Extending Lévy search theory from one to higher dimensions: Lévy walking favours the blind

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A diverse range of organisms, including T cells, E. coli, honeybees, sharks, turtles, bony fish, jellyfish, wandering albatrosses and even human hunter–gatherers have movement patterns that can be approximated by Lévy walks (LW; sometimes called Lévy flights in the biological and ecological literature). These observations lend support to the ‘Lévy flight foraging hypothesis’ which asserts that natural selection should have led to adaptations for Lévy flight foraging, because Lévy flights can optimize search efficiencies. The hypothesis stems from a rigorous theory of one-dimensional searching and from simulation data for two-dimensional searching. The potential effectiveness of three-dimensional Lévy searches has not been examined but is central to a proper understanding of marine predators and T cells which have provided the most compelling empirical evidence for LW. Here I extend Lévy search theory from one to three dimensions. The new theory predicts that three-dimensional Lévy searching can be advantageous but only when targets are large compared with the perceptual range of the searchers, i.e. only when foragers are effectively blind and need to come into contact with a target to establish its presence. This may explain why effective blindness is a common factor among three-dimensional Lévy walkers.

1. Introduction

Lévy walks (LW; sometimes called Lévy flights in the biological and ecological literature) comprise clusters of many short steps with longer steps between them. This pattern is repeated across all scales with the resultant clusters creating fractal patterns that have no
characteristic scale. Because there is no characteristic scale, the overall length of an LW is dominated by the longest step and the step-length variance grows over time but nonetheless remains finite even when unbounded by biological and ecological considerations [1]. The hallmark of an LW is a step-length distribution with a heavy power-law tail: \( p(l) \sim l^{-\mu} \) with \( 1 < \mu \leq 3 \), where \( l \) is the step-length and \( \mu \) is the power-law (Lévy) exponent. Viswanathan et al. [2] showed that the fractal and 'superdiffusive' properties of LW can be advantageous when searching for randomly and sparsely distributed resources. This realization has led to the 'Lévy flight foraging hypothesis' [3] which asserts that since LW can optimize search efficiencies, natural selection should have led to adaptations for Lévy flight foraging. The hypothesis found fledging support in an analysis of the flight patterns of the wandering albatross \( Diomedea exulans \) [4]. This paper led to an explosion of interest in LW as models of movement pattern data. However, many of these early studies, including the seminal study of Viswanathan et al. [4], had wrongly attributed LW to some species because inappropriate statistical techniques had been used and because movement pattern data had been misinterpreted [5, 6].

Edwards et al. [5] introduced robust and accurate statistical methods into LW research. Many subsequent studies have used these methods and the results have provided seemingly compelling evidence for the Lévy flight foraging hypothesis. For example, movement patterns that can be approximated as LW have been identified in: extinct organisms that once occupied ancient sea beds, bacteria, human T cells, honeybees, sharks (and other marine predators), jellyfish, the wandering albatross (once more) and even in human hunter–gatherers [7–17]. It has also become apparent that some organisms, notable mussels (\( Mytilus edulis \), mud snails (\( Hydrobia ulvae \)) and the Australian desert ant \( Melophorus bagoti \) approximate LW as multiphasic walks described by multi-exponential step-length distributions [18–23]. Nonetheless, the theory of Viswanathan et al. [2] only applies when searching is one-dimensional. Its generality has been examined with the aid of numerical simulations because extending the theory from one to higher dimensions appeared to be analytically intractable. Data from numerical simulations suggest that LW can also be advantageous when searching is two-dimensional [24–29] but not necessarily so [30]. The potential effectiveness of three-dimensional LW searches has, however, received scant attention in the literature, possibly because the computational costs of such numerical simulations can be prohibitively high. Perhaps the earliest such study of three-dimensional LW searching was made by Viswanathan et al. [31]. A more extensive study is that of Preston et al. [32], who reported that three-dimensional LW can be evolutionarily favourable in some situations. Nonetheless, the current state of affairs is limiting for two reasons. First, because a robust understanding of three-dimensional LW searching is central to a proper understanding of marine predators and T cells which have provided the most compelling empirical evidence for the Lévy flight foraging hypothesis [11, 12, 33]. Second, because there is no guarantee that the expectations of one-dimensional Lévy search theory will carry over to three dimensions. They do not, after all, carry over in entirety to two dimensions and consequently dimensionality can be an important search parameter [26, 34].

Here I show how Lévy search theory can be extended from one to three dimensions. In the next section, I review the original one-dimensional Lévy search theory of Viswanathan et al. [2]. In §3, I show how this theory can be extended to three dimensions and determine the conditions under which three-dimensional LW searching can be advantageous. This is followed by a Discussion. In appendix A, I develop an approximate theory of two-dimensional Lévy searching and show that it is accurate when targets are large compared with the perceptual range of the searcher.

2. The one-dimensional Lévy search theory of Viswanathan et al.

Viswanathan et al. [2] considered an idealized model of an LW search in which a searcher moves on a straight line towards the nearest target, if the target lies within the searchers’ ‘direct perceptual range’, \( r_s \), otherwise it chooses a direction of travel at random and a distance, \( l \), drawn from a power-law distribution, \( P(l) = (\mu - 1) r_s^{\mu - 1} l^{-\mu} \) for \( l \geq r_s \) and \( P(l) = 0 \) for \( l < r_s \). It then moves
incrementally towards the new location while constantly seeking for targets within a radius, \( r_\ast \) (or within a distance \( r_\ast \) if searching is one-dimensional). If a target is not 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. [2] solved the one-dimensional form of this model analytically. In their theory, which is reviewed by Viswanathan et al. [35], the mean length of a search path was given by \( L = N \langle l \rangle \), where \( N \) is the average number of steps in the search path, and \( \langle l \rangle \) is the mean step-length. The mean step-length is given by

\[
\langle l \rangle \approx \int_{r_\ast}^{\infty} \lambda - \mu \, l \, dl + \int_{r_\ast}^{\infty} \lambda - \mu \, l \, dl.
\]

The second term on the right-hand size is a ‘mean-field’ approximation, because it assumes that the distances between consecutive targets are all equal to the mean free path length, \( \lambda \). The average number of steps in such a search path

\[
N \propto \left[ \frac{x(\lambda - x)}{r_\ast^2} \right]^{(\mu - 1)/2},
\]

where \( x \) is the initial position of the searcher relative to the nearest target [36]. This is essentially the number of steps taken by a Lévy flight before being ‘absorbed’ at either \( x = 0 \) or \( x = L \). Using this simple theory, Viswanathan et al. [2] showed that the mean length of a search path is minimized when \( \mu \approx 2 \), if searching begins sufficiently close to a target. This initial condition is effectively a surrogate for searching for patchily distributed targets, i.e. searching for targets that tend to occur in clusters, or searching for isolated targets that are not depleted or rejected once visited but can instead be profitably revisited. Under these conditions, LW searches with \( \mu \approx 2 \) outperform other LW searches, ballistic (straight line) movements (which arise as \( \mu \to 1 \)) and Brownian (Gaussian) searches, and in this sense are optimal. This theoretical result is of considerable interest because organisms performing Lévy-like walks are typically characterised by \( \mu \approx 2 \) [7,9–12,18,33].

3. Extending Lévy walk search theory from one to three dimensions

The challenge with extending LW search theory from one to three dimensions is to find the average number of steps in the search path because the mean step-length is independent of dimension, and can always be approximated by equation (2.1). This challenge cannot be tackled following the approach of Buldyrev et al. [36], which is strictly limited in scope to one dimension. Nonetheless, Buldyrev et al.’s [36] result, equation (2.2), suggests that expectations for LW can be obtained directly from the expectations for Brownian walks, by a simple rescaling, i.e. by positing that \( N_{\text{LW}} = N_{\text{BW}}^{(\mu - 1)/2} \). Here, I show that this ansatz does, indeed, characterize the number of steps in three-dimensional LW searches. This is achieved in two steps. First, an exact expression is found for the average number of steps in a three-dimensional Brownian search. Then the validity of the resulting ansatz for LW searches is established by making detailed comparisons with simulation data.

Three-dimensional isotropic Brownian motion is governed by the three-dimensional diffusion equation which in spherical coordinates is given by

\[
\frac{\partial p}{\partial t} = \frac{D}{r^2} \frac{\partial}{\partial r} \left( r^2 \frac{\partial p}{\partial r} \right),
\]
where \( p(r, t) \) is the probability density that a Brownian walker is a distance \( r \) from the origin at time \( t \). The appropriate solution to equation (3.1) for \( p(r, t) \) is given by

\[
p(r, t) = \frac{2}{\pi r_0 R} \sum_{n=1}^{\infty} \exp \left( -\frac{D \pi^2 n^2 t}{(R - d)^2} \right) \sin \left( \frac{\pi n(r - d)}{R - d} \right) \sin \left( \frac{\pi n(r_0 - d)}{R - d} \right).
\] (3.2)

This solution satisfies the initial condition that \( r = r_0 \) when \( t = 0 \) and satisfies the boundary conditions that \( p(d, t) = 0 \) and \( p(R, t) = 0 \), i.e. the conditions that a search ends when the walker comes within a distance \( d \) of the origin or has travelled a distance \( R \) from the origin equal to the mean free path length which in the one-dimensional theory was denoted by \( \lambda \). The first boundary condition corresponds to the presence of a target with radius \( d \) at the origin. The second boundary condition is effectively a mean-field approximation, because it assumes that the distances between adjacent targets are all equal to the mean free path length, \( R \). This presupposes that individual targets (or patches of targets when targets are patchily distributed) are randomly and uniformly distributed in space. The boundary conditions are appropriate when searching begins in the vicinity of one target but distant from all other targets. They are not appropriate when searching begins mid-way between adjacent targets. The boundary conditions \( p(d, t) = 0 \) and \( p(R, t) = 0 \) are central to the theory and cannot be imposed in a Cartesian coordinate system. They mirror those used by Viswanathan et al. [2].

The probability, \( q(t) \), that a search is still continuing at time \( t \) is given by

\[
q(t) = 4\pi \int_0^R p(r, t)r^2 dr = \frac{8}{\pi r_0} \sum_{n=1}^{\infty} (-1)^n \exp \left( -\frac{D \pi^2 n^2 t}{(R - d)^2} \right) \sin \left( \frac{\pi n(r_0 - d)}{R - d} \right).
\] (3.3)

The probability, \( P(t) \), that a search ends at time \( t \), i.e. the probability that a target is found at time \( t \), is therefore given by

\[
P(t) = -\frac{dq(t)}{dt} = \frac{8 \pi D}{r_0 (R - d)} \sum_{n=1}^{\infty} n (-1)^n \exp \left( -\frac{D \pi^2 n^2 t}{(R - d)^2} \right) \sin \left( \frac{\pi n(r_0 - d)}{R - d} \right).
\] (3.4)

Consequently, the average duration of the Brownian search path is [37]

\[
\langle t \rangle = \int_0^\infty P(t) dt = \frac{8(R - d)^3}{\pi^3 D r_0} \sum_{n=0}^{\infty} (-1)^n \frac{\pi n(r_0 - d)}{n^3} \sin \left( \frac{\pi n(r_0 - d)}{R - d} \right)
\]

\[
= \frac{2}{3D r_0} (r_0 - d)(R - r_0)(R + r_0 - 2d),
\] (3.5)

Here it is worth noting that Brownian searches cannot be optimized with respect to diffusivity, because the average length of a search \( L \sim D\langle t \rangle \) is independent of \( D \). It follows from equation (3.5) that the average number of steps in the Brownian search path is given by

\[
N \propto \frac{1}{r_0^2} (r_0 - d)(R - r_0)(R + r_0 - 2d),
\] (3.6)

which suggests that the average number of steps in a three-dimensional LW search will be given by

\[
N \propto \left[ \frac{(r_0 - d)(R - r_0)(R + r_0 - 2d)}{r_0^2} \right]^{(\mu - 1)/2}
\] (3.7)

mirroring the scaling obtained by Buldyrev et al. [36] for one-dimensional LW searches. The ansatz, equation (3.7), is in strikingly good agreement with simulation data for three-dimensional LW (figure 1).

In the numerical simulations, which mirror the above theory, LW starting from within a sphere of radius \( R \) where tracked until they first encountered a target of radius \( d \) located at the origin, or first left the sphere; a process mimicking the isotropic mean-field description of searching.

When target sizes are comparable or smaller than the searchers’ perceptual range, a tedious but straightforward calculation shows that the average length of a three-dimensional search path,
Figure 1. Comparison of the ansatz, equation (3.7) (solid lines) and simulation data for the number, $N$, of steps in a three-dimensional Brownian walk (BW) search, and three-dimensional LW searches with Lévy exponent $\mu = 2.5, 2$ and 1.5 (circles). Here $r_0$ is the initial position of the searcher relative to the centre of the nearest target, $d$ is the target radius and $R = 100$ in arbitrary space units is the mean free path. The perceptual range of thesearchers $r_*=0.1$.

Figure 2. Predicted search efficiencies (reciprocals of the average length of a search path) as a function of the Lévy exponent, $\mu$, for three-dimensional LW searches for targets with radius $d = 1$ (a) and $d = 100$ (b) and with a mean free path $R = 10^4$ in arbitrary space units. Searches begin a distance $r_0 = d + r_*$ from a target, where $r_*$ is the perceptual range of the searcher. Predictions are shown for $r_* = 1, 0.1, 0.01$ and 0.001. Shown for comparison (c) is the case when $d = 100$ and $R = 10^6$ which together with (a,b) shows that the target-size effect is more pronounced when $d/R$ remains constant as $d$ decreases.
$L = N\langle l \rangle$, as determined by equations (2.1) and (3.7), is minimal when movements are effectively ballistic, i.e. when $\mu \to 1$. LW per se having $\mu > 1$ are optimal only if the targets are large compared with the searchers’ perceptual range, as illustrated in figure 2. LW with $\mu \approx 2$ become optimal as $r_0/d \to 0$ so that searching begins in the immediate vicinity of a target. This is not an unrealistic scenario. If, for example, the targets are mobile and occasionally evade capture once detected then each new search for the target will begin in the immediate vicinity of a target. The scenario would also arrive if the searchers are effectively blind and so need to come into contact with a target to re-establish its presence. This ‘optimality’ of LW with $\mu \approx 2$ is robust and does not change when the calculations are taken beyond the mean-field approximation (see appendix A). The ramifications of this important finding for the interpretation of three-dimensional movement data in terms of LW are discussed in the next section.

4. Discussion

The LW search theory of Viswanathan et al. [2] led to the ‘Lévy flight foraging hypothesis’ [3] and to the expectation that many predators will have movement patterns that can be approximated by LW with $\mu \approx 2$. The hypothesis is now amply supported by empirical observations [7,9–18]. Theoretical developments have, however, not kept pace with empirical studies. The Lévy flight foraging hypothesis has rested upon Viswanathan et al.’s [2] theory of one-dimensional searching and on data from numerical simulations of two-dimensional searching [24–28]. Largely absent from the literature has been an understanding of three-dimensional LW searching. Here this shortcoming was addressed by establishing a theory of three-dimensional LW searching. The new theory accounts explicitly for key dependencies, i.e. for the relative importance of the searchers’ perceptual range, target spacing and target size (which is not relevant in one dimension). It can also be used to examine the important case of searching near the edge of extinction where targets are very sparsely distributed; a case which will be difficult to study in numerical simulations because obtaining reliable estimates of search statistics will require very long run times.

The key predictions of this new theory are that: (i) ballistic movements are typically optimal when the target size < perceptual range; (ii) LW per se are optimal when the target size is much larger than the perceptual range; (iii) LW with Lévy exponent $\mu \approx 2$, of the kind supported by fits to empirical data [11,12], are optimal when the mean target spacing $\gg$ target size $\gg$ perceptual range.

The new theory shows that the theoretical expectations of Viswanathan et al. [2] for one-dimensional searching carry over to three dimensions but only when targets are large compared with the perceptual range of the searchers. This target-size effect provides new insights into LW searching. The target-size effect suggests that three-dimensional LW searching is only advantageous for foragers that are effectively blind. In this regard, it is interesting to note that the three-dimensional movement patterns of T cells are consistent with their using an LW searching strategy with Lévy exponent $\mu \approx 2$ to locate pathogens, and that target detection in T cells is believed to occur on contact, or perhaps within a short distance of a pathogen [12]. This may also be true of some bacteria. *Escherichia coli*, for instance, use chemotaxis to locate food but, in the absence of external stimuli, noise in the chemotactic pathways that regulate their ‘run-and-tumble’ locomotion, leads to LW movement patterns [7,8]. The new predictions are also consistent with the suggestion made by Sims et al. [11] that fully aquatic marine vertebrates, which feed on ephemeral resources like zooplankton and small pelagic fish, are essentially blind hunters at the spatial and temporal scales over which they typically forage, because their sensory detection ranges are limited by the seawater medium and experience extreme variability in food supply. Effective blindness may, in fact, be common. Karevia [38, p. 192], for example, noted that ‘Although their survival depends on finding suitable host, many [insect] herbivores bumblingly search in a haphazard fashion and must literally bump into a host plant before they recognize it as food’.

The formulation of a robust theory of two-dimensional LW searching remains challenging. An approximate theory valid for large targets is presented in appendix A. This theory captures
well simulation data, and suggests that LW searching is robustly optimal when the targets of the search are sufficiently large compared with the perceptual range of the searcher. This rider may explain why two-dimensional LW searching has not been widely observed. Here it is noteworthy that the most compelling evidence for freely roaming two-dimensional Lévy-like searching comes from observations of foraging mud snails [23], and also from mussel movements made during the formation of mussel patterned beds when individuals are actively searching for conspecifics [18]. Mud snails and mussels are essentially blind and need to make contact with conspecifics or food patches to establish their presence [18,23]. Mussels approximate LW with Lévy exponent $\mu \approx 2$ by adapting an intrinsic multiphasic walk; a process which requires fine tuning of the various modes and so selection pressures for advantageous searching [21]. Mud snails also approximate LW as multiphasic walks [23]. This contrasts with the occurrence of LW in marine predators, T cells and bacteria which may emerge spontaneously and naturally from innate behaviours and innocuous responses to the environment but because they are advantageous there could be selection for keeping them [39].

Predictions from the theory of two-dimensional LW searching are consistent with reports of LW in solitary fallow deer (*Dama dama*) and the absence of such movement patterns in groups of deer with ‘many eyes’ that are better able to detect small patches [40]. The predictions from this theory are also consistent with data from numerical simulations [24–28] and support the Lévy flight foraging hypothesis. Nonetheless, accounting correctly for small targets remains a challenge for future work. Such a theory could potentially bring new insights into the occurrence of LW in human hunter–gatherers and ancient marine organisms [16,17]. To date, the effectiveness of two-dimensional LW searching for small targets has been examined in numerical simulations but such work cannot be regarded as being conclusive.

Finally, it would be interesting to extend the new theory further to account for searchers adapting to conditions found on the search by switching from an extensive LW mode of searching to a more intensive mode of searching upon detection of a target. Such modelling could also account for the risk of predation [34]. This would be a significant development because a growing body of literature has revealed that (i) the cost of predation can be large and comprise the forager’s largest foraging cost, (ii) seemingly small changes in habitat or microhabitat characteristics can lead to large changes in the cost of predation, and (iii) a forager’s cost of predation rises with risk of mortality and the forager’s energy state [41–44]. The theory can also be extended to calculate the variability in foraging rates, and so determine which search strategies minimize the likelihood that a predator will go for long periods without food.

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Appendix A

(a) Extending Lévy walk search theory from one to two dimensions

Here, it is shown how the methodology adopted in §3 can be used to formulate an approximate theory of two-dimensional LW searching. The starting point is the two-dimensional diffusion equation

$$\frac{\partial p}{\partial t} = D \frac{1}{r} \frac{\partial}{\partial r} \left( r \frac{\partial p}{\partial r} \right),$$

those solutions can be expressed in terms of Bessel functions of the first- and second-kind, $J_0(x)$ and $Y_0(x)$. The resulting equations do not appear to be amendable to exact analysis. Progress can,
The appropriate solution to equation (A 1) is then be approximated as follows:

\[
p(r, t) = \sum_{n=1}^{\infty} \lambda_{n}^{2} \left[ J_{0}(\lambda_{n} r) Y_{0}(\lambda_{n} R) - J_{0}(\lambda_{n} R) Y_{0}(\lambda_{n} r) \right] \exp(-D \lambda_{n}^{2} t)
\]

\[
\approx \frac{4}{\pi^{2} R (r_{0})^{1/2}} \sum_{n=1}^{\infty} \left[ \cos \left( \lambda_{n} r - \frac{\pi}{4} \right) \sin \left( \lambda_{n} R - \frac{\pi}{4} \right) - \cos \left( \lambda_{n} R - \frac{\pi}{4} \right) \sin \left( \lambda_{n} r - \frac{\pi}{4} \right) \right]
\times \left[ \cos \left( \lambda_{n} r_{0} - \frac{\pi}{4} \right) \sin \left( \lambda_{n} R - \frac{\pi}{4} \right) - \cos \left( \lambda_{n} R - \frac{\pi}{4} \right) \sin \left( \lambda_{n} r_{0} - \frac{\pi}{4} \right) \right] \exp(-D \lambda_{n}^{2} t)
\]

\[
= \frac{4}{\pi^{2} R (r_{0})^{1/2}} \sum_{n=1}^{\infty} \sin \left( \lambda_{n} (R - r) \right) \sin \left[ \lambda_{n} (R - r_{0}) \right] \exp(-D \lambda_{n}^{2} t).
\]

This approximate solution satisfies the initial condition that \( r = r_{0} \) when \( t = 0 \) and satisfies the boundary conditions that \( p(d, t) = 0 \) and \( p(R, t) = 0 \) when \( \lambda_{n} = n \pi / (R - d) \). Recall that these boundary conditions dictate that a search ends when the walker comes within a distance \( d \) of the origin or has travelled a distance \( R \) from the origin equal to the mean free path length. Equation (A 3) is the approximate two-dimensional analogue of equation (3.2). The approximation is strictly valid only when the minimum value of \( \lambda_{n} r \gg 1/4 \), i.e. only when targets are large so that \( \pi d / (R - d) \gg 1/4 \).

The probability, \( q(t) \), that a search is still continuing at time \( t \) is given by

\[
q(t) = 2 \pi \int_{d}^{R} p(r, t) r \, dr \approx \frac{8}{\pi (r_{0} R)^{1/2}} \sum_{n=1}^{\infty} \lambda_{n}^{-1} \left[ 1 - (-1)^{n} \left( \frac{d}{R} \right)^{1/2} \right] \sin \left[ \lambda_{n} (R - r_{0}) \right] \exp(-D \lambda_{n}^{2} t).
\]

It follows from equation (A 4) that the probability, \( P(t) \), that a search ends at time \( t \), i.e. the probability that a target is found at time \( t \), is given by

\[
P(t) = -\frac{dq(t)}{dt} = \frac{8D}{\pi (r_{0} R)^{1/2}} \sum_{n=1}^{\infty} \lambda_{n} \left[ 1 - (-1)^{n} \left( \frac{d}{R} \right)^{1/2} \right] \sin \left[ \lambda_{n} (R - r_{0}) \right] \exp(-D \lambda_{n}^{2} t).
\]

Consequently, the average duration of a two-dimensional Brownian search path is [37]

\[
\langle t \rangle = \int_{0}^{\infty} P(t) \, dt \approx \frac{8(R - d)^{3}}{\pi^{4} D (r_{0} R)^{1/2}} \sum_{n=0}^{\infty} n^{-3} \left[ 1 - (-1)^{n} \left( \frac{d}{R} \right)^{1/2} \right] \sin \left( \frac{\pi n (r_{0} - d)}{R - d} \right)
\]

\[
= \frac{2}{3 \pi D (r_{0} R)^{1/2}} (r_{0} - d) (R - r_{0}) \left( R + r_{0} - 2d + \left( \frac{d}{R} \right)^{1/2} (2R - d - r_{0}) \right).
\]

This closely resembles the exact result for three-dimensional Brownian search, equation (3.7). Equation (A 6) is in very good agreement with the results of numerical simulations (figure 3) when targets as large \( (d/R \geq 0.1) \). As anticipated its accuracy increases with increasing target size because the accuracy of the approximation introduced at equation (A 2) improves with increasing target size.

The natural generalization of equation (A 6) to the number of steps in two-dimensional LW searches

\[
N \propto \langle t \rangle^{(\mu - 1)/2},
\]

accurately captures simulation data (figure 4). A tedious but straightforward calculation shows that the average length of a two-dimensional LW search path, \( L = N \langle t \rangle \), as determined by equations (2.1) and (A 7) is minimal when \( \mu \approx 2 \) if searches begin sufficiently close to a target.
This strong dependency on initial position has been noted previously, albeit in numerical simulations [34], and is seen in figure 5 to decrease with increasing target size. In accordance with the results of numerical simulations [24–28], LW with \( \mu \approx 2 \) are also predicted to be optimal when searching for small targets even though the theory is imprecise in other regards in this target-size range.

(b) Going beyond the mean-field approximation

Previously, the three-dimensional diffusion equation, equation (3.1), was solved (equation (3.2)) under the assumption that distances between adjacent targets are all equal to the mean free path length, \( R \). An alternative solution to equation (3.1) which takes partial account of variations in the distances between adjacent targets is given by

\[
p(r, t) = \frac{2}{\pi r_0 R} \sum_{n=0}^{\infty} \exp(-Dk_n^2t) \sin(k_n(r - d)) \sin(k_n(r_0 - d)),
\]

where \( k_n = (n + 1/2)\pi/(R - d) \). This solution satisfies the initial condition that \( r = r_0 \) when \( t = 0 \) and satisfies the boundary conditions that \( p(d, t) = 0 \) and \( \partial p(R, t)/\partial R = 0 \). The first boundary condition corresponds to the presence of a target with radius \( d \) at the origin and ensures that a search ends when that target is found. The second boundary condition assumes that the target distribution is statistically homogeneous (with periodicity \( R \)), i.e. assumes that the average distance between adjacent targets is \( R \). By following the steps that led from equation (3.2) to (3.5), it is readily found that the average duration of these Brownian search paths is given by

\[
\langle t \rangle = \frac{2}{r_0 R D} (R - d)(r_0 - d) \left[ (R - d)^2 - \frac{1}{3}(r_0 - d)^2 + d(2R - d - r_0) \right],
\]

which closely resembles the mean-field result (equation (3.5)). The analogue of the mean-field ansatz, equation (3.7), for the number of steps in three-dimensional LW searches is

\[
N = \left[ \frac{2}{r_*^2 r_0 R} (R - d)(r_0 - d) \left[ (R - d)^2 - \frac{1}{3}(r_0 - d)^2 + d(2R - d - r_0) \right] \right]^{(\mu - 1)/2}.
\]

The effective distribution of step lengths is

\[
p(l) = P(l)e^{-l/R} + R^{-1}e^{-l/R} \int_l^\infty P(x)dx \\
\equiv (\mu - 1)r_*^{\mu - 1}l^{-\mu}e^{-l/R} + R^{-1}r_*^{\mu - 1}l^{1-\mu}e^{-l/R}.
\]
Figure 4. Comparison of the ansatz, equation (A7) (solid lines) and simulation data for the number, $N$, of steps in two-dimensional LW searches with Lévy exponent $\mu = 2.0$ (a) and 1.5 (b) (circles). Here, $r_0$ is the initial position of the searcher relative to the centre of the nearest target, $d$ is the target radius and $R = 100$ in arbitrary space unit is the mean free path.

Figure 5. (a) Predictions for the Lévy exponent, $\mu$, characterizing the optimal two-dimensional LW search as a function of the initial position $r_0$. Predictions for obtained using equations (2.1) and (A7) for targets with radius $d = 100$ and 300 and with a mean free path $R = 1000$ in arbitrary space units. (b) Predicted search efficiencies (reciprocals of the average length of a search path $R/L$) as a function of the Lévy exponent, $\mu$, for two-dimensional LW searches for targets of radius $d = 100$ with a mean free path $R = 1000$. 
Figure 6. Predicted search efficiencies (reciprocals of the average length of a search path \( R/L \)) as a function of the Lévy exponent, \( \mu \) for three-dimensional LW searches for targets with radius \( d = 1, 100 \) and \( 1000 \) and with a mean spacing \( R = 10^4 \) in arbitrary space units. Searches begin a distance \( r_0 = d + r_* \) from a target, where \( r_* = 1 \) is the perceptual range of the searcher.

The first term is the probability of making a step length \( l \) and not encountering a target, the second term is the probability of encountering a target during a step, after travelling a distance \( l \). Here as before \( P(l) \) is the intrinsic step-length distribution. Equation (A 11) goes beyond the mean-field approximation, equation (2.1), by allowing for the occurrence of arbitrarily long-steps. It follows from equation (A 11) that the average length step

\[
\langle l \rangle = \int_{r_*}^{\infty} l P(l) \, dl = r_*^{\mu-1} R^{2-\mu} \left[ (\mu - 1) \Gamma(2 - \mu, \frac{r_*}{R}) + \Gamma(3 - \mu, \frac{r_*}{R}) \right],
\]

where \( \Gamma(a, b) \) is an incomplete gamma function. The average length of a search path can be obtained by combining equations (A 10) and (A 12) to give \( L = N(l) \). Numerical evaluation of this expression reveals that LW with \( \mu \approx 2 \) are optimal but only when searchers are effectively blind, mirroring the results obtained with the mean-field theory (figure 6).

References


34. Reynolds AM. 2010 Balancing the competing demands of harvesting and safety from predation: Lévy walk searches outperform composite Brownian walk searches but only when foraging under the risk of predation. *Physica A* 389, 4740–4746. (doi:10.1016/j.physa.2010.06.027)