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CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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The Lévy flight paradigm: random search patterns and mechanisms

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Abstract. Over recent years there has been an accumulation of evidence from a variety of experimental, theoretical, and field studies that many organisms use a movement strategy approximated by Lévy flights when they are searching for resources. Lévy flights are random movements that can maximize the efficiency of resource searches in uncertain environments. This is a highly significant finding because it suggests that Lévy flights provide a rigorous mathematical basis for separating out evolved, innate behaviors from environmental influences. We discuss recent developments in random-search theory, as well as the many different experimental and data collection initiatives that have investigated search strategies. Methods for trajectory construction and robust data analysis procedures are presented. The key to prediction and understanding does, however, lie in the elucidation of mechanisms underlying the observed patterns. We discuss candidate neurological, olfactory, and learning mechanisms for the emergence of Lévy flight patterns in some organisms, and note that convergence of behaviors along such different evolutionary pathways is not surprising given the energetic efficiencies that Lévy flight movement patterns confer.

Key words: Brownian motion; diffusive walks; emergence; foraging; Lévy flight; movement patterns; optimal foraging; power laws; scaling; search pattern.

INTRODUCTION

Many processes of ecological significance are a consequence of the movement of animals around their natural habitats. Movement of animals leads to interactions at the individual or group level, and these interactions are often the most important determinants of the observed population dynamics and species diversity. Such interactions may involve mating, predation, and competition for resources or the spread of communicable disease or parasites, for example. Therefore, it is essential that an understanding of the patterns of animal movement over a broad range of spatial scales is developed in order to better understand the complexities of real ecological systems. As pressure on wildlife habitats continues to increase due to the continual expansion of the human population, an understanding of how animals move will be a key component of future conservation strategies. It is also central to predicting how changes in agricultural practices and climate change will impact upon the search behaviors (e.g., pollination and predation) of beneficial insects and pests.

The question of how individual animals move around has been invigorated in recent years by the development of increasingly compact and durable technologies for locating and recording the coordinates of larger animals. The widespread use of satellite-based methods has offered the possibility of often long runs of geographical coordinate data from tagged animals (Sims et al. 2003, Hays et al. 2006). The exploitation of active radar techniques using resonant antennas has permitted the accurate reconstruction of the flight paths of moths and honey bees at the field scale (Riley et al. 1996, Reynolds et al. 2007a, b, c). Analysis of video of *Drosophila* fruit fly flight patterns, aphid and microzooplankton movement patterns in the laboratory has complemented this development (Bartumeus et al. 2003, Oliver et al. 2007, Reynolds and Frye 2007). Conventional radio tracking using hand-held antennas operating in the VHF band continues to deliver a wealth of animal movement data (Doncaster and Macdonald 1997, Atkinson et al. 2002). Direct visual observation of the subject also continues to yield useful data (Ramos-Fernandez 2004, deKnegt 2007), but this is confined to larger organisms (Sims and Quayle 1998).

The ever-increasing quantity and quality of data provided by ecologists in the field and in the laboratory has stimulated a reappraisal by theorists of underpin-

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ning models for animal movement. It is becoming possible to discriminate between conceptually distinct modeling approaches for how animals move in their natural habitats. Moreover, as will be discussed further, it is now possible to conduct large-scale ecological experiments that are specifically designed to test hypotheses about movement and search strategies (deKnegt et al. 2007, Reynolds et al. 2007c).

For many years, the dominant conceptual model for describing non-oriented animal movement was based on Brownian motion (Kareiva and Sigesada 1983, Bovet and Benhamou 1988, Turchin 1989, 1991, Okubo and Levin 2001). In this framework, an individual's trajectory through space is regarded as being made up of a sequence of distinct, randomly oriented move step-lengths drawn from a Gaussian distribution. Schlesinger and Klafter (1986) were the first to suggest that the movement patterns of some biological organisms may have so-called "Lévy-flight" characteristics. Strictly speaking these should be Lévy-walk movement characteristics patterns because they are continuous movements (usually with a constant velocity) rather than discrete jumps. But here in keeping with much of the literature on random searching, the phrases Lévy-flight and Lévy-walk are used synonymously (Viswanathan et al. 1996, 1999, Atkinson et al. 2002, Bartumeus et al. 2003). Then, around 10 years ago, it was shown that if the animal is searching for resources, the Brownian strategy is inferior to one based on a Lévy flight, where the step-lengths are drawn from a statistical distribution with a power-law tail (Viswanathan et al. 1999). This theoretical observation and initial evidence for Lévy-flight searching in the Wandering Albatross (Viswanathan et al. 1996) prompted the suggestion that the adoption of Lévy flights might be widespread in the animal kingdom. The analysis and interpretation of animal movement data is not, however, wholly straightforward, and some of the analyses claiming Lévy flight behavior in the intervening decade have recently been called into question (Edwards et al. 2007, Sims et al. 2007). Now is an appropriate time to review the theoretical, experimental, and data analysis methods that have been used to investigate ecological applications of Lévy-flight search.

In this review, we address the topic of the application of Lévy flights to animal movement. We begin by looking at some of the key results in search theory and see how these have been elaborated. We review laboratory, field, and experimental studies on search behavior, highlighting the issues that need to be addressed when processing raw tracking data and undertaking trajectory analysis. We discuss candidate neurological and sensory mechanisms for the emergence of Lévy flight patterns in some organisms. Our intention is to provide a synoptic overview of the state of current research in this field. We conclude by drawing attention to a number of future research themes that could shed further light on random searching behaviors and underlying mechanisms.

MOVEMENT AND SEARCH

Animals move in a variety of different ways. In terrestrial ecosystems most organisms propel themselves by locomotion, of which walking, running, or flying are the most readily apparent. In this case, the animal often has full control over where it goes. Flying insects, for instance, usually engage in foraging movements within the "flight boundary layer" and for this reason have control over where they go. By contrast, in moving water (lakes, rivers, or oceans, for example) the effect of turbulent currents can be significant, so movement may take place through a combination of swimming and passive advection in a turbulent velocity field; the trajectory is then a combination of the two processes (Rhodes and Reynolds 2007).

Animals move for many different reasons. One of their principal motivations to move is the search for food resources. Generally, regularly renewable sources of food are not accessible in the immediate vicinity of the animal, so they have to conduct a search of their habitat to locate them. Other reasons for moving might include searching for a mate, avoiding predators, visiting a watering hole, looking for a den site, maintaining and marking territorial claims, migration, or searching for a site (or host) on which to lay eggs. At a given time an animal may be moving for any one of these reasons, or possibly for combinations of reasons, such as searching for food while avoiding becoming prey themselves. If the environment is unchanging or wholly predictable, animals may develop knowledge of where to locate resources and they will exploit that knowledge (Stephens and Krebs 1986, Doncaster and Macdonald 1997). But where resource availability is unknown or unpredictable, animals have to conduct non-oriented searches with little or no prior knowledge of where resources will be found. Consequently, the greatest reproductive success will go to those that are able to locate resources most efficiently, as they will minimize their risk of starvation, maintain their health, permit the diversion of energy to activities other than resource search, and potentially minimize their exposure to competitors and predators.

Any model of animal movement has to take into account both how and why animals move. To neglect these reasons and to attempt to fit a movement model without acknowledging this yields little additional insight. These ecological considerations have to be integrated into the analysis from the outset, and this necessitates interaction between modelers and ecologists with a detailed knowledge of the animal subject and the wider ecological context.

In what follows we will be focused and concern ourselves only with animal movements that are motivated by search. Of all the determinants of why animals move, this is the preeminent one. It is the one that is undertaken most frequently (daily in most cases) and success ensures individual survival, thereby permitting the possibility of reproduction and replacement of the population.

LÉVY-FLIGHT SEARCH THEORY

Random walk (RW) models emerged from the analysis of short-scaled movement data acquired in experiments usually lasting less than an hour and performed in arenas extending over no more than several meters (Kareiva and Shigesada 1983, Bovet and Benhamou 1988, Turchin 1991). Analysis of animal movements over much larger spatial scales and/or longer temporal scales has given rise to Lévy flight models (Viswanathan et al. 1996, 1999, Atkinson et al. 2002). Lévy flights comprise sequences of randomly orientated straight-line movements. Frequently occurring but relatively short straight-line movement randomly alternate with more occasionally occurring longer movements, which in turn are punctuated by even rarer, even longer movements, and so on with this pattern repeated at all scales (Fig. 1). As a consequence, the straight-line movements have no characteristic scale, and Lévy flights are said to be “scale-free.” The distribution of straight-line movement lengths, l , does, in fact, have a power-law tail:

$$P(l) \sim l^{-\mu} \quad (1)$$

where $1 < \mu \leq 3$. For $\mu \geq 3$, the search path corresponds to Brownian motion by virtue of the central limit theorem, whereas for $\mu \leq 1$, it emerges as distributions that cannot be normalized (Viswanathan et al. 1999). It should be emphasized that Lévy flights (LFs) are a random process and do not require complex calculation to execute. Instead, it is akin to rolling a fictitious many-sided die on which there are more low numbers than high numbers. Over much iteration, a Lévy flight will be distributed much farther from its starting position than a Gaussian (i.e., Brownian) random walk of the same length. The mean-square displacement of a Brownian walker has a linear dependence on time whereas that of a Lévy flier grows faster and depends on time raised to some power >1 . Lévy flights are therefore said to be “super-diffusive.”

Bartumeus et al. (2005) argued that RW can be interpreted as being the by-product of local scanning mechanisms whereas LFs have fundamental properties (super-diffusivity and scale-invariance) that allow for higher search efficiencies in random search scenarios. This prompted them to propose that some animals may have evolved the ability to perform LF when confronted with uncertainty. The notion is supported by the theoretical analysis of Viswanathan et al. (1999). Viswanathan et al. (1999) showed that $\mu = 2$ Lévy flights are optimal for the location of stationary targets that are randomly and sparsely distributed, and once visited are not depleted but instead remain targets for future searches. This is true irrespective of the dimensionality of the search space. Such movement patterns minimize the mean distance traveled before locating a target. Lévy flights with $\mu \rightarrow 1$ are optimal for the location of targets in one-dimensional environments that, once visited, become depleted and are no longer targets for future searches. This search pattern corre-

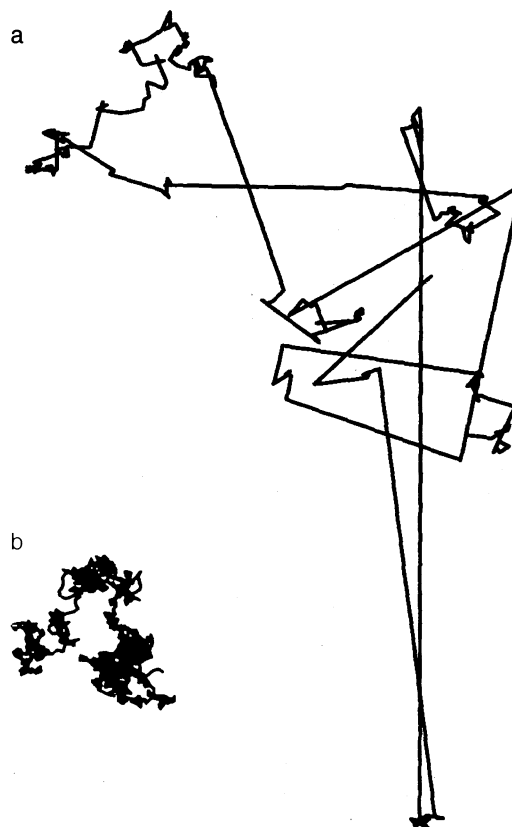


FIG. 1. (a) An example of a simulated $\mu = 2$ Lévy flight (LF) movement pattern. Frequently occurring short movements are interspersed with more rarely occurring longer movements. (b) An example of a Brownian walk composed of randomly oriented movements of fixed length. The LF movement pattern and the Brownian walk have the same overall lengths.

sponds to straight-line “ballistic” movement between targets.

There is a widely held view that the infinite variance implicit in Eq. 1 is an unrealistic modeling assumption. This is unwarranted because Lévy searches, unlike Lévy flights per se, are truncated whenever a target is located. As a consequence, the distribution of move lengths has a finite cutoff, comparable to the mean distance traveled between successive encounters with targets when traveling in a straight line (i.e., the “mean-free path”) and this corresponds to a “truncated” Lévy distribution (Viswanathan et al. 1999). The finite size of the animal’s environment or territory sets an even larger natural truncation scale which is relevant in situations of very low target densities as demonstrated in the context of random searches on regular lattices (Santos et al. 2005, 2008). Such cutoffs render the variance finite. This causes a convergence to Gaussian behavior but only after a very large number of steps (Mantegna and Stanley 1994). It is also worth noting that even without truncation, the variance of LF within a data set containing a large but finite number of moves, N , is not infinite but instead is proportional to $N^{(3-\mu)/(\mu-1)}$

(Bouchaud and Georges 1990). This is distinctly different from Brownian movements whose statistics are independent of the size of the data set.

It is tempting to interpret the results of Lévy-flight search models with reference to how animals search for food. In common with other useful models in ecology, it has a simplicity and generality that invites comparison with empirical data. The analysis of Viswanathan et al. (1999) demonstrates the existence of maximum search efficiencies, and it would be expected that there would be greater selection pressures for these movement patterns. Animals expend energy while searching, so the more efficient their search strategy, the more energy is left over for other purposes. Before attempting this interpretation, and to guide future comparisons with empirical data, it is worth stating more thoroughly the assumptions that the model imposes: (1) the animal is searching for stationary resource; (2) the animal is determining its own trajectory; (3) the animal is only searching for the resource; (4) the search domain is open and is not restricted by the presence of boundaries; (5) the resource is randomly and "sparsely" distributed, i.e., the animals have no prior knowledge of target locations; and (6) the searcher has perfect perceptual and prey-capture capabilities so that targets within the searcher's perceptual range are never missed and are always captured.

In contrast with Brownian searches, where the scale of movement is set by the organism, in LF searching the larger scales of movement are not intrinsic to the organism but instead are determined by the distribution of prey. According to LF theory, only the smallest scale of movement, the perceptual range, is intrinsic to the organism (Viswanathan et al. 1999). This fundamental difference between Brownian and LF searches has important ramifications when attempting to predict how animal movement patterns will change in response to environmental changes.

These initial observations about maximizing search efficiency using scale-free strategies stimulated many studies that sought to test for Lévy-flight search in empirical ecological data, and this will be discussed in more detail in the next section. However, in parallel with this, further work has taken place on developing the theory of search. We now discuss some of these developments.

Lévy flights have the advantage over other representations (e.g., correlated random walks and composite Brownian walks) of being a potentially more flexible and economic paradigm that encompasses several different search scenarios (e.g., collective searching and searching for moving targets) and these extensions of the standard Lévy flight theory have provided new biological insights into the orientation flights of bumble bees and honey bees, and into visually cued mate location behaviors in butterflies (Reynolds 2006a, b). "Orientation flights" are all the flights performed by a bee before making her first "bee-line" flight to and from a known forage location, which may be located several kilometers from the hive.

Orientation flights enable individual bees to acquire knowledge about the surrounding terrain. The orientation flights of honey bees may also contribute to the hive's collective knowledge of the surrounding terrain because honey bees, unlike bumble bees, can communicate the location of forage patches through the waggle dance. The orientation flights of honey bees consist of single hairpin loops that extend between 10 and 300 m out from the hive followed by straight-line return flights (Capaldi et al. 2000). This contrasts with the complex looping patterns made by naive bumble bees. The orientation flights of honey bees are consistent with their having adopted a Lévy-flight exploration strategy that is optimal for communicative explorers, while the orientation flights of bumble bees are consistent with their having adopted a Lévy flight exploration that is optimal for noncommunicative explorers (Reynolds 2006a). In accordance with observations, it is predicted that the waggle dance can be disrupted without noticeable influence on a hive's ability to maintain mass when forage is plentiful. Similarly, it has been suggested that visually cued mate location behavior in butterflies and in some other insects can be understood within the context of optimal Lévy-flight searching strategies for the location of moving targets (Reynolds 2006b).

Extensions of Lévy flight theory are also shedding light on the movement patterns of central-place foragers and foragers with a preferred feeding ground. Many of these animals adopt a stereotypical searching strategy that begins at the location where the forager initially expects to find the target and is comprised of loops of ever-increasing size that start and end at this location, and are directed in different azimuthal directions (Wehner and Srinivasan 1981). This strategy ensures that the area where the target is expected to lie is searched most intensively. It has been shown these movement patterns are consistent with the adoption of an optimal random Lévy-looping searching strategy for the location of a *single* target whose location is uncertain (Reynolds 2008a). The difference between freely roaming Lévy-flight searching patterns and Lévy-looping searching can be attributed to differences in the information that the searchers have about the likely location(s) of the target(s) of their search. Lévy-loopers center their searches on the origin because, initially at least, that is the most likely location of the target. Lévy-fliers, on the other hand, have no prior information about the most likely locations of their targets of their search, and as a consequence, their search patterns are freely roaming and there is no looping back to the origin after each straight line movement. Lévy-loopers should not be confused with the helical Lévy flight patterns observed in microzooplankton (Bartumeus et al. 2003). When searching in three-dimensional environments these cork-screw movements may reduce the likelihood of missing nearby targets.

It is also becoming apparent that other complex models can be subsumed within a Lévy flight paradigm (Reynolds 2008b). For example, Benhamou (2007)

introduced the composite Brownian walk (CBW) to explain search patterns within a landscape of patchily distributed resources. In a CBW, a searcher moves in a straight-line between patches and adopts more localized Brownian movements within a patch. The search pattern is therefore “adaptive” because detection of a food item triggers switching from an extensive mode of searching for clusters of food to intensive within-cluster searching for individual prey items. Benhamou (2007) showed that this CBW outperforms any Lévy-flight searching strategy with constant μ . The CBW can, however, be interpreted as an “adaptive” Lévy-flight searching pattern in which the inter-patch straight-line motions correspond to Lévy flights with $\mu \rightarrow 1$ and where the intra-patch motion corresponds to a Lévy flight with $\mu = 3$. Following from Viswanathan et al. (1999), this adaptive Lévy flight is an optimal strategy because $\mu \rightarrow 1$ is optimal for the location of randomly, sparsely distributed patches that once visited are depleted and because $\mu = 3$ flights are optimal for the location of densely but random distributed within-patch resources (Reynolds 2008b).

LÉVY SEARCHING IN AN ECOLOGICAL CONTEXT

The observation that in different situations there are demonstrably more efficient search strategies suggests that animals may also have developed correspondingly efficient search strategies. The results of the models described here suggest that Lévy-flight search is a particularly useful strategy that can accommodate a wide variety of different search scenarios, and this has stimulated comparison with ecological data. Sims et al. (2007) recently noted that over 30 biological and ecological studies relating to Lévy flight behavior have been published since the year 2000. Observations have been made in a wide variety of species spanning a body-size length scale from $\sim 10^{-5}$ m to $\sim 10^1$ m.

Here we look at the connection between search theory and empirical studies in greater detail and look at the type of studies that have been undertaken. The number of species reported to undertake Lévy-flight search behavior is increasing and it is not our intention here to exhaustively review each study in detail. Instead we identify a number of different study types and discuss the strengths and weaknesses of each approach when attempting to identify patterns of search.

Tracking during field trials

Honey bees (*Apis mellifera*) are regularly faced with the task of navigating back to their hives from remote food sources, and they have evolved several methods to do this. They use path integration (i.e., monitoring distances traversed) while foraging for new sources (Collett and Collett 2000, Collett et al. 2006), and once one is found, they travel in straight, compass-directed “vector” flights, to and fro, between the food source and hive (Riley et al. 2003). Landmarks may also be used, particularly on long flights (Collett et al. 2002). However, impressive though these methods are, they

are not perfect. For example, the bees’ path integration system will always be subject to cumulative errors, especially on long-range flights over unfamiliar terrain, and particularly if compass information is made less precise by heavy overcast. The strong winds and limited visibility associated with sudden summer thunderstorms, for example, may induce navigational errors, and the question arises, how do honey bees find their hives when their usual navigation methods fail to bring them home? It has been known for 80 years that if bees’ hive-centered navigational mechanisms are *artificially* disrupted, they adopt what appear to be looping, searching flights, and usually manage to (eventually) find their hives (Wolf 1927). With the advent of the harmonic radar it became possible to monitor the flight paths of honey bees over field-sized length scales (Riley et al. 1996, Riley and Smith 2002). Recently, harmonic radar was used to record the flight paths of bees that had been captured at a feeder, artificially displaced to a location away from the hive, and then released (Reynolds et al. 2007b). As expected, the paths showed that the bees initially tended to make long, looping flights away from the release point, as though they were searching systematically for their hive. Subsequent analysis of the harmonic data demonstrated that the bees were flying an optimal Lévy-looping flight pattern for the location of a single target (Reynolds et al. 2008a). The analysis of the flight patterns of displaced bees also showed that their Lévy-flight searching strategy can occasionally and temporarily be disrupted when the bees encounter localized landscape features (e.g., tents that were placed within the experimental arena) but that the overall flight paths remain close to the optimal search pattern. In particular, upon encountering a linear landscape feature that passed through the hive position, most bees flew repeatedly back and forth along a portion of it before arriving at the hive, or resuming an off-feature flight pattern which usually brought them back to the hive. Honey bees trained to an artificial feeder were also found to adopt the optimal Lévy-looping strategy when the feeder was removed (Reynolds et al. 2007c) suggesting that bees exploit this strategy when known food sources become depleted. More recently, optimal Lévy-looping flights have been identified in the flight patterns of peacock or small tortoiseshell butterflies after arriving at a cluster of flowering suitable for oviposition (E. Cant, A. Smith, D. Reynolds, and J. Osborne, *unpublished data*). Presumably the internal energy levels of these butterflies are not influencing the search patterns, as might be the case in food foraging situations.

The random Lévy-looping searching strategy is clearly less reliable than an equidistant (Archimedian) spiral search pattern. Such a spiral search could, however, work only if the bees’ navigation were precise enough and their visual detection ability were reliable enough, to ensure that all areas are explored and that no intervening regions escape scrutiny. Should the hive be missed, there would be no chance of encountering it a

second time because the flight path is an ever-expanding spiral. Relying on a spiral search pattern would therefore be disastrous where navigational and detection systems are less than ideal, and even then, this method could be used only for short searches before the inevitable cumulative navigational error became too large to allow a true spiral to be maintained.

The bee experiments provide strong evidence for LF searching, as the organism is being tracked while it is performing its natural behavior in the habitat to which it is adapted. When away from the hive it can be confidently assumed that the bees are engaged in search behavior and (in northern temperate regions, at least) are not subject to predation. As yet the scanning harmonic radar technology that permitted these field trials has not been extended beyond a few types of insects that are radar-detectable because they consistently fly a few meters above the plant canopy.

Laboratory studies of tracking

Lévy flight patterns with $\mu = 2$ have also been found in a laboratory-scale study of starved fruit flies (*Drosophila melanogaster*) using high speed video (Reynolds and Frye 2007). During their trajectories in still air, fruit flies explore their landscape using a series of straight flight paths punctuated by rapid 90° body saccades. Some saccades are triggered by visual expansion associated with collision avoidance. Yet many saccades are not triggered by visual cues but rather appear spontaneously. Analysis of high-speed video data revealed that the control of these visually independent saccades and the flight intervals between them constitute an optimal scale-free active-searching strategy. It was also shown that searching is intermittent, such that active searching phases randomly alternate with relocation phases. Behaviorally, this intermittency is reflected in frequently occurring short, slow, straight-line flights randomly alternating with rarer longer faster straight-line flights. This suggests, in accordance with recent theoretical developments (Reynolds 2006c), that scale-free and intermittent behaviors are not manifestations of two distinctly different kinds of searching strategy, but rather are constituent parts of a single, complex, widely adopted searching strategy.

Laboratory studies of tracking are useful and can work well for smaller organisms, yielding accurate and plentiful data. However, it can be challenging to replicate realistic stimuli and cues from the natural environment in such studies, thereby giving confidence that the organism is behaving as it would in the wild.

Wild animal tracking

Some of the most challenging data gathering on animal movement involves the long-term tracking of wild animals in their natural habitats. Radio-tracking of tagged animals using portable antennas has provided a wealth of data on the movement patterns of animals that are large enough to carry the requisite transmitter. Though the method is less controlled and less accurate

than laboratory or field trials, there is the advantage that the animal is likely to be engaged in its usual behavior in its familiar habitat. Bradshaw et al. (2007) showed, for instance, that Lévy flights from simulated data cannot be “recovered” when the spatial geolocation error is about 10% of the maximum move distance per day. A study of a number of radio-tracked side-striped jackals in Zimbabwe (*Canis adustus*) is illustrative of this approach (Atkinson et al. 2002) that has been refined by field ecologists over many years. Eight jackals were sequentially tracked for three eight-hour nighttime foraging expeditions and one twelve-hour nighttime session. Fixes were taken every 10 minutes with a measured accuracy within 100 m of the jackals’ true position (i.e., within the criterion set by Bradshaw et al. [2007]). The jackals were known to be foraging for small mammals and fruit. Other species that have been tracked include spider monkeys in their natural forest habitats (Ramos-Fernandez 2004), though this was done by visual observation. More recently an analysis of over a million movement displacements from animal-attached electronic tags as revealed that the vertical movements of a diverse range of marine predators, including sharks, bony fishes, sea turtles, and penguins, were power-law distributed and so consistent with the presence of Lévy-flight movement patterns (Sims et al. 2008).

When interpreting wild animal tracking data it is essential that there is a clear understanding of the ecological and behavioral context in which the data were gathered. In the jackal study (Atkinson et al. 2002) this involved detailed field observations of the animals in their natural habitats before any spatial tracking was done. Without this understanding it is not possible to confidently assert that searching is actually occurring at a given time. Additionally, it is also essential to understand the limitations of the tracking technology that has been used (not only spatial accuracy obtainable from any given method as highlighted by Bradshaw et al. [2007]). For instance, the wet-dry data loggers used in the albatross-tracking studies (Viswanathan et al. 1996) could not distinguish between in-flight and nest-sitting phases, thereby compromising the quantitative analysis.

HOW LÉVY FLIGHTS MAY ARISE IN SUCH A WIDE VARIETY OF ORGANISMS

The key to prediction and understanding lies in the elucidation of mechanisms underlying the observed patterns. It is becoming evident that Lévy flight patterns can emerge from a diverse range of mechanisms. Nevertheless, convergence of behaviors along such different evolutionary pathways is not surprising given the energetic efficiencies that Lévy-flight movement patterns confer. Our view is that the universality of the phenomenon indicates that it is unlikely to be the consequence of environmental factors. A possible exception is the scale-free movements of spider monkeys (Ramos-Fernandez et al. 2004), which have been attributed to complex interactions with their environment (Boyer et al. 2006).

It has been found that $\mu = 1.5$ Lévy flights can arise from naive tracking of odor plumes dispersing with the atmospheric boundary layer (Reynolds 2005), and such flight patterns have been identified in male *Agrotis segetum* moths flying in the presence of female sex pheromone (Reynolds et al. 2007a). An organism naively tracking an odor plume will fly upwind whenever the perceived odor concentration is above a threshold high and will otherwise cast back and forth in a crosswind direction, in an attempt to re-establish contact with the plume. The distribution of times during which odor concentrations remain above threshold levels has a $-3/2$ power-law tail (Yee et al. 1994). It has also been shown how $\mu = 2$ Lévy-flight searching patterns can emerge from conspecific avoidance, i.e., behavior designed to avoid locations previously traversed by individuals of the same species (Reynolds 2007). The findings may account for the scale-free foraging movements of jackals because they (like all Canids) are well equipped to detect scent trails (Moulton et al. 1960). This mechanism may also account for the fractal scaling (i.e., scale-free) properties of the movement patterns of ground-foraging beetles (Johnson et al. 1992). Indeed, in a recent study the movements of a starved model predator, the carabid beetle *Pterostichus melanarius*, was monitored in arenas containing test papers, upon which beetles had previously walked, and unexposed control papers (Guy et al. 2008). Significantly, beetles accumulated on the unexposed controls, indicating conspecific odor trail avoidance behavior. More recently it has been shown that $\mu = 2$ Lévy flight patterns are a robust emergent property of predators that use chemotaxis to locate randomly and sparsely distributed stationary prey items (Reynolds 2008c). This may account for the Lévy-flight movement patterns of *Oxyrrhis marina* micro-zooplankton in still water containing prey items.

It has been suggested that Lévy flights in *Drosophila* may have neurophysiological underpinnings. Segev et al. (2002) recently reported that Lévy-stable distributions with an inverse-square-law tail characterize the electrical activity of some neuronal networks. Such spontaneous electrical activity could provide the timing signals necessary for the execution of Lévy flights. In fruit flies, locomotor activity is coordinated by a region called the central complex, often referred to as the insect's "motor cortex." Martin et al. (2001) found that blocking synapses within the ellipsoid-body, a subregion of the central complex, leads to a loss of the fractal (i.e., Lévy-like) properties of adult walking behavior. They concluded that fractal patterns of locomotor activity are somehow regulated in the ellipsoid body. It would therefore be fruitful in future work to investigate whether genetically or mechanically inactivating the ellipsoid body also interrupts the Lévy structure of flight behavior.

Viswanathan et al. (1996) suggested that Lévy-flight movement patterns of predators arise in response to scale invariant distributions of food within the environment, i.e., some animal search patterns may be adapted stochastically to their prey field. The suggestion finds

support in the recent study of Sims et al. (2008) who reported Lévy flights in marine predators coexisting with Lévy-like fractal distributions of prey density. This, of course, leaves open the establishment of an underlying mechanism.

DATA ANALYSIS ISSUES

The identification of a Lévy-flight search pattern (or any other hypothesized pattern) in data obtained from tracking studies will ultimately depend upon the judicious application of appropriate analysis methods. The raw material for this analysis process is positional data (spatial x, y coordinates) for a tracked animal, and the z data from vertical dive time-series for a marine predator. This data may have certain spatial accuracy associated with it, and it will have been recorded at either regular or irregular time intervals. While it is generally desirable to have long runs of tracking data, depending on the scenario and the animal under observation, search behavior might only be undertaken at certain times; often insight has to be derived from low accuracy, irregularly recorded and short-duration time-series of tracked coordinates. Methods are needed that can produce robust insight from limited data.

To identify a Lévy-flight search strategy we are concerned with diagnosing a scale-free trajectory. From Eq. 1, the Lévy flight should have a scale-free distribution of step lengths. Additionally, the turning points of the trajectory should have a fractal distribution in space. So the first task is to construct a trajectory from the raw positional data. This yields a set of step-lengths and turning points.

How should LFs be constructed from tracking data?

Ideally, searching flights should be represented as sequences of straight-line segments between the points at which significant changes in direction, "turns," occur (Bartumeus et al. 2003, Benhamou 2007, Reynolds et al. 2007b, c). This is because LF movements, when strictly defined, consist of straight-line movements and "reorientation" events during which the direction of travel changes abruptly. Turns should be identified using objective measures. A turn can, for instance, be taken to arise when the angle between two movement segments joining three successive positional fixes is less than a critical angle (Reynolds et al. 2007b, c). An example of how an LF trajectory can be constructed from bee tracking data is shown in Fig. 2. The robustness of any subsequent analyses with respect to the choice for the critical angle should then be tested. In the case of honey bees and *Drosophila* fruit flies the critical angle was taken to be 90° and the results of analyses did not change significantly when this angle was changed by $\pm 30^\circ$ (Reynolds and Frye 2007, Reynolds et al. 2007b, c). The representations of the "searching" flights in terms of straight-line flights and turns can then be analyzed in detail by using "random walk methods," which can detect the presence of long-term correlations. This analysis is based on the fact that the number of

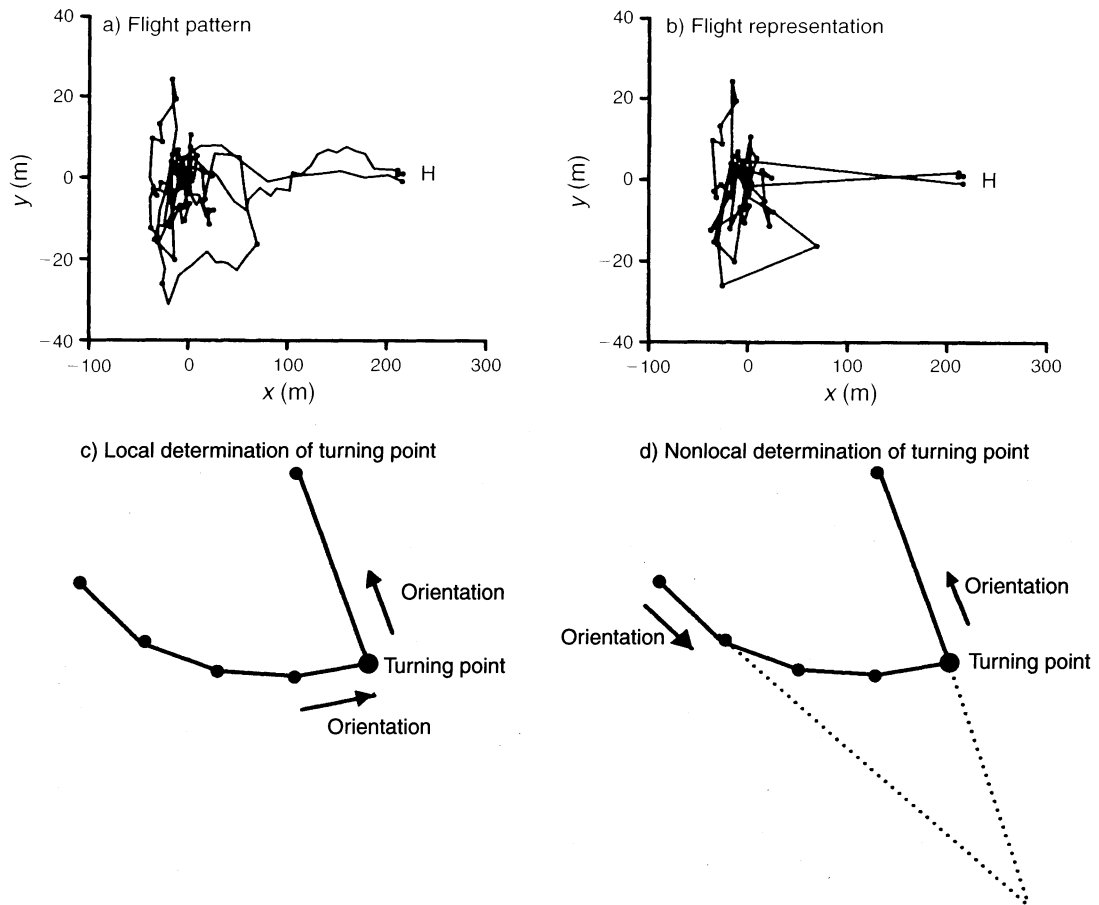


FIG. 2. (a) A typical flight pattern of a honey bee (*Apis mellifera*) trained to an artificial feeder, which was then removed, resulting in a localized search around the former position of the feeder. The location of the honey bee was recorded every 3 s unless the radar failed to detect the radar transponder. The hive was located at $(x, y) = (210 \text{ m}, 0 \text{ m})$, and the feeder was located at $(x, y) = (0 \text{ m}, 0 \text{ m})$ (approximately). The flight begins and ends in the vicinity of the hive (marked with an "H"). The locations where there are significant changes in flight orientation are indicated with solid circles. A change in flight direction is deemed to have arisen when the direction of the current flight segment (joining two successive recorded positions) and that of the flight segment immediately following the last deemed change in direction, is less than 90° (i.e., when the interior angle of the turn is acute). (b) Representation of the honey bee flight in terms of straight-line flights and changes in flight orientation. The statistical properties of these representations do not differ significantly from representations in which *local* abrupt changes in orientation are taken to arise when the angle between two successive flight segments (i.e., between three successive recorded positions) is $< 90^\circ$. (c) Local determination of the turning point using three successive recorded positions. (d) A non-local determination of the turning point. The close correspondence between these two [local (c) and non-local (d)] representations indicates that most changes in flight orientation occur abruptly rather than through the accumulation of small changes.

turning points occurring within the time intervals t to $t + \Delta t$ defines a time series, $u(t)$, and an associated net "displacement," $n(t) = \sum_{i=0}^N u(i\Delta t)$. If the values of $u(t)$ are completely uncorrelated and behave like "white noise," then the root-mean-square displacement,

$$F = \sqrt{\langle [n(t) - \langle n(t) \rangle]^2 \rangle} \propto t^\alpha.$$

where $\alpha = 1/2$ and where the angular brackets denote an ensemble average over all flights in the data set (Peng et al. 1995). Short-term correlations in the data may cause the initial slope of a plot of $\log(F)/\log(t)$ to differ from one half, although it will still approach one-half at longer times. Long-term power-law correlations, how-

ever, will generate α values $\neq 0.5$. Care must be exercised because apparent power-law scaling can arise when analyzing small data sets (Viswanathan et al. 2005, Bartumeus et al. 2008). The use of multiple measures serves to increase confidence. Other analyses could consist of a determination of the fractal dimension of the represented flight patterns and an examination of the distributions of the lengths and durations of the straight-line segments in those representations. A raft of methods has been devised for the latter, most recently by Sims et al. (2007), who advocated logarithmic binning of data, and by Edwards et al. (2007), who advocated the use of the Akaike Information Criteria (AIC) to distinguish between power laws and exponentials. This issue is hotly

contested, and debate about the reliability of methods used to test for the presence of power-law tails are likely to run and run (see e.g., Clauset et al. 2007, Edwards et al. 2007, Sims et al. 2007).

In applying these techniques, it is important to distinguish between the scaling properties of indefinitely long LF, which are a mathematical abstraction, and the scaling properties of finitely long LF that may represent the movement patterns of some animals. Note, in particular, that the longest straight-line movement in an LF search will be comparable with the mean-free path between targets because an LF search will be truncated whenever a target is located. As a consequence, the distribution of move lengths has a finite cutoff. And in the presence of multiple prey encounters, the extreme tail of the distribution of move lengths is not a power law but is, instead, exponential.

The effect of varying levels of measurement error in the tracking data has been investigated by Bradshaw et al. (2007) and some of the difficulties of estimating the Lévy exponent from data have been highlighted by Sims et al. (2007).

Sampling search trajectories at nonconstant and constant time intervals

Some analyses of animal movement are not based on the straight-line movements made between successive reorientations but instead are based on move lengths made between arbitrary location fixes (Atkinson et al. 2002, Seuront et al. 2007). This technique is appealing because it obviates the need to judge when a turn has been made. Benhamou (2007) rightly questioned the validity of this approach. The hallmark power-law tail of Lévy flights is, in fact, quite robust with respect to this form of subsampling (Reynolds 2008b).

OUTLOOK

Knowing how animals move around their environment is essential to understanding many ecological and population processes. Continuing development of tracking technology will ensure that an ever-increasing supply of data on animal movement will become available for analysis (Sims et al. 2008). Much of that analysis will be concerned with discriminating between different candidate models for animal movement. One intention of this work is to explore the extent to which Lévy-flight searching is applicable in a wide variety of ecological circumstances and to indicate the key steps (and potential pitfalls) in processing and analyzing raw movement data. This continues to be a topic of active research and further developments and insight into diagnosing movement patterns from raw data are expected. Even if falsified, the LF hypothesis is important because it will be a step towards more sophisticated theories. Moving beyond detailed issues relating to analyzing data, there are some more general topics that require further attention, and we believe, these too should be a focus for future research:

- 1) A recent paper in *Nature* (Edwards et al. 2007) questioned the claim for Lévy flight behavior in the Wandering Albatross, first reported by Viswanathan et al. (1996). Additionally, Edwards et al. (2007) identify some other data sets (Viswanathan et al. 1999) in which the analysis is unable to definitively discriminate the presence of an LF. Central to the resolution of the issue is the identification of underlying processes that can give rise to LF patterns because convergence to a consensus view about reliable indicators of LF has not been attained despite much effort over many years. The key to prediction and understanding does, after all, lie in the elucidation of mechanisms underlying the observed patterns. Some progress has been made in this direction by Reynolds (2005, 2007, 2008c) and by Reynolds and Frye (2007), who have identified candidate mechanisms underlying the occurrence of LF in some organisms. Mechanisms underlying the occurrence of LF patterns in the marine predators' wandering (Sims et al. 2008) do, however, remain elusive.
- 2) Traditionally, movement data has been discretized (Turchin 1989), and distances traveled along with orientations taken during fixed increments have been used to construct random walk models. This procedure precludes the identification of LF because no account is taken of abrupt but occasional changes in direction. Studies of animal search that use this kind of data analysis should be revisited, so that the Brownian walk hypothesis can be scrutinized.
- 3) LF searching may be a universal strategy applicable across spatial scales ranging from less than a meter in the case of microzooplankton, amoeba, and *Drosophila* fruit flies (Levandowsky et al. 1997, Bartumeus et al. 2003, Reynolds and Frye 2007) to several kilometers in the case of the jackal (Atkinson et al. 2002), and adopted by swimming, walking, and airborne organisms. This advance in the understanding of innate searching in homogeneous environments leaves open the impact that landscape heterogeneity and physical barriers can have on movement patterns. Benhamou (2007) was the first to consider optimal searching in heterogeneous environments containing clusters of targets, and this work highlighted the benefits that adaptive searching can have over nonadaptive searching. In an adaptive search, detection of a prey item triggers switching from an extensive mode of searching for clusters of prey to intensive within-cluster searching for individual prey items. Underlying this notion is the assumption that searchers have reliable information about target distributions (in the presence of unpredictability due to predators, for example, and target detection errors, it may be advantageous to adopt a nonadaptive search strategy). It would be interesting to determine the relative merits of adaptive and nonadaptive LF searching in the presence of uncertainty and to extend the approach to non-destructive foraging.

- 4) Many central-place foragers, and foragers with preferred feeding ground, adopt a stereotypical searching strategy that begins at the location where the forager initially expects to find the target, and is comprised of loops of ever-increasing size that start and end at this location, and are directed in different azimuthal directions (Wehner and Srinivasan 1981, Hoffman 1983, Fourcassié and Traniello 1994, Durier and Rivault 1999). This strategy ensures that the area where the target is expected to lie is searched most intensively. These movement patterns are closely akin to the LF looping patterns made by displaced honey bees (Reynolds et al. 2007b) and by honey bees searching after a known food becomes depleted (Reynolds et al. 2007c). It is hoped that the honey bee studies will motivate ecologists to reexamine the searching patterns of central placed foragers and foragers with preferred feeding grounds as part of the development of a unifying theory of searching patterns in animals.
- 5) It is of considerable interest to test whether animal responses to environmental changes are consistent with (yet to be determined) expectations obtained under the assumption that LFs are innate, evolved behaviors. This would provide a stern test of the predictive capabilities of the LF hypothesis.

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