreover, it may help us understand the processes of diffusion and migration. In this paper, however, we focus our discussion on the implications for optimal foraging theory in cultural ecology and archaeology.

Optimal foraging theory is not really a single theory, but rather a diverse suite of formal models that are used to understand foraging patterns of both animals and humans. The approach usually taken is to analyze a quantitative model of decisions made by foragers to see whether or how they maximize some kind of "currency" (often some quantity like the net amount of energy gained) under a set of specified constraints. Most models fall into one of two categories: (1) those that analyze diet choices, often called "prey models," and (2) those that examine when a forager should leave a patch of resources, the so-called "patch" models (Stephens and Krebs, 1986, pp. 5–6). The prey or diet model has generally examined the proportions of different foods in the diet or the likelihood of pursuing one prey versus another. In contrast, the patch models generally evaluate the time spent in resource patches and the timing of the move to the next resource patch after the presence of the forager has depressed the availability of the resource in the patch. Stephens and Krebs (1986, pp. 33–36) have also offered a combined model that considers both prey choices and patch residence times. All these models include travel times between resource patches or prey search times as an important variable and therefore should take into account spatial patterns of foraging behavior. So as not to oversimplify our discussion, we note that many different specific foraging models have been developed that consider the outcomes of varying assumptions or constraints.

Lévy Flights

Lévy flights, named after the French mathematician Paul Lévy, are a class of random walks in which the step lengths are drawn from a probability distribution with a power law tail. These probability distributions are known as Lévy distributions or stable distributions. The lengths, l, of the steps or jumps of the walks are distributed as a power law, $P(l) = l^{-\mu}$ with $1 < \mu \le 3$ (Viswanathan *et al.*, 1999).

Many different kinds of random walks have been described and analyzed. Brownian motion is probably the best known of all random walks. It is the special case of a random walk for which the step lengths are distributed in accordance with a Gaussian probability distribution, or when $\mu \ge 3$ (Viswanathan *et al.*, 1999). Brownian motion describes the random motion of particles in a colloid. In contrast, in Lévy flights, as mentioned before, the step lengths are distributed according to a power law. This statistical difference gives Lévy flights a very distinctive appearance, one in which the pattern can be described subjectively by "clumps" of small steps separated by dramatic jumps. The pattern contrasts visually with the more homogenous patterns of Brownian motion (Bartumeus *et al.*, 2003, p. 12772).

Lévy flights are commonly used in physics to model a variety of processes including diffusion. Whereas Brownian motion and the resulting Gaussian statistics are normally used to model the patterns of motion in regular diffusion, Lévy flights create an enhanced kind of diffusion that is referred to as "anomalous diffusion" or "superdiffusion."

Lévy flights are intimately related to fractals. Lévy processes, not Gaussian ones, describe diffusion in fractal objects (ben-Avraham and Havlin, 2000, pp. 33–61). Because of the power law distribution of step lengths in a Lévy flight, the resulting pattern is a fractal: it is scale invariant and self-similar, characteristics that are diagnostic of fractals (Mandelbrot, 1983; Shlesinger *et al.*, 1993).

In recent years, biologists have discovered that Lévy flights describe foraging patterns in a number of species of animals and insects: ants, bumble bees, Drosophila melanogaster (Cole, 1995), albatrosses (ben-Avraham and Havlin, 2000, pp. 48-49; Viswanathan et al., 1996, 1999), jackals (Atkinson et al., 2002) and reindeer (Mårell et al., 2002). Even zooplankton have been observed to forage in Lévy flight patterns (Bartumeus et al., 2003: 12772). Recently, primate ethologists have observed nonhuman primates foraging in patterns that obey Lévy statistics (Boyer et al., 2004; Ramos-Fernández et al., 2003). This latter research, which recorded the behavior of Ateles geoffroyi (spider monkeys) in the Yucatán Peninsula, is important both because of its focus on primates and because Ateles forage in groups, which influences the model and the results. Earlier studies had all focused on lone foragers. Group foragers exhibit patterns of movement that may imply that groups are more efficient than individuals in locating food, an argument that has long been offered as one explanation for the existence of social groups of primates. The fission-fusion group dynamic found in spider monkeys is also characteristic of the primates most closely related to humans, the chimpanzees (Pan spp.). Thus, these findings may carry implications for the behavior of the common ancestor of Pan and the hominid clade.

Optimal Searching

Viswanathan et al. (1999, 2000, 2002) have demonstrated that Lévy flights are optimal search patterns for foragers searching for scarce targets that are randomly placed and can be visited any number of times. Optimal searches occur specifically when the step lengths are distributed according to a power law with an exponent of -2, that is, when P(l) = l^{-2} (da Luz *et al.*, 2001; Viswanathan *et al.*, 2001). It has been proposed that animal and insect foragers may perform Lévy flights because the probability of returning to a previously visited site is lower than for Brownian walks. Consequently, the number of newly visited sites is higher for Lévy flight searchers. Optimal foraging theory predicts, or sometimes assumes, that foragers (human or animal) will exhibit optimizing behavior, normally measured in terms of maximizing the net return in energy for their investment of effort in foraging. The study of foraging movement allows us to evaluate one aspect of this idea, namely that foragers minimize the energy expended in searching for food by optimizing their search patterns.

The Ju/'Hoansi: Human Foragers

Here we present evidence that human foragers use Lévy flights as search patterns as part of their subsistence strategies, and furthermore that they indeed perform optimal searches. We have analyzed data published by Yellen (1977) describing the movements of the Dobe Ju/'hoansi during hunting and collecting trips made in 1968.

The Dobe Ju/'hoansi1 are-or were until their recent resettlement-hunters and foragers living in and around the Kalahari Desert in Botswana and Namibia. They speak a "click" language of the Khoisan family. They have been intensively studied with special attention to their subsistence system and economy (Lee, 1979, 1993; Lee and DeVore, 1976). In the traditional subsistence system of the Ju/'hoansi men hunted and women gathered plant foods. In the 1960s, when these observations were made, meat, procured by men hunting, provided 30% of the overall caloric intake. Plants provided the remaining 70% of calories in the diet (Lee, 1993, p. 50). Men did perform some gathering, raising their total contribution to the diet to about 45%, but, interestingly, women never hunted (Lee, 1993, p. 56; Marshall, 1976, p. 96). A wide variety of game was pursued and over 100 species of plants were considered edible (Lee, 1993, p. 45). The most important plant food by far was the mongongo or mangetti nut (Ricinodendron rautanenii), a highly nutritious food which is virtually a staple in the Ju/'hoansi diet.

The Dobe band of the Ju/'hoansi lived at the Dobe waterhole (whence the name) during the winter-spring dry season. Like other San groups, they spent the dry season at a permanent water source. During and after the rains, the social group broke up into smaller subgroups that moved out into the hinterland and built short-term camps near seasonal or temporary water sources. At each camp, the people exploited the nearby food sources and, after consuming most of the desirable nearby food, they moved to another temporary camp. After some days or a few weeks, they returned to Dobe for a few days or weeks before setting out on another trip. The data analyzed here consist of the locations of those rainy season camps that were occupied by one small kin group from January 27 to July 11, 1968 (Yellen, 1977). This kin group was composed of two married men and their families. They made a total of 37 moves and occupied 28 different camps in the course of their five trips from the Dobe waterhole (Yellen, 1977, p. 59). In this article, we examine the statistical patterning of these moves.

To understand the meaning of these data, one must appreciate the considerations that enter into the choice of camp location. Generally speaking, in this hot and dry climate water is the most important determinant of settlement location, but the way in which it affects camp location is not simple and absolute. For example, Marshall (1976, pp. 75–76) recounts an occasion when a Ju/'hoan band camped in a mongongo tree grove six miles from a temporary waterhole. Every day for as long as the water lasted they sent their boys on the 12-mi round trip to bring water. In addition to water, many other factors enter into the decision of where to make camp, including the presence of plant food or game. The landscape and environment are complex. The patchy distributions of plants and animals are affected by geomorphology, soils, and rainfall patterns (Yellen and Lee, 1976). It is not, therefore, surprising that the locations of camps form a complex spatial pattern. Mongongo nut groves, for example, are an important influence on camp location. In the Dobe area, the groves are only found on dune crests (Yellen, 1977, p. 21). The dunes in turn are not randomly distributed; they form long, east-west trending ridges from 8-80 km in length between dry river courses (Yellen, 1977, pp. 18-20). Elsewhere in the region, the mongongo groves form other kinds of patches that closely correlate with geomorphology and soil types (Lee, 1979, pp. 182-185). The essential point is that camp location represents a decision about resource patch location that is identical to the decisions analyzed by optimal foraging theory patch models.

Ju/'hoan foraging has been studied using diet breadth models (Belovsky, 1987, 1988; Hawkes and O'Connell, 1981, 1985). It can be argued, however, that the patch model is equally if not more relevant to understanding their foraging patterns because patch models generally consider the problem of when a forager should decide to move to a new patch after having depressed the resources available in his present patch. This is precisely the decision that the Ju/ 'hoansi make as they shift their camps, and therefore the patch model is clearly relevant to understanding the behavior that created our data set.

Materials and Methods

Our data come from Yellen's 1977 book on the Dobe Ju/'hoansi settlement patterns and camp structure. That research was undertaken as part of the long-term Harvard University !Kung Bushman ethnology and human ecology project. The data we used were drawn from Table 3 (Yellen, 1977, p. 60) and Map 7 (note that Maps 5 and 7 were accidentally switched by the printer although their captions were not). Yellen (1977, pp. 61–63) discusses the strengths and weaknesses of this data set, including the potential influences of his anthropological team and of nearby Bantu settlers. He concludes, nevertheless, that "[h]ad neither Bantu nor anthropologists been there, I believe that the basic pattern would have been the same but less time would have been spent at the permanent waterhole." This statement leads us to believe we can rely upon the camp location data but that the occupation times may be somewhat less accurate.

¹ The Ju/'hoansi have in the past been known by other names including !Kung and Bushmen.

We measured the distances between camps on Map 7 in the order in which they were occupied, and we drew the lengths of the camps' occupations from Table 3. The lengths of camp occupations are also given in Table 5, and the analysis of those data yield results very similar to those presented here. We analyzed the geographic distances between camps in the order in which they were occupied to see if they conformed to a power law distribution of step lengths predicted by a Lévy flight. We also analyzed the lengths of camp occupations to see if they conformed to a power law distribution as they would if they were the wait times at the turning points of a Lévy flight. A delicate issue in these calculations is the use of histograms to measure the probability density functions (PDFs) of the data sets. The PDF will tell us whether the step lengths and wait times come from power law distributions or from some other kind of distribution. The PDFs can be determined from histograms of step lengths or wait times, but the results will depend on the widths of the bins used to construct the histograms. Narrow bins will be good estimators of short distances or times, but poor estimators of long ones, while the opposite will be true of wide bins (that is, the latter will be good estimators of long distances or times, but poor estimators of short times or

Table I This Table Lists the Distances Between Successive Camps in kilometers. They were scaled off Map 7 of Yellen's (1977) monograph using calipers. The distances were measured from the mid-points of the numerals on the map. When a particular camp number did not appear on the map, we measured to the number of the first camp of the same name on the list. This camp number is given in the "Remarks" column. To convert from millimeters on the printed map to geographic distance we used a scaling factor of 5/27

From camp	To camp	Measured distance (mm)	Geographic distance (km)	Remarks
1	2	94.3	17.46296296	
2	3	14.7	2.722222222	
3	4	14.7	2.722222222	Measured to no. 2
4	5	34.7	6.425925926	
5	6	24.2	4.481481481	
6	7	19.4	3.592592593	
7	8	53.7	9.94444444	Measured to no. 1
8	9	44.8	8.296296296	
9	10	26.7	4.94444444	
10	11	28.9	5.351851852	Measured to no. 2
11	12	14.7	2.722222222	Measured to no. 3
12	13	18.8	3.481481481	
13	14	10.9	2.018518519	
14	15	10.9	2.018518519	
15	16	9.3	1.722222222	
16	17	16.8	3.11111111	Measured to no. 14
17	18	42.8	7.925925926	
18	19	82.7	15.31481481	Measured to no. 1
19	20	25.7	4.759259259	
20	21	67.1	12.42592593	
21	22	16.6	3.074074074	
22	23	22.8	4.222222222	
23	24	68	12.59259259	Measured to no. 1
24	25	44.8	8.296296296	Measured to no. 9
25	26	26.1	4.833333333	
26	27	27.8	5.148148148	
27	28	12.1	2.240740741	
28	29	14.6	2.703703704	
29	30	70.9	13.12962963	
30	31	28.4	5.259259259	Measured to no. 1
31	32	20.2	3.740740741	
32	33	28.5	5.27777778	
33	34	37.1	6.87037037	
34	35	21.2	3.925925926	
35	36	32.3	5.981481481	
36	37	21.8	4.037037037	
37	38	85	15.74074074	Measured to no. 1

lengths). Therefore, to estimate the PDFs of the data sets we used the "multihistogram" or "fractal" method developed by Liebovitch et al. (1987, 1999, 2001). We computed histograms of different bin sizes, evaluated the PDF from each histogram, and then combined those values to form the completed PDF (Liebovitch et al., 1999, pp. 3313-3314). Compared to conventional methods, the fractal method offers several important advantages. It uses the PDF determined from each histogram rather than the histogram itself. These PDFs can be combined into a single function while the histograms themselves cannot. It generates more points in the PDF function at scales that have more data so that the functions used to fit the PDF are properly weighted by the relative amount of data at different scales. Finally, it is accurate and efficient, particularly when the number of measurements is small (Liebovitch et al., 2001, pp. 362-363).

Results

The application of these numerical methods to the data sets yielded the following results. The step lengths, that is, distances between the Ju/'hoansi camps, are distributed as a power law with an exponent of -1.9675 ($r^2=0.965$; Fig. 1). This is a clearly a power law relation, indicating that these movements conform to a Lévy flight. Similarly, the wait times (i.e., lengths of occupations of the camps) are distributed as a power law with an exponent of -1.4503 ($r^2=0.828$; Fig. 2). Note that, as mentioned earlier, the occupation times may have been influenced by external factors.

To determine whether the Lévy flights model was the best description of our data, we also examined several other plausible models. We feel that evaluating alternate hypotheses is an appropriate means for identifying and supporting the best choice among competing explanations (Johnson and Omland, 2004). The falsification of alternative possibilities reinforces and buttresses a scientific argument. The choice of model, however, is not necessarily simple. The number of possible models is a potentially infinite. How to choose from among this sea of possibilities? We believe that one should start from concepts with clear social interpretations and implications, rather than beginning with the quantitative possibilities. In other words, model selection should not be an exercise in curve fitting, followed by an attempt to understand the social implications of the curve that fits best. One should first conceptualize the social model and then evaluate its quantitative implications.

Considering these ideas, we selected three alternatives to the Lévy flight model, which implies a power law distribution of step length. The alternative models were: a normal distribution, a uniform distribution, and an exponential distribution. We tested these models in two ways. First, we tested the exponential distribution of step lengths (which seemed the most likely of the alternative possibilities) by using the multihistogram method, so it would be directly comparable to the Lévy flight test described above. Then, we examined all three alternatives (including the exponential distribution again) by examining the distributions of step lengths using One-sample Kolmogorov– Smirnov tests in SPSS Release 12.0.

Normal Distribution

A normal distribution of step lengths is probably the most common model of human movements across the landscape. For example, Ammerman and Cavalli-Sforza's (1979) famous "wave of advance" model for the spread of agriculture assumes a Gaussian distribution of steps. The approach originated in Fisher's (1937) model for the diffusion of advantageous alleles across the landscape. This model is effectively a stochastic one, which would arise in



distances (Km)

Fig. 1 Power law distribution of distances between campsites, exhibiting an exponent of 1.9675.



wait times (days)

Fig. 2 Power law distribution of camp residence times, exhibiting an exponent of 1.4503.

the event of a spatially random distribution of campsites. This kind of model is, of course, common for two reasons. First, the existence of random effects in natural (or cultural) processes such as these seems innately reasonable to some investigators. Second, Gaussian statistics have traditionally

 Table II
 One-sample
 Kolmogorov–Smirnov
 Test
 Comparing the Ju/'hoansi
 Step Length
 Data to a Normal Distribution
 Description
 <thDescription</th>
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		Distance
N		37
Normal parameters ^{a, b}	Mean	6.1762
-	Std. deviation	4.21463
Most extreme differences	Absolute	0.226
	Positive	0.226
	Negative	-0.145
Kolmogorov-Smirnov Z		1.376
Asymp. sig. (2-tailed)		0.045

^a Test distribution is Normal.

^bCalculated from data.

been used in modeling because they were mathematically tractable. The Gaussian model of step lengths can, however, be rejected as a model of the Ju/'hoansi data set because p < 0.05, as shown in Table II.

Uniform Distribution

To our knowledge, no one has hypothesized that humans move about the landscape in a uniform spatial pattern, but it is not an unreasonable possibility. If resources were uniformly, or at least redundantly, distributed across the landscape, then groups of foragers might move relatively similar distances each time they shifted camp. In such a case, the step lengths might be driven by external forces, such as the locations of other social groups, rather than by the distribution of resources. Other scenarios might also be imagined that would lead to a relatively even pattern of movements. Regardless of the possible reason, the Ju/'hoansi step length data do not match well to a uniform distribution, as shown in Table III. The test statistic yields p = 0.000, allowing us to reject the hypothesis.

Exponential Distribution

Exponential distributions arise for the length of a set of walks when, at each step in a walk, there is a constant probability that the walk will end. Sometimes the walk ends after only a few steps, sometimes after many steps. Longer walks are less likely because they must survive many more equally likely terminations. It can be shown that if the probability per unit length to terminate the walk remains constant, that the distribution of lengths of many walks has an exponential form. (See, for example, Liebovitch, *et al.*, 1987, where this is derived in terms of durations of time, which are here analogous to the lengths of the walks.) This model could represent human behavior. The band continues a walk, at each moment deciding whether it has been worthwhile and whether, with the same chance, it should be continued or ended. We also wish to test an exponential

 Table III One-sample Kolmogorov–Smirnov Test Comparing the Ju/'hoansi Step Length Data to a Uniform Distribution

		Distance
Ν		37
Uniform parameters ^{a, b}	Minimum	1.72
	Maximum	17.46
Most extreme differences	Absolute	0.418
	Positive	0.418
	Negative	-0.027
Kolmogorov-Smirnov Z		2.543
Asymp. sig. (2-tailed)		0.000

^a Test distribution is Uniform.

^bCalculated from data.

function because Ju/'hoansi migration distances (in the sense of the distance between the birthplaces of spouses (see below)) seem to resemble an exponential distribution. Interestingly, the step lengths of the Ju/'hoansi data do not appear to match an exponential distribution well, as shown by the Kolmogorov–Smirnov test statistic of p=0.018 (Table IV). We also tried to fit an exponential curve to the step length data using the multihistogram method (Fig. 3). The coefficient of determination (R^2) for the exponential distribution is 0.910, markedly lower than the same coefficient for the power law ($R^2=0.965$). This, of course, suggests that the power law is a better fit to the data.

We conclude that the power law distribution of step lengths, which implies a Lévy flight model of movement, is the best fit to the data of the alternatives tested.

Discussion

First, of primary importance is the fact that the pattern of camp movement comprises a Lévy flight. The movements are not distributed in a Gaussian or exponential mode, as might be expected, but as a power function. When migration and diffusion are modeled, researchers typically assume a Gaussian distribution of migration distances, for example in the well-known "wave of advance" model (Ammerman and Cavalli-Sforza, 1979, p. 280; Wijsman and Cavalli-Sforza, 1984). Several aspects of this model have been questioned (Anthony, 1990, pp. 901-902). Lévy flight movements may help explain rapid, long-distance migrations that advance through processes such as leapfrogging (Anthony, 1990). Lévy flights can produce faster long-distance migration than Brownian motion because the latter will have few long jumps and many medium-length jumps, whereas the former will produce some surprisingly long leaps.

The assumption of a Gaussian distribution of migration distances is also undermined by some real migration data. For example, migration distances often seem to be modeled

 Table IV
 One-sample
 Kolmogorov–Smirnov
 Test
 Comparing the Ju/'hoansi
 Step
 Length
 Data to an Exponential Distribution
 Description
 Descrindescription
 Description

		Distance
N		37
Exponential parameter ^{a, b}	Mean	6.1762
Most extreme differences	Absolute	0.252
	Positive	0.072
	Negative	-0.252
Kolmogorov-Smirnov Z		1.531
Asymp. sig. (2-tailed)		0.018

^a Test Distribution is Exponential.

^bCalculated from data.



distances (Km)

Fig. 3 The distribution of distances between campsites fit to an exponential distribution.

by an exponential relation (Wijsman and Cavalli-Sforza, 1984). Interestingly, Ju/'hoansi migration distances do seem to follow an exponential distribution (Harpending, 1976). "Migration distance" among these highly mobile people is defined as the distance between the birthplaces of spouses, not the pattern of band movement around the land. As Fig. 4 illustrates, the Ju/'hoansi migration data (Harpending, 1976) fit a single negative exponential function quite well ($R^2=0.97$). In the simplest terms, this tells us that the probability of two individuals marrying declines exponentially with the distance between their birthplaces. Of course, marriage patterns are influenced by the network of kin relations among the Ju/'hoansi, including factors such as rules of exogamy and marriage preferences. So the migration distance data must relate to the Lévy flight foraging model in an indirect and complex way that is difficult to specify based on the available data.

Second, we find it extremely interesting that the power law exponent of the step distances is very close to -2. Recall that an exponent of -2 implies a maximally efficient

Fig. 4 Statistical distribution of Ju/'hoansi migration distances of spouses showing a fit to an exponential function.





Exponential function of Ju/'hoan migration distances

(data from Harpending 1976)

 $\begin{array}{c}
350 \\
300 \\
250 \\
200 \\
150 \\
100 \\
50 \\
0 \\
0
\end{array}$

search for randomly placed, scare targets that can be revisited (Viswanathan et al., 1999, 2000). We were surprised to find this because, notwithstanding the extensive theorizing about optimality in human behavior, concrete empirical cases of optimizing behavior in the literature are scarce (Salmon, 1989). The case discussed here may be an instance of optimizing behavior. We hasten to add, however, that we do not interpret this finding to imply that Ju/'hoansi are automatons whose behavior has been programmed by natural selection. The only reasonable interpretation is that the Ju/'hoansi achieved an optimal search pattern while behaving rationally in adapting to a spatially complex and unpredictable environment. Indeed, the Ju/'hoansi know where the waterholes, mongongo groves, and salt licks are in their territory, and they place their camps accordingly. Thus, the Ju/'hoansi Lévy flight exponent may well reflect the spatial distribution of resources as well as their decision-making processes.

Third, we believe that the conclusions drawn here should influence the application of optimal foraging theory to hunter–gatherer studies. In optimal foraging models, search times or travel times are essential elements in the basic equations (Charnov, 1976, p. 131; Charnov and Orians, 1973; *cf.* MacArthur and Pianka, 1966).² Both prey and patch models derive from Holling's disk equation. This equation assumes a linear relationship between search time and the number of prey/patch encounters (Stephens and Charnov, 1982; Stephens and Krebs, 1986, pp. 14–15). The power law function of the travel distances documented here clearly violates that assumption of linearity.

The nonlinearity inherent in Lévy flights presents other challenges for conventional optimal foraging models. For example, the prey and patch models commonly assume that prey or patch encounters are distributed as a Poisson process (Stephens and Krebs, 1986, pp. 19, 28). This cannot be true if the Ju/'hoansi are foraging in a Lévy flight pattern because it is so strongly nonlinear in space and time that it cannot be reconciled with a Poisson process.

Travel times figure prominently in patch models (Charnov, 1976; Kelly, 1995, pp. 90-110; Smith, 1991, pp. 245-285), which, as we observed earlier, are directly relevant to understanding Ju/'hoansi camp movements. The model examines how patches are chosen and at what point a forager should leave an exploited patch for a fresh one. This model is clearly relevant to understanding Ju/'hoansi foraging behavior in the Kalahari given (1) the scarce and patchy distribution of food in the Ju/'hoansi environment; (2) the tendency for the Ju/'hoansi to camp in or at resource patches; and (3) the propensity for the Ju/'hoansi to "eat out" (substantially exploit) an area before moving on to a fresh patch. The generic patch model predicts that a forager will leave a patch when the marginal rate of gain declines to the point at which it equals the long-term average rate of energy intake in the habitat (Stephens and Krebs, 1986, p. 29). In the basic and common formulation of the model, the average travel time between patches is taken to be the inverse of the patch encounter rate. Thus, when the encounter rate is maximized, time is minimized, and in

 $^{^2}$ Travel and search times seem to be proportional to distance in the Ju/'hoansi case. Lee (1979, p. 193) reports that the Ju/'hoansi travel 4–5 km/h with a load, and we know of no ethnographic evidence indicating that this rate varies nonlinearly with distance.

fact some models have explicitly examined time minimization as a model goal (e.g., Abrams, 1984). So, average search time is a key variable in the calculation of most models. In the case of a Lévy flight, however, there is no average travel time between patches. The mean simply does not exist because power laws do not have stable means (Liebovitch, 1998, pp. 74–105; Liebovitch and Scheurle, 2000; Liebovitch and Todorov, 1996; Liebovitch *et al.*, 1999). This tells us that the standard formulation of the patch model cannot be accurately calculated for a forager who forages using a Lévy flight pattern. We do not assert that this "disproves" optimal foraging theory, but we do believe that optimal foraging models that analyze human behavior should employ more realistic assumptions about forager behavior.

How might models of human optimal foraging take into account these kinds of assumptions? A number of existing models do take into account Lévy flights of foragers (e.g., Bartumeus et al., 2005). For example, da Luz et al. (2001) define foraging efficiency as the ratio of total energy gained in visited sites to the total distance traveled by the forager. They then show, relying in part on the theoretical work and simulations performed by Viswanathan et al. (1999), that foragers performing Lévy flights maximize their foraging efficiency when their Lévy flight exponent $\mu=2$. Difficulties remain, however, in applying this model to humans. Since the model is designed to apply to animal or insect searching, it assumes little or no learning or memory, assumptions which are clearly not true in the case of human foragers. Since the Ju/'hoansi do know their environment well, their movement patterns are unlikely to be analogous to a random search. This leads us to consider the other possible cause of their Lévy flights: a fractal distribution of resources. Fractals are closely related to Lévy flights because the turning points of a Lévy flight form a fractal pattern of points. The mathematical relationship between them is simple. The exponent of the Lévy flight, μ , relates to the fractal dimension of the pattern by $F_D = \mu - 1$. Viswanathan et al. (1999, p. 914) examined the Lévy flight model for a fractal distribution of resources and found it consistent with their model. There is a modest literature describing fractal models of foraging (e.g., Hoddle, 2003; Russell et al., 1992) that examine foraging in a fractal environment.

Fourth, and last, because the turning points of a Lévy flight form a fractal pattern we can predict that the spatial distribution of camps will form a fractal pattern. This fact is of primary importance to archaeologists because they, more than anyone else, quantitatively study hunter–gatherer settlement patterns. Archaeologists not only conduct surveys to find hunter–gatherer archaeological sites, but they are also concerned with sampling the landscape to locate these sites and with analyzing their spatial distributions.

Summary

We analyzed published data on Ju/'hoansi settlement patterns and showed that the shifting of their rainy season foraging camps formed a Lévy flight pattern. This finding is consistent with recent observations for a variety of other foraging species. Startlingly, the exponent of the step lengths of the Lévy flight implies that their search pattern is highly efficient, and approaches maximal efficiency. This discovery carries significant implications for optimal foraging theory as applied to hunter–gatherers and for archaeological studies of hunter–gatherer settlement patterns.

References

- Abrams, P. A. (1984). Foraging Time Optimization and Interactions in Food Webs. *American Naturalist* 124(1): 80–96.
- Ammerman, A. J., and Cavalli-Sforza, L. L. (1979). The wave of advance model for the spread of agriculture in Europe. In Renfrew, C., and Cooke, K. L. (eds.), *Transformations: Mathematical Approaches to Culture Change*, Academic, New York, pp. 275–293.
- Anthony, D. W. (1990). Migration in Archaeology: The Baby and the Bathwater. American Anthropologist 92(4): 895–914.
- Atkinson, R. P. D., Rhodes, C. J. D., Macdonald, W., and Anderson, R. M. (2002). Scale-free Dynamics in the Movement Patterns of Jackals. *Oikos* 98: 134–140.
- Bartumeus, F., Peters, F., Pueyo, S., Marrasé, C., and Catalan, J. (2003). Helical Lévy Walks: Adjusting Searching Statistics to Resource Availability in Microzooplankton. *Proceedings of the National Academy of Sciences* 100(22): 12771–12775.
- Bartumeus, F., da Luz, M. G. E., Viswanathan, G. M., and Catalan, J. (2005). Animal Search Strategies: A Quantitative Random Walk Analysis. *Ecology* 86(11): 3078–3087.
- Belovsky, G. E. (1987). Hunter–gatherer Foraging: A Linear Programming Approach. *Journal of Anthropological Archaeology* 6(1): 29–76.
- Belovsky, G. E. (1988). A Optimal Foraging-based Model of Huntergatherer Population Dynamics. *Journal of Anthropological Archaeology* 7(4): 329–372.
- ben-Avraham, D., and Havlin, S. (2000). Diffusion and Reactions in Fractals and Disordered Systems, Cambridge University Press, Cambridge.
- Boyer, D., Miramontes, O., Ramos-Fernández, G., Mateos, J. L., and Cocho, G. (2004). Modeling the Searching Behavior of Social Monkeys. *Physica A* 342: 329–335.
- Charnov, E. L. (1976). Optimal Foraging, the Marginal Value Theorem. *Theoretical Population Biology* 9(2): 129–136.
- Charnov, E. L., and Orians, G. H. (1973). Optimal Foraging: Some Theoretical Expectations. Unpublished MS. Available at http://www.biology.unm.edu/Charnov/73OptimalForaging.pdf>.
- Cole, B. J. (1995). Fractal Time in Animal Behavior: The Movement Activity of Drosophila. Animal Behaviour 50: 1317–1324.
- da Luz, M. G. E., Buldyrev, S. V., Havlin, S., Raposo, E. P., Stanley, H. E., and Viswanathan, G. M. (2001). Improvements in the Statistical Approach to Random Lévy Flight Searches. *Physica A* 295: 89–92.
- Fisher, R. A. (1937). The Wave of Advance of Advantageous Genes. Annals of Eugenics 7: 355–369.

- Green, R. F. (1987). Stochastic models of optimal foraging. In Kamil, A. C., Krebs, J. R., and Pullman, H. R. (eds.), *Foraging Behavior*, Plenum, New York, pp. 273–302.
- Harpending, H. (1976). Regional variation in !Kung populations. In Lee, R. B., and DeVore, I. (eds.), *Kalahari Hunter–Gatherers*, Harvard University Press, Cambridge, pp. 152–165.
- Hawkes, K., and O'Connell, J. (1981). Affluent Hunters? Some Comments in Light of the Alyawara Case. American Anthropologist 83: 622–626.
- Hawkes, K., and O'Connell, J. (1985). Optimal Foraging Models and the Case of the !Kung. American Anthropologist 87: 401–405.
- Hoddle, M. S. (2003). The Effect of Prey Species and Environmental Complexity on the Functional Response of *Franklinothrips* orizabensis: A Test of the Fractal Foraging Model. *Ecological Entomology* 28: 309–318.
- Johnson, J. B., and Omland, K. S. (2004). Model Selection in Ecology and Evolution. *Trends in Ecology and Evolution* 19(2): 101–108.
- Kelly, R. L. (1995). The Foraging Spectrum: Diversity in Hunter– Gatherer Lifeways, Smithsonian Institution, Washington.
- Lee, R. B. (1979). *The !Kung San: Men, Women, And Work in a Foraging Society*, Cambridge University Press, Cambridge.
- Lee, R. B. (1993). The Dobe Ju/'hoansi, Harcourt Brace, New York.
- Lee, R. B., and DeVore, I. (eds.) (1976). Kalahari Hunter–Gatherers: Studies of the !Kung San and their Neighbors, Harvard University Press, Cambridge.
- Liebovitch, L. S. (1998). Fractals and Chaos Simplified for the Life Sciences, Oxford University Press, New York.
- Liebovitch, L. S., and Scheurle, D. (2000). Two Lessons from Fractals and Chaos. *Complexity* 5(4): 34–43.
- Liebovitch, L. S., and Todorov, A. T. (1996). Fractal Dynamics of Human Gait: Stability of Long-range Correlations in Stride Interval Fluctuations. *Journal of Applied Physiology* 80: 1446–1447.
- Liebovitch, L. S., Fischbarg, J., and Koniarek, J. (1987). Ion Channel Kinetics: A Model Based on Fractal Scaling Rather than Multistate Markov Processes. *Mathematical Biosciences* 84: 37–68.
- Liebovitch, L. S., Todorov, A. T., Zochowski, M., Scheurle, D., Colgin, L., Wood, M. A., Ellenbogen, K. A., Herre, J. M., and Bernstein, R. C. (1999). Nonlinear Properties of Cardiac Rhythm Abnormalities. *Physical Review E* 59(3): 3312–3319.
- Liebovitch, L. S., Scheurle, D., Rusek, M., and Zochowski, M. (2001). Fractal Methods to Analyze Ion Channel Kinetics. *Methods* 24: 359–375.
- MacArthur, R. H., and Pianka, E. R. (1966). On Optimal Use of a Patchy Environment. *American Naturalist* 100(916): 603–609.
- Mandelbrot, B. B. (1983). *The Fractal Geometry of Nature*, Freeman, New York.
- Mårell, A., Ball, J. P., and Hofgaard, A. (2002). Foraging and Movement Paths of Female Reindeer: Insights from Fractal Analysis, Correlated Random Walks, and Lévy Flights. *Canadian Journal of Zoology* 80: 854–865.

- Marshall, L. (1976). The !Kung of Nyae Nyae, Harvard University Press, Cambridge.
- Ramos-Fernández, G., Mateos, J. L., Miramontes, O., Cocho, G., Larralde, H., and Ayala-Orozco, B. (2003). Lévy Walk Patterns in the Foraging Movements of Spider Monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology* 55(3): 223–230.
- Russell, R. W., Hunt, G. L., Coyle, K. O., and Cooney, R. T. (1992). Foraging in a Fractal Environment: Spatial Patterns in Marine Predator–Prey System. *Landscape Ecology* 7(3): 195–209.
- Salmon, M. H. (1989). Efficient explanations and efficient behavior. In Pinsky, V., and Wylie, A. (eds.), *Critical Traditions in Contemporary Archaeology*, Cambridge University Press, Cambridge, pp. 10–13.
- Shlesinger, M. F., Zaslavsky, G. M., and Klafter, J. (1993). Strange Kinetics. *Nature* 363: 31–37.
- Smith, E. A. (1991). Inuijuamiut Foraging Strategies: Evolutionary Ecology of an Arctic Hunting Economy, Aldine de Gruyter, New York.
- Stephens, D. W., and Charnov, E. L. (1982). Optimal Foraging: Some Simple Stochastic Models. *Behavioral Ecology and Sociobiology* 10: 251–263.
- Stephens, D. W., and Krebs, J. R. (1986). *Foraging Theory*, Princeton University Press, Princeton.
- Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A., and Stanley, H. E. (1996). Lévy Flight Search Patterns of Wandering Albatrosses. *Nature* 381: 413–415.
- Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P., and Stanley, H. E. (1999). Optimizing the Success of Random Searches. *Nature* 401: 911–914.
- Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P., and Stanley, H. E. (2000). Lévy Flights in Random Searches. *Physica A* 282: 1–12.
- Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P., and Stanley, H. E. (2001). Lévy Flights Search Patterns of Biological Organisms. *Physica A* 295: 85–88.
- Viswanathan, G. M., Bartumeus, F., Buldyrev, S. V., Catalan, J., Fulco, U. L., Havlin, S., da Luz, M. G. E., Lyra, M. L., Raposo, E. P., and Stanley, H. E. (2002). Lévy Flight Random Searches in Biological Phenomena. *Physica A* 314: 208–213.
- Wijsman, E. M., and Cavalli-Sforza, L. L. (1984). Migration and Genetic Population Structure with Special Reference to Humans. *Annual Review of Ecology and Systematics* 15: 279–301.
- Yellen, J. E. (1977). Archaeological Approaches to the Present: Models for Reconstructing the Past, Academic, New York.
- Yellen, J. E., and Lee, R. B. (1976). The Dobe-/Du/da environment: Background to a hunting and gathering way of life. In Lee, R. B., and DeVore, I. (eds.), *Kalahari Hunter–Gatherers: Studies of the !Kung San and their Neighbors*, Harvard University Press, Cambridge, pp. 27–46.