Scale-free animal movement patterns: Lévy walks outperform fractional Brownian motions and

fractional Lévy motions in random search scenarios

Scale-free animal movement patterns: Lévy walks outperform fractional Brownian motions and fractional Lévy motions in random search scenarios

A M Reynolds

Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK

Abstract

The movement patterns of a diverse range of animals have scale-free characteristics. These characteristics provide necessary but not sufficient conditions for the presence of movement patterns that can be approximated by Lévy walks. Nevertheless, it has been widely assumed that the occurrence of scale-free animal movements can indeed be attributed to the presence of Lévy walks. This is, in part, because it is known that the super-diffusive properties of Lévy walks can be advantageous in random search scenarios when searchers have little or no prior knowledge of target locations. However, fractional Brownian motions (fBms) and fractional Lévy motions (fLms) are both scale-free and super-diffusive, and so it is possible that these motions rather than Lévy walks underlie some or all occurrences of scale-free animal movement patterns. Here this possibility is examined in numerical simulations through a determination of the searching efficiencies of fBm and fLm searches. It is shown that these searches are less efficient than Lévy walk searches. This finding does not rule out the possibility that some animals with scale-free movement patterns are executing fBm and fLm searches, but it does make Lévy walk searches the more likely possibility.

PACS numbers: 02.50.Ey, 05.10.Gg, 05.40.Fb

1. Introduction

Over recent years there has been an accumulation of evidence that many animals, including microzooplankton (Bartumeus *et al* 2003), a species of African jackal (Atkinson *et al* 2002), honeybees (Reynolds *et al* 2007a, 2007b), fruit flies (Reynolds and Frye 2007) and some marine predators (Sims *et al* 2008), have scale-free characteristics. Some earlier studies claiming evidence for scale-free characteristics (Viswanathan *et al* 1996, 1999) have, however, been overturned (Edwards *et al* 2007). The later studies have so far stood up to scrutiny (Buchanan 2008). One of the simplest indicators of scale-free behaviour is power-law scaling

of the distribution of movement lengths made between successive, significant changes in direction. For microzooplankton, honeybees and marine predators, these distributions exhibit approximate inverse-square power-law scaling over about one or two decades (Bartumeus *et al* 2003, Reynolds *et al* 2007a, 2007b, Sims *et al* 2008). The results of 'random-walk analyses' of movement patterns can provide stronger evidence for scale-free behaviour (Atkinson *et al* 2002, Reynolds *et al* 2007a, 2007b, Sims *et al* 2008). In these analyses, time series, $u(t)$, of the numbers of turns made within time intervals from t to $t + \Delta t$, are treated as increments in a random walk. The analysis is meaningful when the turns are biologically significant because they represent abrupt changes in otherwise nearly straight-line motion (Bartumeus 2009). The flight patterns of *Drosophila* fruit flies in still air are the archetypical example of this, as fruit flies explore their landscape using a series of straight-flight paths punctuated by rapid $90°$ body saccades. Similarly, the flight directions of honeybees change abruptly over several seconds rather than gradually through the accumulation of many small turns over much longer times (Reynolds *et al* 2007a, 2007b). The net 'displacement' is just the running sum $n(t) = \sum_{i=0}^{N=t/\Delta t} u(i)$. If values of $u(t)$ are completely uncorrelated and behave like 'white noise', then the root mean square of the running sum would obey the scaling relation $F = \sqrt{\langle (n(t) - \langle n(t) \rangle)^2 \rangle} \propto t^\alpha$, where $\alpha = 1/2$ and where the angular brackets denote an ensemble average over all walks in the data set (Peng *et al* 1993). Short-term correlations in the data may cause the initial slope of a plot of $\log(F)/\log(t)$ to differ from 1/2, although it will still approach 1/2 at longer times. Movement patterns that can be approximated by correlated random walks (Turchin 1998) would produce this scaling as would multi-scale movements, e.g. bouts of ballistic motion punctuated by bouts of Brownian motion that are representative of some movement patterns in the presence of patchily distributed resources (Reynolds 2008a). Long-term *power-law* correlations (Peng *et al* 1993) will generate α values different from 1/2. The movement patterns of honeybees, jackals and some marine predators are characterized by $\alpha \neq 1/2$ and this implies that long-term power-law correlations exist in these data (Atkinson *et al* 2002, Reynolds *et al* 2007a, 2007b, Sims *et al* 2008). The movement patterns of jackals and honeybees also exhibit fractal scaling over 1–2 decades of scale and this provides further evidence for the presence of scale-free movement patterns (Atkinson *et al* 2002, Reynolds *et al* 2007a, 2007b).

The occurrence of scale-free characteristics in the movement patterns of some animals has been attributed to the presence of Lévy walks (Atkinson *et al* 2002, Bartumeus *et al* 2003, Ramos-Fernandez *et al* 2004, Reynolds *et al* 2007a, 2007b, Sims *et al* 2008). Lévy walks, named after the French mathematician Paul Pierre Lévy, are comprised of random sequences of movement segments (such as flying, swimming or walking), with lengths, l, drawn from a probability distribution function having a power-law tail, $p(l) \sim l^{-\mu}$, where $1 < \mu < 3$. For $\mu > 3$, sums of length, i.e. total displacements, converge to a Gaussian distribution by virtue of the Central Limit Theorem so that motions are effectively Brownian at sufficiently large scales. Levy indices $\mu \leqslant 1$ do not correspond to normalizable distributions with probabilities that sum to unity. Lévy walks with $\mu \to 1$ correspond to randomly oriented straight-line movements. Qualitatively, a Lévy walk is characterized by frequently occurring but relatively short move lengths punctuated by rarely occurring longer lengths that in turn are punctuated by even more rarely and longer lengths, and so on. Over much iteration, a Lévy walk will be distributed much farther from its starting position than a Gaussian (i.e. Brownian) random walk of the same length and is said to be 'super-diffusive'. In some cases, Lévy walk movement patterns may be emergent properties of the manner in which the animals interact with their environments (Boyer *et al* 2006, Reynolds 2007, 2008b). Other examples have been attributed to innate evolved searching behaviours. This is principally because the scale-free and super-diffusive properties of Lévy walks can lead to advantages over Gaussian motions in random search

scenarios when searchers have little or prior knowledge of target locations (Bartumeus *et al* 2005). For example, Viswanathan *et al* (1999) demonstrated that $\mu = 2$ constitutes an optimal Lévy walk search strategy for locating randomly and sparsely distributed targets that once visited are not depleted but instead remain targets for future searches; a scenario mimicking searches for patchily distributed resources and searching when prey items can evade capture (Reynolds and Bartumeus 2009). Under such conditions, a $\mu = 2$ Lévy search strategy minimizes the mean distance travelled and so minimizes the mean energy expended before encountering a target. More recently, Reynolds and Bartumeus (2009) reported that Lévy walks with $\mu \leqslant 2$ and straight-line ballistic motions can be equally effective when searching destructively in two- and three-dimensional environments.

Inverse-square power-law distribution of move lengths, power-law scaling of the random-walk time series data, and fractal scaling of entire trajectories provide necessary but not sufficient conditions for the presence of $\mu \approx 2$ Lévy walks in the movement patterns of some animals. This is because, as shown later, these indicators of scale-free behaviour do not discriminate among Lévy walks, fractional Brownian motions (fBm) and fractional Lévy motions (fLm) (Mandelbrot and Van Ness 1968). It is therefore necessary to examine these alternative models. Indeed, this is crucial because the key to prediction and understanding lies in the elucidation of mechanisms underlying the observed patterns (Levin 1992). Frontier (1987) was perhaps the first to propose that fBms could be used to characterize the movements of some animals (insects). The conjecture finds support in recent measurements of natural conductance fluctuations in lipid membranes that can be approximately modelled as fBms and fLms (Kotulska 2007). Such fluctuations could in principle provide timing signals necessary for the execution of fBms and fLms movement patterns.

In the pioneering work of Mandelbrot and Van Ness (1968), fBm was defined by its stochastic representation,

$$B_H(t) = \frac{1}{\Gamma(H + 1/2)} \left(\int_{-\infty}^{t} (t - s)^{H-1/2} \, \mathrm{d}B(s) + \int_{-\infty}^{0} s^{H-1/2} \mathrm{d}B(s) \right), \quad (1)$$

where Γ is the gamma function, $0 < H < 1$ is the Hurst parameter and t is time. The integrator B is an ordinary Brownian motion. Ordinary Brownian motion is recovered from (1) when $H = 1/2$. fBm is uniquely characterized by the following properties: $B_H(t)$ has statistically stationary increments, the initial value $B_H(0) = 0$, the mean and variance obtained by ensemble averaging over many walks evolve according to $\langle B_H(t) \rangle = 0$, $\langle B_H^2(t) \rangle = t^{2H}$ and $B_H(t)$ has a Gaussian distribution when $t > 0$. fBms are, therefore, sub-diffusive when $H < 1/2$ and super-diffusive when $H > 1/2$, because the position variance then grows faster than linearly in time.

Increments in fBms have autocorrelation

$$\langle [B_H(k+1) - B_H(k)][B_H(1) - B_H(0)] \rangle$$
$$= \tfrac{1}{2}[|k-1|^{2H} - 2|k|^{2H} + |k+1|^{2H}] \underset{k \to \infty}{\sim} H(2H-1)k^{2H-2}. \quad (2)$$

This span of interdependence between increments is infinite. The autocorrelations (2) are negative when $0 < H < 1/2$ and positive when $1/2 < H < 1$. Positive correlations lead to paths that are straighter and smoother than Brownian walks (figure 1). It is evident from figure 1 that fBms, like Lévy walks, tend to cluster in self-similar patterns that are characteristic of fractals, and that occasionally occurring long moves initiate new clusters. The longer the move, the less likely is its occurrence.

It is possible that these scale-free and super-diffusive properties lead to advantages over Lévy walks in random searches scenarios. This would have significant ramifications for the interpretation of scale-free animal movement patterns because animals can be expected to
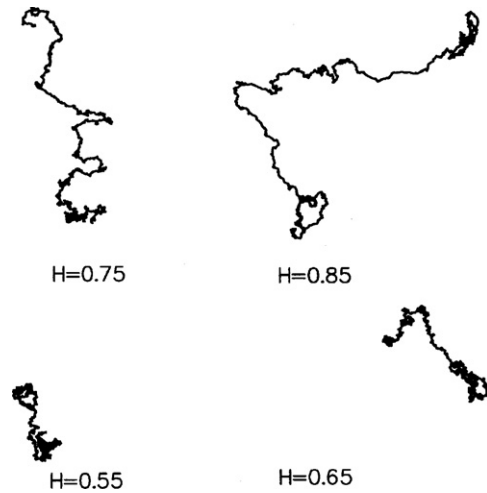
Figure 1. Examples of simulated fBm generated using (4). Each example contains 1000 increments with unit variance. Directional persistence becomes more evident, has the Hurst parameter, *H*, increases from 1/2 to 1.

adopt advantageous searching strategies. Here, the efficiencies of fBm and also fLm searches are examined in numerical simulations. fLm can be defined by its stochastic representation

$$L_H(t) = \frac{1}{\Gamma(H+1/2)} \left(\int_{-\infty}^{t} (t-s)^{H-1/2} \, \mathrm{d}L(s) + \int_{-\infty}^{0} s^{H-1/2} \, \mathrm{d}L(s) \right), \quad (3)$$

where the integrator *L* is ordinary Lévy walks. Ordinary Lévy walks are recovered when *H* = 0.5. The orientation of successive walk segments is positively correlated (directional persistence) when $H > 0.5$ and negatively correlated (directional anti-persistence) when $H < 0.5$.

　　The simulation of fBms and fLms, their possible correspondence with scale-free animal movement patterns and the searching efficiencies of fBm and fLm searches are presented in sections 2 and 3. This is followed, in section 4, by a discussion.

2. Optimal fractional Brownian motion searching

2.1. Simulating fBm

fBms were simulated by approximating the stochastic integrals in (1) by stochastic sums. The approximation is given by

$$B_H^{/}(n) = C_H \left(\sum_{i=-N}^{n} (n-\mathrm{i})^{H-1/2} B(\mathrm{i}) - \sum_{i=-N}^{0} \mathrm{i}^{H-1/2} B(\mathrm{i}) \right), \quad (4)$$

where *B*(i) are independent Gaussian random quantities with mean zero and unit variance, and C_H is chosen so that increments $B_H(k+1) - B_H(k)$ have unit variance. The approximation is not appropriate in a strict sense because the Brownian paths in (1), although continuous, are non-differentiable and, more importantly, because they do not have bounded variation with probability one (Dieker 2004). Here, these issues are set aside and approximation (4) is adopted because animal movement patterns cannot possibly adhere to the strict definition of

an fBm (1) but could, at least in principle, adhere to its discrete analogue (4). Following Qian *et al* (1998), two-dimensional fBms are simulated using two independent one-dimensional fBm for movements in the *x*- and *y*-directions. The results of numerical simulations (not shown) reveal that the mean square displacements of exactly represented and approximately represented fBms, (1,4), have the same power-law scaling: $\langle B_H^2 \rangle = t^{2H}$ and $\langle B_H'^2 \rangle = t^{2H}$. It is also found that the self-affine curves (plots of the *x*-coordinate as a function of time) of approximately and exactly represented fBm have, to close approximation, the same fractal (box-counting) dimension, $D = 2 - H$. Estimates for the fractal dimension were based on 250 independent fBms, each with 1000 increments for $H = 0.5, 0.6, 0.7, 0.8$ and 0.9. The average number of boxes n_{box} of size l_{box} required to enclose the fBms was plotted against l_{box}. A power-law relationship of the form $n_{box} \propto l^{-D}$ would be indicative of fractal scaling with fractal dimension *D*. Here the fractal dimension was estimated by least-squares regression on $\log(n_{box})$ of $\log(l_{box})$ for $10 < n < 10^3$. Correlation coefficients (r^2 values) are greater than 0.99 indicating that over 99% of the data were well represented by $n_{box} \propto l^{-D}$. The results of these numerical simulations do not depend sensitively upon the value of the lower bound *N* in the stochastic sums in (4) when $N \geqslant 1000$. For this reason, the results of all further analyses are presented for $N = 1000$.

2.2. Correspondence between fBm and scale-free animal movement patterns

To facilitate analysis and to draw a direct analogy with the analysis of animal movement patterns, fBm trajectories are represented as sequences of straight-line moves between successive significant turns. Here significant directional changes are deemed to have arisen when the angle between two successive incremental movements (i.e. between three successive positions) is acute (figure 2, insets). Distributions of movement lengths do not change significantly when the critical angle used to define a turn is changed by $\pm 30°$. Irrespective of the discretization employed, the tail of the distribution of straight-line move lengths when plotted on log–log scales becomes straighter as the Hurst parameter increases from 0.5 to 1.0 (figure 2). This is indicative of the distribution of straight-line move lengths becoming better approximated by a power law. Perhaps the most robust approach for testing the presence of power-law scaling is to utilize maximum likelihood estimates (MLE) and the Akaike information criteria (AIC), as advocated by Edwards *et al* (2007). Here, following Edwards *et al* (2007), this approach is used to test whether the simulation data provide more evidence for distributions of straight-line movement lengths, *l*, having power law

$$P_1(l) = Cl^{-\mu}, \qquad l \geqslant a \tag{5}$$

or exponential tails

$$P_2(l) = \lambda \, e^{-\lambda(l-a)}, \qquad l \geqslant a, \tag{6}$$

where $C = (\mu - 1)a^{\mu-1}$ is a normalization constant. The key quantities of interest in this analysis are the MLE for the exponent, μ, that characterizes the best-fit power-law tail and the Akaike weights. The Akaike weight, w, for the power-law tail can be considered as the weight of evidence in favour of the power-law tail being the better model of the simulation data, i.e. the Akaike weight for a power-law can vary from 0 (no support) to 1 (complete support). A power-law tail is convincing favour over an exponential tail when $H > 0.8$ (e.g. $H = 0.85$, $w = 1.00$, $\mu = 2.93$; $H = 0.95$ and $w = 1.00$, $\mu = 2.2$). This analysis was based on 250 independent fBm with 1000 increments for each *H*. For $H < 0.8$ exponential tails are convincingly favoured over a power-law tails.

The results of a random-walk analysis applied to the time series of turns data are more revealing. It provides clear evidence of scale-free behaviour. As *H* increases from 0.5 to 1.0,
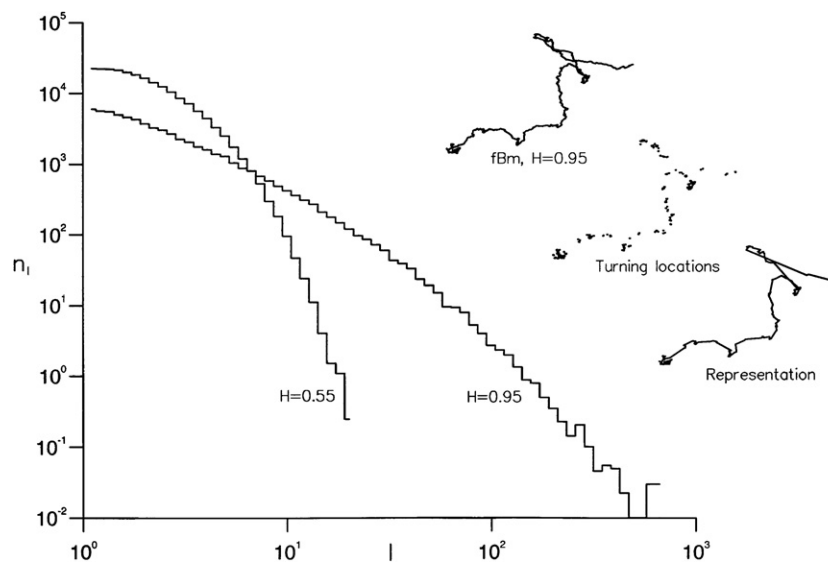
Figure 2. Numbers, n_l, of straight-line moves of lengths, l, made between successive, significant changes in direction. Here directional changes are deemed to have arisen where the direction between two successive walk segments (i.e. between 3 successive positions) is less than $90°$ (i.e. when the angle is acute). Distributions of movement lengths do not change significantly when the critical angle used to define a turn is changed by $\pm30°$. The sizes of the data collection bins are logarithmically distributed and numbers of straight-line walk segments have been normalised by the bin sizes. Distributions were determined from 250 independently simulated fBm. The inserts show an example of a fBm with 1000 increments, the location of the $90°$ turns, and its representation in terms of straight line moves between turning locations.

the value of scaling exponent α increases monotonically from 0.5 to about 0.75 (figure 3). This saturation value is less than the values of α that characterize the movement patterns of jackals and honeybees (Atkinson *et al* 2002, Reynolds *et al* 2007a, 2007b).

2.3. Optimal fBm searching strategy

Viswanathan *et al* (1999) considered an idealized Lévy walk model in which a searcher moves on a straight line towards the nearest target if the target lies within the 'direct perception' distance, r, otherwise it chooses a direction at random and a distance, l, drawn from a power-law distribution $p(\ell) = (\mu - 1)r^{\mu-1}|\ell|^{-\mu}$ when $\ell > r$, otherwise $p(\ell) = 0$, where $1 < \mu < 3$. It then moves incrementally towards the new location whilst constantly seeking for targets within a radius, r. If no target is detected, it stops after traversing the distance l and chooses a new direction and a new distance, otherwise it proceeds to the target. Viswanathan *et al* (1999) found that $\mu = 2$ Lévy walks are optimal for the location of randomly and sparsely distributed targets that once visited are not depleted but instead remain targets for later searches. Straight-line motions are optimal for destructive searching and these correspond to fBm (and fLm) with $H = 1$.

Here the efficiencies of fBm searches are investigated using a natural adaptation of the model of Viswanathan *et al* (1999) in which the Lévy walk movement patterns are replaced by fBm movement patterns whilst retaining all other model ingredients. When $0 < H < 1/2$, fBm are sub-diffusive and as a consequence, searching is necessarily less efficient than a
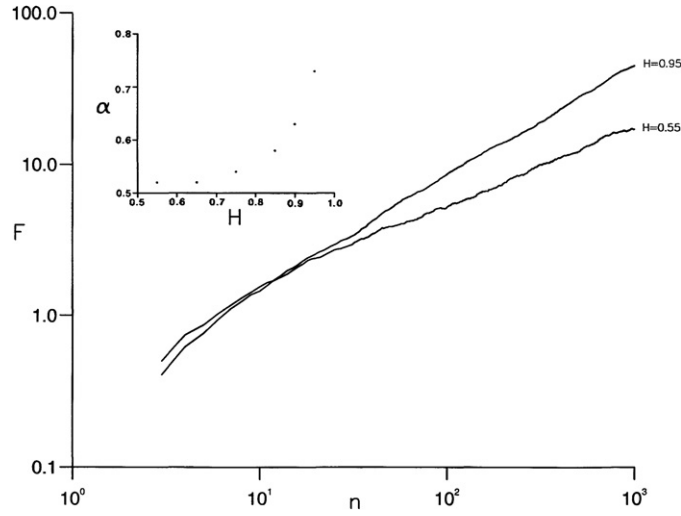
Figure 3. The net root mean square displacement, F, associated with the time series of turning points. The inset shows the least-squares best fit, scaling exponent, α, characterising the power-law scaling of the displacement F as a function of the Hurst parameter, H. The least-square fit is obtained from a linear regression of $\log F$ on $\log n$ for $10 < n < 10^3$. Correlation coefficients (r^2 values) are greater than 0.9 indicating that over 90% of the data are well represented by $F \propto t^\alpha$. Displacements were determined from 250 independently simulated fBm.

Brownian search. The results of numerical simulations reveal that the searching efficiency decreases monotonically as H increases from 1/2 to 1, i.e. decreases with increasing directional persistence of the fBm (figure 4). These fBm searches are therefore less efficient than Brownian searches ($H = 1/2$) and so less efficient than Lévy walk searches which outperform Brownian searches (Viswanathan *et al* 1999).

3. Optimal fractional Lévy-motion searching

fLms were simulated by approximating the stochastic integrals in their stochastic representation (3) by stochastic sums. The approximation is given by

$$L_H^{/}(n) = C_H \left(\sum_{i=-N}^{n} (n-i)^{H-1/2} L(i) - \sum_{i=-N}^{0} i^{H-1/2} L(i) \right), \qquad (7)$$

where $L(i)$ are independent Lévy walks and the constant C_H is chosen so that the smallest increment, $L_H(k+1) - L_H(k)$ has unit size. Step lengths, l, are drawn from a power-law distribution $p(\ell) = (\mu - 1)r^{\mu-1}|\ell|^{-\mu}$ when $\ell > r$ otherwise $p(\ell) = 0$. Two-dimensional fLms are simulated using two independent one-dimensional fLms for movements in the x- and y-directions. The results of numerical simulations do not depend sensitively upon the value of the lower bound N in the stochastic sums in (7) when $N \geqslant 1000$. For this reason, results are shown for $N = 1000$.

Persistence ($H > 1/2$) leads to a reduction in searching efficiencies, and as a consequence, fLm searches are less effective than Lévy walk searches ($H = 0.5$) (figures 5(*a*) and (*b*)). Nevertheless, the optimal value $\mu_{\text{opt}} \approx 2$ is robust with respect to H, i.e. robust with respect to long-range persistent 'memory effects'. This new result complements that of Viswanathan *et al* (2001) and Bartumeus *et al* (2005), who reported that the optimal value $\mu_{\text{opt}} \approx 2$ is
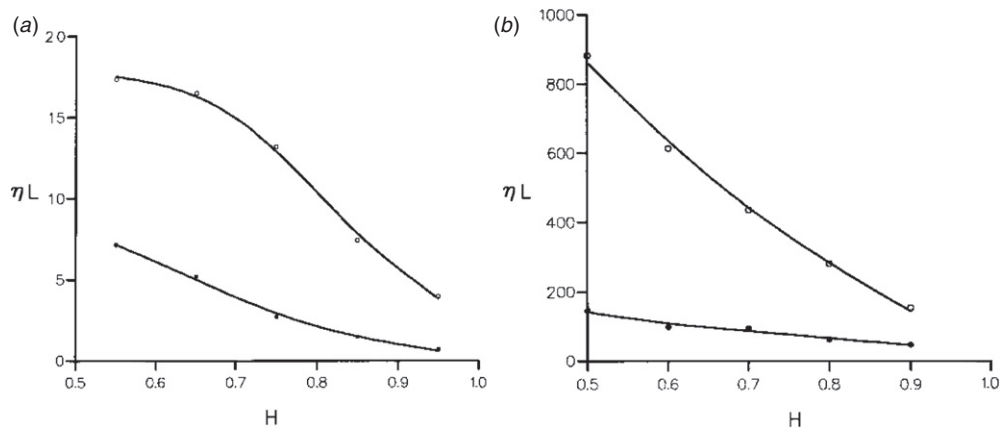
Figure 4. (*a*) The searching efficiency, η, of one-dimensional fBm searches as a function of the Hurst parameter, H. The searching efficiency is the reciprocal of the mean distance travelled before first arriving at a target. The distance between adjacent targets has been approximated by the mean distance, L, between adjacent targets. Targets are therefore located at $x = 0$ and $x = L$. Searching commences from $x = 10$ (i.e. in the immediate vicinity of a target) and ends when the searcher is within one unit of length of a target. In these units of length, increments in the fBm have unit variance. Searching efficiencies were determined from 250 independently simulated fBm. Simulation data are shown for $L = 10^3$ (●) and $L = 10^4$ (○). The lines are added to guide the eye. The emergence of Brownian motion ($H = 1/2$) as an optimal strategy is not sensitively dependent upon L when $L > 10^3$. (*b*) The searching efficiency, η, of two-dimensional fBm searches as a function of the Hurst parameter, H. Data is shown for searches in arena of size 2000^2 containing 100 (○) and 10 000 (●) randomly distributed targets. Searches commence in the immediate vicinity of a target that is closest to the centre of the arena. Statistical stationary averages are formed by ensemble averaging over 1000 searches each of length 1000. Searching efficiencies increase with decreasing H. The same trends are seen for other arena sizes and search lengths. The lines are added to guide the eye.

robust with respect to short-range 'memory effects'. It is evident from figure 5(*c*) that the inverse-square power-law distribution of move lengths that characterizes optimal $\mu = 2$ Lévy walks is also robust with respect to the inclusion of long-range persistence associated with small departures from $H = 0.5$.

4. Discussion

The movement patterns of a diverse range of animals (microzooplanktons, *Drosophila* fruit flies, honeybees, jackals and some marine predators) have scale-free characteristics (Atkinson *et al* 2002, Bartumeus *et al* 2003, Reynolds *et al* 2007a, 2007b, Reynolds and Frye 2007, Sims *et al* 2008). The results of these analyses provide necessarily but not sufficient conditions for the presence of Lévy walks, since it is possible that either fBm or fLm rather than Lévy walks underlie some or all of these movement patterns (figures 2, 3 and 5). The case for Lévy walks is bolstered by the fact that Lévy walks can optimize the success of random encounters in a wide range of search scenarios, and consequently represent robust solutions to general search problems. It is undermined, some what, by the fact that the scale-invariant and super-diffusive properties of Lévy walks which lead to advantages over Gaussian movements in random search scenarios (Bartumeus *et al* 2005) are shared by fBm and fLm (Mandelbrot and Van Ness 1968).
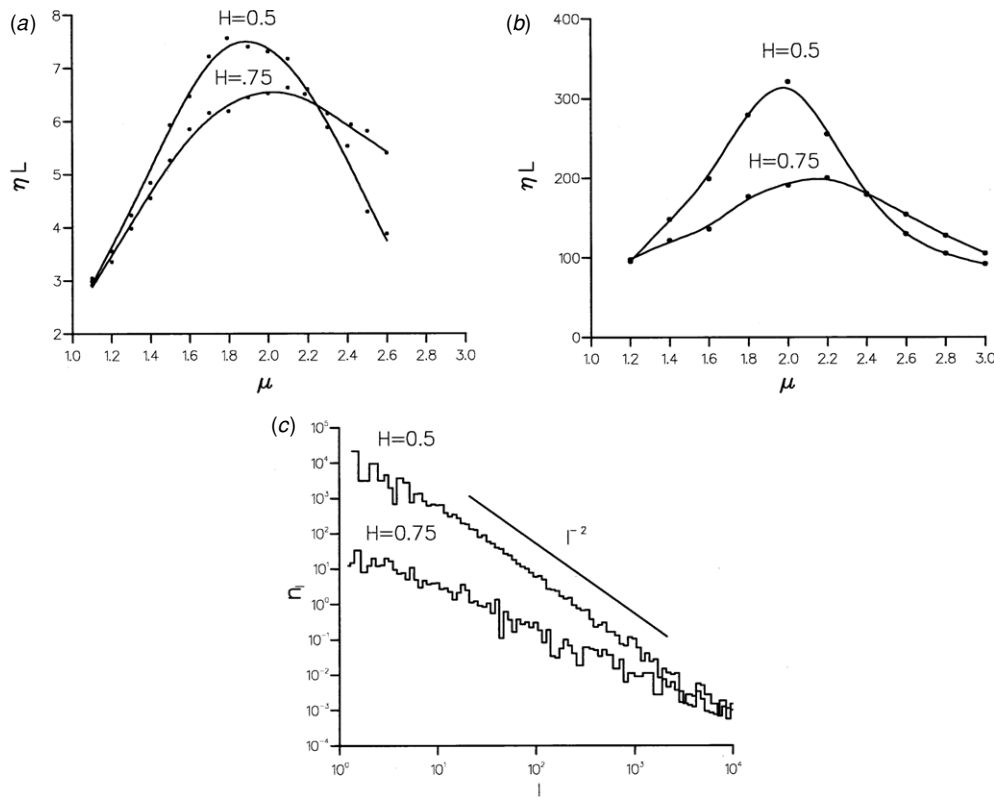
Figure 5. (*a*) The searching efficiency, η, of one-dimensional Lévy walk searches ($H = 0.5$) and fLm searches ($H = 0.75$) as a function the Lévy parameter, μ. The searching efficiency is the reciprocal of the mean distance travelled before first arriving at a target. The distance between adjacent targets has been approximated by the mean distance, L, between adjacent targets. Targets are located at $x = 0$ and $x = L$. Searching commences from $x = 10$ (i.e. in the immediate vicinity of a target) and ends when the searcher is within one unit of length of a target. Searching efficiencies were determined from 250 independently simulated fLm. Simulation data are shown for $L = 10^3$ (●). The lines are added to guide the eye. The optimality of $\mu \approx 2$ ($H = 0.5$) Lévy walks is not sensitively dependent upon L when $L > 10^3$. (*b*) The searching efficiency, η, of two-dimensional Lévy walk searches ($H = 0.5$) and fLm searches ($H = 0.75$) as a function the Lévy parameter, μ. Data is shown for searches in arena of size 2000^2 containing 10 000 randomly distributed targets. Searches commence in the immediate vicinity of a target that is closest to the centre of the arena. Statistical stationary averages are formed by ensemble averaging over 1000 searches each of length 1000. The same trends are seen for other arena sizes and search lengths. The lines are added to guide the eye. (*c*) The distribution of move lengths for optimal ($\mu = 2$) Lévy walk searches ($H = 0.5$) and for the best fLm search with $H = 0.75$. Inverse-square power-law scaling is indicated.

In this paper, it was shown that fBm and fLm searches are less efficient than Lévy walk searches (figures 4 and 5). For $H < 0.5$, this was because motions are sub-diffusive rather than super-diffusive. For $H > 0.5$, it is mainly because the directional persistence reduces the likelihood of revisiting previously visited territory and so increases the likelihood that nearby targets will be missed. These findings do not rule out the possibility that animals with innate scale-free searching patterns are executing fBm and fLm searches, but it does make Lévy walk searches the more likely possibility. Underlying this assertion is an evolutionary hypothesis, i.e. the notion that Lévy walks can be considered as adaptive strategies when the

empirical data are consistent with the specific conditions that led to advantageous or optimal Lévy walks (Bartumeus 2007). According to this evolutionary hypothesis, organizational levels (physiological, sensorial) that are plastic and acted upon selection pressure may tune up Lévy walk search strategies. Lévy walk search strategies may, for instance, arise from conspecific odour trail avoidance, a behaviour designed to avoid locations previously visited traversed by individuals of the same species (Reynolds 2007). Lévy search patterns in airborne and some marine animals, on the other hand, may have neurological underpinnings. Inverse-square power-law distributions of spontaneous neuron firing signals, that could provide the timing signals necessary for the execution of optimal Lévy searches have been observed in *in vitro* studies (Segev *et al* 2002, Beggs and Plenz 2003, Mazzoni *et al* 2007). This warrants further investigation because recent analytical and numerical studies suggest that inverse-square power-law distributions of spontaneous firing times are a robust, emergent property of neuronal systems (Levina *et al* 2007). Timing signals sufficient for the execution of optimal Lévy searches may therefore be ubiquitous. The problem is that living neural networks grown *in vitro* show network behaviour that is decidedly different from any neural network in the living animal (Eckmann *et al* 2007). The applicability of outcomes of *in vitro* studies to the understanding of scale-free movements must therefore be treated with a modicum of doubt.

Acknowledgments

References

Atkinson R P D, Rhodes C J, MacDonald D W and Anderson R M 2002 Scale-free dynamics in the movement patterns of jackals *Oikos* **98** 134–40
Bartumeus F 2007 Lévy processes in animal movement: an evolutionary hypothesis *Fractals* **15** 151–62
Bartumeus F 2009 Behavioral intermittence, Lévy patterns, and randomness in animal movement *Oikos* **118** 488–94
Bartumeus F, da Luz M G E, Viswanathan G M and Catalan J 2005 Animal search strategies: a quantitative random-walk analysis *Ecology* **86** 3078–87
Bartumeus F, Peters F, Pueyo S, Marrasé C and Catalan J 2003 Helical Levy walks: adjusting searching statistics to resource availability in microzooplankton *Proc. Natl Acad. Sci.* **100** 12771–5
Beggs J M and Plenz D 2003 Neuronal avalanches in neocortical circuits *J. Neurosci.* **23** 11167–77
Boyer D, Ramos-Fernandez G, Miramontes O, Mateos J L, Cocho G, Larralde H, Ramos H and Rojas F 2006 Scale-free foraging by primates emerges from their interaction with a complex environment *Proc. R. Soc.* B **273** 1743–50
Buchanan M 2008 The mathematical mirror to animal nature *Nature* **453** 714–6
Dieker A B 2004 Simulation of fractional Brownian motion *Master's thesis*, Vrije Universiteit Amsterdam, The Netherlands
Eckmann J P, Feinerman O, Gruendlinger L, Moses E, Soriano J and Tiusty T 2007 The physics of living neural networks *Phys. Rep.* **449** 54–76
Edwards A M *et al* 2007 Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer *Nature* **449** 1044–8
Frontier S 1987 Applications of fractal theory to ecology ed P Legendre and L Legendre *Developments in Numerical Ecology* (Berlin: Springer) 335–78
Kotulska M 2007 Natural fluctuations of an electropore show fractional Levy stable motion *Biophys. J.* **92** 2412–21
Levin S A 1992 The problem of scale in ecology *Ecology* **73** 113–31
Levina A, Herrmann J M and Geisel T 2007 Dynamical synapses causing self-organised criticality in neural networks *Nature Phys.* **3** 857–60

Mandelbrot B B and Van Ness J W 1968 Fractional Brownian motions, fractional noises and applications *SIAM Rev.* **10** 422–37

Mazzoni A, Broccard F D, Garcia-Perez E, Bonifazi P, Ruaro M E and Torre V 2007 On the dynamics of the spontaneous activity in neuronal networks *PloS One* **5** e439

Peng C K, Hausdorff J M, Mietus J E, Havlin S, Stanley H E and Goldberger A L 1993 Long-range anticorrelations and non-Gaussian behaviour in the heartbeat *Phys. Rev. Lett.* **70** 1343–6

Qian H, Raymond G M and Bassingthwaighte J B 1998 On two-dimensional fractional Brownian motion and fractional Brownian random field *J. Phys.* A **31** L527–L535

Ramos-Fernandez G, Mateos J L, Miramontes O, Cocho G, Larralde H and Ayala-Orozco B 2004 Levy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*) *Behav. Ecol. Sociobiol.* **55** 223–30

Reynolds A M 2007 Avoidance of conspecific odour trails results in scale-free movement patterns and the execution of an optimal searching strategy *Europhys. Lett.* **79** article 30006

Reynolds A M 2008a How many animals really do the Lévy walk? *Ecology* **89** 2347–51

Reynolds A M 2008b Deterministic walks with inverse-square power-law scaling are an emergent property of predators that use chemotaxis to locate randomly distributed prey *Phys. Rev.* E **78** article 011906

Reynolds A M and Bartumeus F 2009 Optimizing the success of random destructive searches: Lévy walks can outperform ballistic motions *J. Theor. Biol.* submitted

Reynolds A M and Frye M A 2007 Free-flight odour tracking in Drosophila is consistent with an optimal intermittent scale-free search *PLoS One* **2** e354

Reynolds A M, Smith A D, Menzel R, Greggers U, Reynolds D R and Riley J R 2007a Displaced honeybees perform optimal scale-free search flights *Ecology* **88** 1955–61

Reynolds A M, Smith A D, Reynolds D R, Carreck N L and Osborne J L 2007b Honeybees perform optimal scale-free searching flights when attempting to locate a food source *J. Exp. Biol.* **210** 3763–70

Segev R, Benveniste M, Hulata E, Cohen N, Palesvki A, Kapon E, Shapira K and Ben-Jacob E 2002 Long term behaviour of lithographically prepared *in vitro* neuronal networks *Phys. Rev. Lett.* **88** article 118102

Sims D W *et al* 2008 Scaling laws of marine predator search behaviour *Nature* **451** 1098–102

Turchin P 1998 *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants* (Sunderland, MA: Sinauer)

Viswanathan G M, Afanasyev V, Buldyrev S V, Havlin S, da Luz M G E, Raposo E P and Stanley H E 2001 Lévy flight search patterns of biological organisms *Physica* A **295** 85–8

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** 413–5

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** 911–4