Beyond Optimal Searching: Recent Developments in the Modelling of Animal Movement Patterns as Lévy Walks

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Abstract Lévy walks first entered the biological literature when Shlesinger and Klafter (Growth and Form, Martinus Nijhof Publishers, Amsterdam, 1986, pp 279–283) proposed that they can be observed in the movement patterns of foraging ants. The fractal and superdiffusive properties of Lévy walks can be advantageous when searching for randomly and sparsely distributed resources, prompting the suggestion that Lévy walks represent an evolutionary optimal searching strategy. The suggestion is supported by a plethora of empirical studies which have revealed that many organisms (a diverse range of marine predator, honeybees, *Escherichia coli*) have movement patterns that can approximated by Lévy walks. Nonetheless, Lévy walks with their strange fractal geometry appear alien to biology and their relevance to biology has been hotly debated. Here I describe some of my own recent contributions to Lévy walk research. This research has sought to identify biologically plausible mechanisms by which organisms can execute Lévy walks and to demonstrate that these movement patterns have a utility beyond the understanding and prediction of optimal searching patterns. This work has made apparent that Lévy walks do not stand outside of the now well-established correlated random walk paradigm but are instead natural consequences of it. I also describe some recent advances in Lévy walk search theory.

> Where then but there see another.
> Bit by bit an old man and child.
> In the dim void bit by bit an old man and child.
> Any other would do as ill.
> Samuel Beckett

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1 Introduction

In 1828 the Scottish botanist Robert Brown reported that minuscule pollen particles suspended in water have seemingly random movements. Einstein's subsequent 1905–6 [29, 30] mathematical description of these random "Brownian" movement patterns has been hugely successful and now lies at the heart of the "correlated random walk paradigm"—the dominant conceptual framework for modelling animal movement patterns [104]. Then just over two decades ago, physicists suggested that some animals have Lévy walk movement patterns. Lévy walks, named after the French mathematician Paul Lévy, arose in a purely mathematical context in the first half of the last century [54]. Lévy walks first entered the biological literature when [94] proposed that they can be observed in the movement patterns of foraging ants. Lévy walks comprise clusters of short step lengths with longer movements between them. This pattern is repeated across all scales with the resultant clusters creating fractal patterns that have no characteristic scale and such that the distribution of move lengths has an inverse power-law tail, $p_l(l) \sim l^{-\mu}$ where $1 < \mu < 3$. Over much iteration, a Lévy walk will be distributed much further from its starting position than a Brownian walk of the same length. The fractal and "superdiffusive" properties of Lévy walks can be advantageous when searching for randomly and sparsely distributed resources [108], prompting the suggestion that Lévy walks represent an evolutionary optimal searching strategy [9, 11]. Nonetheless, Lévy walks with their strange fractal geometry appear alien to biology and their relevance to biology has been hotly debated [18, 40, 101], Auger-Méthé et al. (2011). It seemed to some that physicists and mathematicians had lost touch with biology, and especially so after it became apparent that early empirical analyses of the flight patterns of the wandering albatross [107] (Fig. 1), which had provided the impetus for nearly two decades of research into Lévy walks, were flawed [27].

But the humble pollen has other tales to tell (which show that Lévy movements are pertinent even in the simplest of situations). Occasionally, one of Robert Brown's pollen grains would have come into contact with the bottom of the dish. It is readily seen that the distribution of straight-line distances between successive contact points has an inverse-square power-law tail. The contact points thus form a "Lévy flight" pattern with $\mu = 2$, a random jump process in which the distribution of jump lengths has an inverse-square power-law tail. The distribution of time intervals between consecutive contacts has an inverse power-law tail, $p(t) \propto t^{-3/2}$, by virtue of the Sparre Andersen Theorem [99, 100]. Net horizontal displacements made in a time interval, t, are Gaussian distributed with mean zero and variance $\sigma^2 = 2D't$ where D' is the bulk diffusivity. Taken together these two characteristics imply that the distribution, of distances $p_l(l) \propto \int\limits_0^\infty \frac{e^{-l^2/4D't}}{4\pi D't} t^{-3/2} dt \propto l^{-2}$, between consecutive contact points has an inverse-square power-law tail. Observations of the pollen grains made at the bottom of the dish can therefore be modelled as Lévy flights with $\mu = 2$ (Fig. 2). Analogous behaviour has been predicted for bulk-mediated effective surface diffusion at liquid surfaces [20]. The Lévy flights have fractal dimension $D = \mu - 1$ [95]. The key ingredients of a Lévy walk movement pattern,

Fig. 1 Lévy walk research owes much to the wandering albatross. Early analyses of flight pattern data were flawed but fruitful and continue to provoke and inspire. Photograph courtesy of Corbis

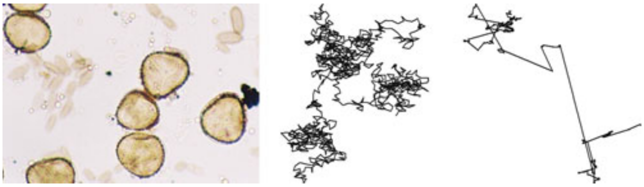

Fig. 2 The humble pollen does both the Brownian walk and the Lévy flight. Bracken pollen (*left*). An example of a simulated Brownian walk representative of pollen movements within a fluid (*middle*). An example of a Lévy flight representative of pollen movements across the bottom of the Petridish. Photograph by Jon S. West, Rothamsted Research

a power-law distribution of move lengths and fractal scaling, are thus lurking within Brownian walks and so are present within the correlated random walk paradigm, despite qualms about the biological plausibility of such properties [13, 103]. Lévy flights also abound once the pollen grains are liberated from watery confines and are at the mercy of the wind [4, 79, 93]. Although these airborne movements are clearly divorced from searching they are not without consequence as they result in a patchy, fractal-like, spatial population structures very different from the structure of a homogeneous front produced by Brownian movements [21, 53, 92, 112]. Here I take up this theme and describe some of my own recent contributions to Lévy walk research, made since my last review with Christopher Rhodes [85]. This research has sought to identify biologically plausible mechanisms by which organisms can execute Lévy walks and to demonstrate that these movement patterns have a utility beyond the understanding and prediction of optimal searching patterns. This work has made apparent that observations of Lévy walks do not stand outside of the correlated random walk paradigm but are instead natural consequences of it. I also describe some recent advances in Lévy walk search theory.

2 Underlying Mechanisms: The Key to Prediction and Understanding

Following the seminal work of [108], Lévy walk research has been mainly focused on establishing the conditions under which Lévy walks constitute an optimal searching strategy, and on establishing statistically reliably means of identifying such movement patterns in telemetry data [8,9,11,13,27,28,110]. Nonetheless, the key to prediction and understanding of movement patterns lies in the elucidation of mechanisms underlying the observed patterns [52]. "Without an understanding of mechanisms, one must evaluate each new stress on each new system *de novo*, without any scientific basis for extrapolation; with such an understanding, one has the foundation for understanding" [52].

One of the simplest candidate mechanisms could give rise to Lévy walk movement patterns in terrestrial ecotones such as riparian forests, dune systems or rocky shores where strong environmental gradients force animals to forage within a narrow strip [10]. This restriction would be realised by an animal with straight-line movements, if each time it arrives at an edge of the strip it is "deflected" back at a random angle, $0 < \theta < \pi$ drawn from the distribution $p_\theta = 1/\pi$. The horizontal distance travelled along the strip before encountering the opposing edge is $l = L \tan\theta$ where L is the width of the strip. The probability density function of l is determined by $p_l dl = p_\theta d\theta$ and so $p_l = \frac{1}{\pi}\frac{L}{l^2+L^2}$. These movement patterns are a Lévy walk with $\mu = 2$. Random changes in direction at the edges of an ecotone could thus have adaptive value, as $\mu = 2$ Lévy walk movement patterns can be advantageous in random search scenarios [8, 86, 108]. Random scattering from locations on the perimeter of broad two-dimensional landscapes (that do not have strip-like geometries), on the other hand, does not result in Lévy walk movement patterns. Nonetheless, two-dimensional Lévy walk movement patterns with $\mu < 2$ would be produced if the random scattering occurred within the landscape at markers (e.g. vegetation patches) that have a patchy fractal distribution [38]; a scenario which pollen dispersal studies have made plausible [21,53,92,112].

I next describe four other biologically plausible mechanisms that can give rise to two-dimensional observed Lévy walk movement patterns:

- Serial correlation
- Random reorientation at cues left by correlated random walkers
- By products of advantageous foraging behaviours
- Innate physiology

2.1 Serial Correlation

For many years the dominant conceptual framework for describing non-oriented animal movements has been the correlated random walk (CRW) model in which an individual's trajectory through space is regarded as being made up of a sequence of distinct, independent randomly-oriented "moves" [104]. It has long been recognized that the transformation of the animal's continuous movement path into a broken line is necessarily arbitrary and that probability distributions of move lengths and turning angles are model artefacts [104, and references therein]. Dunn and Brown [26], and Alt [1, 2] were perhaps the first to address the problem. They formulated "continuous-time" CRW models. In these models, velocities rather than positions evolve as a Markovian process and are exponentially autocorrelated. Integration of the velocity process gives the position process. The approach pioneered by Dunn and Brown [26], and by Alt [1, 2] has recently been developed by Johnson et al. [46] who demonstrated its utility in an analysis of telemetry data for harbor seals (*Phoca vitulina*) and northern fur seals (*Callorhinus ursinus*). Reynolds [75] showed that velocity autocorrelation inevitable leads to Lévy walk movement patterns on timescales less than the autocorrelation timescale.

Autocorrelation must be present in all movements but is not captured in discrete correlated random walk modelling. Autocorrelation has been quantified in cell motility studies [91, and references therein] but until recently it has received scant attention in the literature on the movement patterns in "higher" animals. A notable exception to this is the analysis by Johnson et al. [46] of seal telemetry data, where it was reported that autocorrelation timescales are several hours long. Lévy walks should be discernible over these timescales.

This advance has resonance with recent developments in the understanding of spontaneous movement of HaCaT and NHDF cells (cells of the epidermis) made in the absence of external guiding stimuli. These movements are well represented by generalizations of the Langevin equation [91]. This modelling is phenomenological as model components are *inspired* by fits to experimental data. Nonetheless, a slight re-parameterization and re-interpretation of the model components leads to the model of [59] which realises Lévy walks as Markovian stochastic processes [76]. This suggests that spontaneous cell movement patterns can be approximated by Lévy walks, as first proposed by Schuster and Levandowsky [89] and that Lévy walks could be lurking under the skin! These movement patterns could have adaptive value because cells of the epidermis form new tissue by locating and then attaching on to one another—a random search scenario.

2.2 Random Reorientation at Cues Left by Correlated Random Walkers

Traces of movement patterns in the form of odour trails can remain within the landscape for some time. In addition to these unintentional and perhaps unavoidable trails animals may also make deliberate scent marks. Mammalian scent marks might, for instance, act as: a deterrent or a substitute for aggression to warn conspecifics away from occupied territory; a sex attractant or stimulant; a system for labeling the habitat for an animal's own use in orientation or to maintain a sense of familiarity with an area; an indicator of individual identity; an alarm signal to conspecifics; and an indicator of population size [44].

Reynolds [77] noted that the odour trails left behind by correlated random walkers will be fractal with fractal dimension $D = 1.33$, illustrating once again that fractal scaling is a property of Brownian motion. By disrupting the movements of other animals these odours can result in reorientation. The locations at which these changes in the direction of travel occur will therefore be fractal. Odour-cued reorientation is therefore expected to give rise to movement patterns that can be approximated by Lévy walks since the turning points in a Lévy walk have fractal dimension $D = \mu - 1$. With the aid of numerical simulations [77] showed that animals which randomly reorient whenever they encounter the odour trail of a Brownian walker but otherwise move in straight-lines because of "directional persistence" will, indeed, have $\mu = 2.33$ Lévy walk movement patterns. These movement patterns are advantageous when searching for sparsely distributed resources without prior knowledge of resource locations or when information obtained during the search is difficult to process so that deterministic search rules cannot be used [8,86,108]. Consequently there will be strong selection pressures for the aforementioned reorientation process when resources are sparsely distributed within unpredictable environments inhabited by correlated random walkers. The presence of correlated random walkers may therefore drive the evolution of Lévy walks when the fitness advantage exceeds the environmental noise. Stochasticity in the form of random reorientations upon encountering odour cues could therefore have adaptive value when sensorial or cognitive animal skills do not override the need for randomness.

In this picture the emergence of Lévy walks from within the correlated random walk paradigm is dependent upon just three simple and well established ingredients: (1) landscapes are inhabited by animals that have CRW movement patterns and either intentionally or unintentionally leave behind odour trails; (2) some other animals also trace out near-straight line paths through the landscape; (3) but after encountering an odour trail abruptly change their direction of travel.

2.3 Lévy Walks as by Products of Advantageous Foraging Behaviours

The flight patterns of foraging bumblebees are of considerable interest because these bees, with a specialized worker caste, do nothing but forage uninterrupted for long periods of time (Fig. 3). They are not distracted by sex or territorial defence and have few predators [33]. They are therefore ideal for testing the clear-cut outcomes of predictive mathematical models of foraging. And this has led to a long running debate about whether bumblebees forage optimally within patches, and whether it matters [34, and references therein], This debate has been enriched by the possibility that bumblebees are executing optimal Lévy flight searching patterns when foraging within patches [27]; an analysis based on Heinrich's [33] classic observational study of bumblebee (*Bombus terricola*) movements (distances and turning angles) at clover (*Trifolium repens*) patches.

Bumblebees foraging within a flower patch tend to approach the nearest flower but then often depart without landing or probing it, if it has been visited previously; unvisited flowers are not rejected in this manner. Reynolds [73] replicated this foraging behaviour in numerical simulations. Lévy walk patterns with $\mu \approx 2$ were found to be an inconsequential emergent property of a bumblebees' foraging behaviour and, in this case, are not part of an innate, evolved optimal searching strategy.

Fig. 3 Bumblebees are ideal for testing the clear-cut outcomes of predictive mathematical models of foraging. Their foraging flights are consistent with Lévy searching theory but they are not necessarily Lévy searching. Photograph courtesy of Corbis

The results thereby provide a vivid demonstration that the key to understanding the biological, ecological and evolutionary consequences of any movement pattern lies in the elucidation of underlying mechanisms [52]. The significance of a particular movement patterns can, in fact, vary markedly even across closely related species and perhaps even within the same organisms under different scenarios. Honeybees (*Apis mellifera*), for example, unlike foraging bumblebees, do seem to execute Lévy flights as part of an innate, evolved searching strategy, at least when searching for their hive and when searching after a known food resource has become depleted [83, 84, 87].

Lévy walk patterns with $\mu \approx 2$ are also known to be an emergent property of predators that use chemotaxis (odour gradient following) to locate randomly and sparsely distributed prey items [71]. Chemotaxis also provides good solutions to the "travelling salesman problem" often minimising the total distance travelled between prey items and so often minimising the energetic costs of foraging [80]. Taken together these findings suggest that $\mu \approx 2$ Lévy walk *patterns* are a frequent emergent property of advantageous searching when searchers have some information about target locations (i.e. when the position of the nearest potential food source is known or when predators can detect the presence of odours emanating from distant food sources). This intriguing possibility complements the widely held view that Lévy walk *processes* are symptomatic of advantageous searching when searchers have little or no knowledge of target locations, and provides a new perspective on the ongoing debate about whether Lévy walks are patterns or processes [13, 68]. Much of this debate is a rerun of earlier deliberations about what "randomness" actually means in the context of random walks [104]. Turchin [104] remarked "that even if animals were perfect automaton we might still choose to model such behaviour stochastically because we might not have perfect knowledge of the deterministic rules driving these animals or, if we did, because including them would require very accurate representation of all environmental "micro-cues". Randomness is thus a modelling convention which is useful when deterministic modelling is impractical or even unhelpful." The approach termed "behavioural minimalism" [55] is directly analogous to thermodynamic theory in which the essentially unpredictable motion of individual molecules is described probabilistically. The underlying philosophy is not that the finer detail does not exist, but that it is irrelevant for producing the observed patterns [52]. That is, the collective behaviour of large numbers of automaton may be indistinguishable (at the scale of the population) from that of random walkers.

2.4 Innate Physiology

Over recent years there has been an accumulation of evidence that many animal behaviours are characterised by common scale-invariant patterns of switching between two contrasting activities over a period of time. This is evidenced in mammalian wake–sleep patterns [15, 56, 57], in the intermittent stop–start locomotion of *Drosophila* fruit flies [60], and in even the nest building behaviours of Large White x Landrace gilts (a species of the wild boar *Sus scrofa*) [35]. Reynolds [81] showed that these dynamics can be modelled by a stochastic variant of Barabási's model [6] for bursts and heavy tails in human dynamics. The new model captures a tension between two competing and conflicting activities. The durations of one type of activity are distributed according to an inverse-square power-law, mirroring the ubiquity of inverse-square power-law scaling seen in empirical data. The durations of the second type of activity follow exponential distributions with characteristic time-scales that depend on species and metabolic rates. This again is a common feature of animal behaviour. In contrast to animal dynamics, "bursty" human dynamics, are characterised by power-law distributions with scaling exponents close to -1 and -3/2. The model may account for some occurrence of Lévy walk movement patterns where an animal is resolving a tension between two competing and conflicting actions: moving in a straight line and turning. And in this regard Lévy walks are no stranger than sleep–wake patterns, stop–start locomotion, and nesting building where construction competes with the need for vigilance.

3 Translating Observations Taken at Small Spatiotemporal Scales into Expected Patterns at Greater Scales

Translating observations taken at small spatial and temporal scales into expected patterns at greater scales is a major challenge in spatial ecology [48]. The ability to scale up from observational scales is of crucial importance when assessing the potential effects of landscape heterogeneity and changes in behaviour, and in applying traditional behavioural ecology to landscape-level ecological problems [55]. To scale from limited observations to the landscape, we must understand how to aggregate and simplify, retaining essential information without getting encumbered by unnecessary detail. In principle this can and has been achieved by associating different modes of movement with different parameterizations of a single CRW model [32, 45, 46, 61, 62, 66, 67]. Depending on the diffusivity (mode), K, a CRW model could, for instance, produce either long straight movements, random meanderings, or more circuitous movements. Difficulties arise when the available observational data are not sufficient to parameterize accurately the probability distribution function of the modes, $p(K)$. In these cases the principle of scientific objectivity dictates that we be maximally uncommitted about what we do not know concerning the distribution $p(K)$. The most conservative, non-committal $p(K)$ that is consistent with the data (e.g. with estimates for the mean value of K) is obtained by maximising Shannon's differential entropy [41–43]. Any other distribution would assume more information than is known from the data. In this context, Shannon's differential entropy, $H = -\int\limits_{K} p(K) \log_e p(K) dK$, is a measure of the average surprise of seeing an animal in a particular movement mode, K, given a distribution of modes $p(K)$. A highly improbable outcome is very surprising. If there are two movement modes, K_1 and K_2, then the entropy is zero when there is no uncertainty, i.e. when $p(K_1) = 1$ and $p(K_2) = 0$ or when $p(K_1) = 0$ and $p(K_2) = 1$. It is maximized when $p(K_1) = p(K_2) = 1/2$ as there is less uncertainty when $p(K_1) \neq p(K_2)$ because then one or other of the modes is more likely to be seen.

Reynolds [82] showed that truncated $\mu = 2$ Lévy walk movement patterns are the most conservative, maximally non-committal model of movement patterns beyond the scale of data collection when (a) CRW models embody observed movement patterns and (b) minimal or partial information/assumptions about landscape and behavioural heterogeneity are in the form of reliable estimates for the lower order moments of diffusivity (e.g. when given estimates for the mean diffusivity, or the mean and variance of the diffusivity). Lévy walks therefore provide a robust, universal scaling-law which describes how movement patterns change across scale, and which has the potential to become a valuable modelling tool when scaling up from limited observational data in order to assess the likely effects of landscape heterogeneity and changes in behaviour. Reynolds' [82] result also indicates that with landscape and behavioural heterogeneity, the unusual thing is not truncated Lévy walk movement patterns but their absence. In fact, large-scale, Gaussian, diffusive movement patterns, if they arise at all, would be an emergent phenomenon, not a mathematically self-evident state from which any deviation is a worrisome anomaly. Standard methods in spatial ecology do, however, consider Gaussian statistics and diffusion as two basic ingredients of animal movement at the long-time limit [14, 65].

4 Enlarging the Framework of Lévy Walk Search Theory

The foregoing as illustrated that a diverse range of processes can give rise to Lévy walk movement patterns. Some of these processes are not selected for, thus illustrating that Lévy walk movement patterns may have utility beyond the understanding and prediction of optimal searching patterns. Other processes (e.g. random reorientation at cues left by correlated random walkers) will only operate if there are selection pressures for of Lévy walks.

The association of Lévy walks with optimal searching can be traced back to the theoretical and computational work of [108] which produced an idealised model of Lévy walk searching. In this model a searcher moves on a straight-line towards the nearest target if this target lies within the "direct perceptual range", r; otherwise it chooses a direction at random and a distance, l, drawn from a power-law distribution, $P(l) = (\mu - 1)r^{\mu-1}l^{-\mu}$ for $l \geq r$ and $P(l) = 0$ for $l < r$. The searcher 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. [108] showed that $\mu = 2$ Lévy walks are an optimal Lévy walk searching strategy for the location of randomly and sparsely distributed targets that can be repeatedly revisited because they are not depleted or rejected once visited. Lévy walks with $\mu < 2$ are nearly equally effective and outperform their $\mu > 2$ counterparts when searching "destructively" in either two- or three-dimensional arenas [8, 86]. From a mathematical perspective the difference between non-destructive and destructive searching lies in the specification of the initial conditions for the search. In a non-destructive search each new search begins close to a previously visited target but distant from many other targets. In a destructive search, each new search begins from a location that is distant from the surviving targets. Reynolds [78] and then James et al. [40] noticed that the optimal Lévy walk search strategy can be extremely sensitive to the initial conditions. The advantages that Lévy walks have over ballistic movements in random search scenarios are greatly reduced or removed if searches do not begin in the immediate vicinity of a target. James et al. [40] suggested that this sensitivity shows that the optimality of Lévy walk search is not as robust as previously thought thereby creating the impression that Lévy walk searches are optimal in just a few special circumstances. For two-dimensional searches this sensitivity stems, in part, from the use of point targets in numerical simulations and is less pronounced when targets are large compared with the perceptual range of the forager (Fig. 4), or are patchily distributed. Previously, it had been suggested wrongly that target size does not affect the optimality of searching patterns [39]. Nonetheless, this revised understanding leaves open the specification of biologically-realistic initial conditions for Lévy walk searches. In the next sections I show how the ambiguity in the specification of the initial conditions for a Lévy walk search can be resolved and argue that Lévy walk searches can be optimal when searching under the risk of predation [78]. I also show that Lévy walks searches are expected to be optimal when searching for prey that can occasionally evade capture [86], and when searching is intermittent such that bouts of active searching alternate with relocation bouts during which prey cannot be detected [70, 58]. This strand of research enlarges the framework of Lévy search theory, and may provide a new insights into the movement patterns of a diverse range of marine predator (basking shark *Cetorhinus maximus*, Atlantic cod *Gadus morhua*, bigeyed tuna *Thunnus obesus,* leatherback turtles *Dermochelys coriacea*, and Magellanic penguins *Spheniscus magellanicus*) and *Escherichia coli* which can be modelled as Lévy walks with $\mu \approx 2$ [37, 49, 96, 102]. It is, however, important to acknowledge from the outset that foragers may show plasticity and

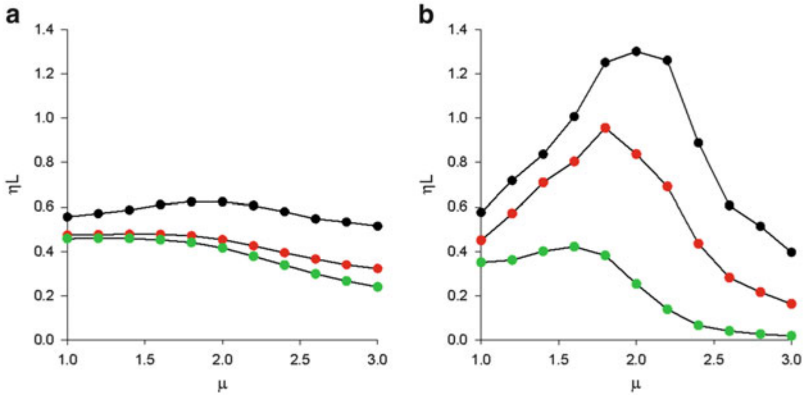

Fig. 4 Simulation data for the searching efficiencies, η, of non-destructive foragers with Lévy walks movement patterns as a function of the Lévy exponent μ. The searching efficiency is taken to be the reciprocal of the mean distance travelled before encountering a target. In other words, it is the mean number of targets located during a search divided by the total length of the search. The two-dimensional square search arena with side length $L = 1000$ arbitrary space units contains 50,000 stationary point-sized targets. The perceptual range of the searchers is $r = 0.1$ space unit. Data ensemble averaged over 5,000 realisations are shown for (**a**) random and uniformly distributed targets and for (**b**) for patchily distributed targets. Each patch contains 10,000 targets that are uniformly distributed within non-overlapping circles of diameter 100 arbitrary space units. Patches were randomly and uniformly distributed within the search arena. Data are shown for the cases when each new search begins $r(black)$, $5r(red)$ and $50r(green)$ from the last target to be located

change strategies depending on circumstances (as illustrated in Fig. 5) and that trade-offs might prevent a universal solution [12].

4.1 Balancing the Demands of Foraging and Safety from Predation

Benhamou [13] and then Plank and James [68] devised a composite Brownian walk model for the location of patchily distributed targets that once visited become temporally unavailable either because they have become depleted or because of the increased risk of predation. In this model searchers travel out from the origin of their search in a straight line until they encounter a target and then proceed to search destructively within the patch that contains this target using Brownian movements, i.e. using an area restricted search. If a target is not located within a prescribed time, the "giving up time" then the searcher switches back to the original straight-line motion. Benhamou [13] showed that his composite Brownian walk model is more efficient than any Lévy walk that is not responsive to conditions found in the search. Reynolds [71, 72] subsequently pointed out that the composite Brownian walk model can, in fact, be interpreted as being an "adaptive" or responsive Lévy

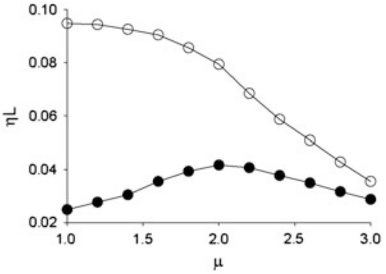

Fig. 5 Optimality hanging in the balance. The presence of a gentle breeze could be sufficient to switch the optimal searching strategy from a ballistic walk to a Lévy walk. Simulation data (unpublished) is shown for the efficiency, η, of Lévy walk searches as a function of the Lévy exponent μ. The searching efficiency is the mean number of prey items encountered per unit distance travelled. The search arena, a square with side length L, contains 10^5 prey items that are randomly and uniformly distributed. Prey are consumed once detected. The perceptual range of the predator $r = 10^{-4}L$ arbitrary space units. Data are shown for the cases when prey can be detected equally well when approached from any direction (*open circle*) and only when approached from an upwind location (*filled circle*) because unbeknown to the predator, prey flee from olfactory cues produced by predators

walk search. This correspondence arises because straight-line movements between targets correspond to truncated $\mu \to 1$ Lévy walks. Benhamou [13] and Plank and James [68] have therefore demonstrated that an adaptive Lévy walk is better than any non-adaptive Lévy walk when searching destructively in patchy environments. Moreover, predictions from the composite Brownian walk are entirely consistent with standard Lévy walk search theory; this predicts that straight-line movements are advantageous when searching destructively for sparsely distributed patches whilst Brownian movements are optimal for within-patch searching [108].

Reynolds [74] then developed a new class of adaptive Lévy walk searching model which encompassed composite Brownian models as a special case. In these models, bouts of Lévy walk searching alternate with bouts of more intensive Brownian walk searching. As with the composite Brownian model switching from extensive to intensive searching is prompted by the detection of a target and switching back to extensive searching arises if a target is not located after travelling a distance equal to the giving-up time. The model reconciles Lévy walk search theory with the ubiquity of two modes of searching by predators and with their switching searching model immediately after finding a prey [50]. This model reduces to the “composite Brownian walk” model when $\mu \to 1$. It should be noted that the model presupposes that the prey are patchily distributed and that the predator perhaps through past experience is aware of this. The models are thus fundamentally different from non-adaptive Lévy walk search models [108] where it is assumed that animals have *no* prior knowledge of the target distribution.

Prey capture does not always trigger an area restricted search [111]. This is probably because decisions to modify behaviour after prey capture are dependent on many parameters, including the presence of other predators, the state of the forager, the cost of catching the prey, the quality of the prey patch, or predation risks. Adaptive Lévy walk searching models have been used to examine the trade-offs between searching efficiency and safety from predation [78]. Only if the benefits of advantageous foraging outweigh these costs can there be strong selection pressures for Lévy walk movement patterns. In the absence of predation the giving-up time can be chosen to maximise foraging efficiency and in this case the searching efficiency of adaptive Lévy walks is no better than that of composite Brownian walks. But when foraging under the risk of predation this unconstrained optimal may not be realised because a forager must trade off food harvesting with safety [17]. When the realised giving-up distance is much shorter than the unconstrained optimal one, Lévy walks with $\mu \approx 2$ are advantageous. This finding has resonance with that of [109] who argued that convoluted movement patterns confer greater fitness than straight-line paths because they reduce the risk of predation. Straight-line paths present the most efficient means of searching for prey while also exposing the forager to maximum predation risk. Animals that manage to trade-off food and safety by vigilance to predators while feeding from a food patch can remain within the patch for long times and are not be expected to have Lévy walk movement patterns. Animals that use little vigilance and manage risk via time allocation by demanding a higher feeding rate to compensate for a higher risk of predation may have Lévy walk movement patterns. And so despite having fundamentally different properties, Lévy walks and composite Brownian walks can compete a priori as possible models of foraging movements. Lévy walks are expected in tritrophic systems and where intra-guild predation (a ubiquitous interaction, differing from competition or predation, defined as killing and eating among potential competitors) operates.

4.2 Red Queen Dynamics

The co-evolution of predators and their prey can lead to situations in which neither improves its fitness because both populations co-adapt to each other [25, 106]. In these evolutionary arms races, improvements in the ability of a predator to detect and capture prey (e.g., heightened sensitivity to chemical, mechanical or visual signals, stronger attack reactions) are matched by compensating improvements in the ability of prey to evade detection and capture (e.g. crypsis, feigning death, strong jumps, sudden increase of size, confounding signals). These "Red Queen" type of dynamics [105] preclude the possibility of a perfect searching/capture process. Reynolds and Bartumeus [86] showed that $\mu \sim 2$ Lévy walks can be optimal when searching destructively if targets occasionally evade detection and/or capture. Searches for escapees begin close to escaped prey but distant from other prey—a scenario mirroring "non-destructive" foraging which favours $\mu \sim 2$ Lévy walk searching. This suggests that accounting for the co-evolutionary arms races at the predator–prey detection/reaction scales can explain to some extent the $\mu \sim 2$ Lévy walks searching patterns at larger scales.

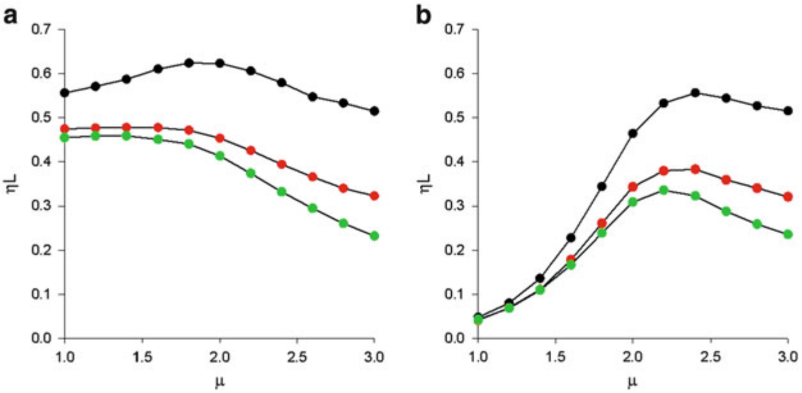

Fig. 6 Simulation data for the searching efficiencies, η, of non-destructive foragers with Lévy walks movement patterns as a function of the Lévy exponent μ. The searching efficiency is taken to be the reciprocal of the mean distance travelled before encountering a target. In other words, it is the mean number of targets located during a search divided by the total length of the search. Fifty thousand stationary targets were randomly and uniformly within a two-dimensional square search arena with side length $L = 1000$ arbitrary space units. The perceptual range of the searchers is $r = 0.1$ space unit. Data are shown for (**a**) non-intermittent (i.e. standard) Lévy walk searching and (**b**) intermittent Lévy walk searching where targets can be only detected using relatively short moves with length $l < 100r$. Data are shown for the cases when each new search begins $r(black)$, $5r(red)$ and $100r(green)$ from the last target to be located. Similar results (not shown) were obtained for patchily distributed targets

4.3 Intermittent Searches

The movements of many foragers (e.g. planktivorous fish, ground-foraging birds, and lizards) are intermittent with pauses or bouts of relatively slow movements lasting from milliseconds to minutes [51, 63]. This intermittency can have a variety of energetic benefits. Endurance can also be improved by partial recovery from fatigue. Perceptual benefits can arise because pauses increase the capacity of the sensory systems to detect relevant stimuli. Several processes, including velocity blur, relative motion detection, foveation, attention and interference between sensory systems could be involved [51]. Searching could therefore be salutatory such that "scanning" phases during which prey can be detected alternate with "relocation" phases during which prey cannot be detected. This trait can be incorporated into Lévy walk searching models by associating the short moves ($l < l_0$) with the scanning phases whilst longer moves are associated with the relocation phases. Intermittent Lévy walks with $\mu \approx 2$ are an optimal search strategy for both destructive and non-destructive foragers [58, 70]. In other words, this strategy is robustly optimally with respect to the initial conditions of the search, and so markedly different from non-intermittent Lévy walk searching which are extremely sensitive to initial conditions [78] (Fig. 6).

Here following [108] the searching efficiency is taken to be the reciprocal of the mean distance travelled before encountering a targets, i.e., it is the mean number of targets located during a search divided by the total length of the search. Foragers that minimize the average distance travelled between targets will therefore maximize their expected energy gain when energy expenditure increases linearly with distance travelled. The energy costs of intermittent locomotion are, however, more complex and the energy expended in accelerations and decelerations can be more than offset by a variety of energetic benefits and by recovery from fatigue [51, and references therein], Fish such as cod and Pollack can, for instance, save energy by "burst-coasting swimming" as the drag while coasting with the body straight is only about one third of the drag while swimming. The energetic costs of intermittent locomotion warrant further investigation because they could favour $\mu \neq 2$ Lévy walk movement patterns for some taxa.

4.4 Optimizing the Encounter Rate in Biological Interactions

Encounter rates set bounds on prey-consumption, the risk of predation, the likelihood of mate-location and the spread of infectious diseases and so play a crucial role in population dynamics. To date, however, there have not been any reported studies on the relative merits of Lévy walk search strategies for the location of mobile targets in two-search arenas.

James et al. [39] reported that ballistic movements outperform Lévy walks and Brownian walks when searching randomly and destructively for mobile prey in one-dimensional environments, thereby overturning the previous analysis of [7]. Data (previously unpublished but comparable to that reported on by [10]) from numerical simulations of destructive searching in two-dimensional arenas show that Lévy walks with $\mu \leq 2$ are equally effective and outperform Lévy walks with $\mu > 2$ when predators move with speeds that are faster than or comparable to that of their prey (Fig. 7a–c). Maximal encounter rates are then largely insensitive to the movement pattern of the prey. This is not surprising and entirely consistent with numerical simulations of destructive searching for immobile targets [8, 86]. It is evident from Fig. 7a–c that the prey cannot adapt their movement patterns so as to reduce the likelihood of predation. This suggests that prey movement patterns are determined by their foraging and mating-location requirements and not by the costs of predation. Predator movement patterns do, of course, become irrelevant when predators move much more slowly than their prey (Fig. 7d). A "sit-and-wait" strategy and a Brownian search are then just as effective as a Lévy walk search. It is thus possible for Brownian searches to have evolved naturally as one search strategy. Nonetheless, Lévy searches are more versatile and outperform Brownian walks when (if) searching for slowly moving prey (Fig. 7a–c) in addition to fast moving ones. This leads to the expectation that Lévy searches are predominant in generalist predators whilst Brownian and correlated random walk searching is likely in some specialist predators with a narrow prey range. Note also that ballistic movements are predictable, making the forager more vulnerable to predation (Fig. 8).

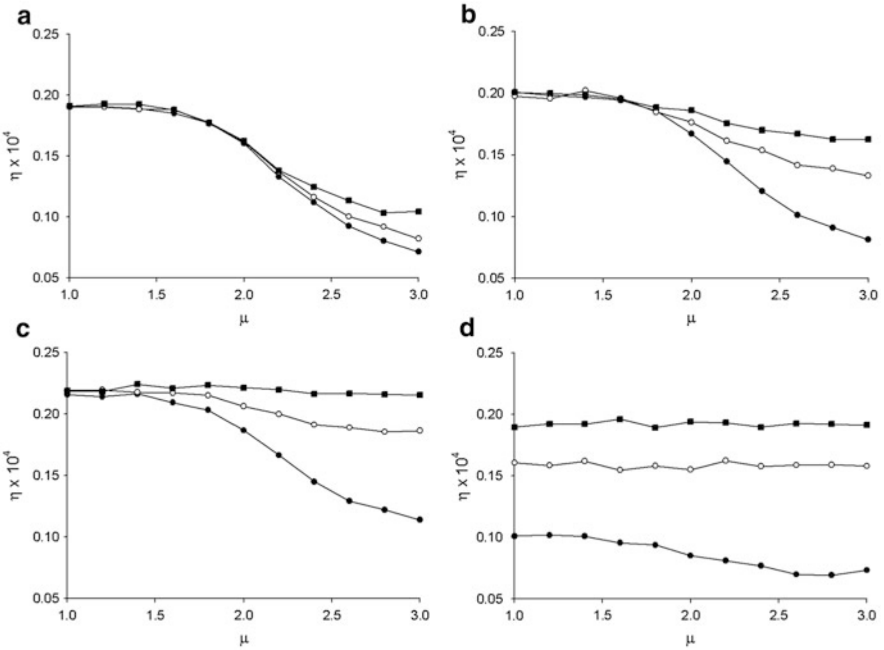

Fig. 7 Simulation data for the mean encounter rates, η, for predators with Lévy walks movement patterns as a function of the Lévy exponent, μ. Predators search within a two-dimensional square arena with size 1,000×1,000 arbitrary space units containing ten prey. The encounter rate is the average number of prey items encountered per unit distance travelled. Data are shown for predators that move ten times faster than their prey (1.0 and 0.1 space units in unit time) (**a**), for predators that move two times faster than their prey (1.0 and 0.5 space units in unit time) (**b**), for predators that move at the same speed as their prey (1.0 space units in unit time) (**c**) and for predators that move ten times slower than their prey (0.1 and 1.0 space units in unit time) (**d**). In all cases the perceptual range $r = 1$ space unit and predators travel for a time of 10^5 time units. Encounter rates for each case were obtained by ensemble averaging for 500 realizations of the initial prey distribution. Simulation data are shown for prey with Brownian walk ($\mu = 3$) (*filled circle*), $\mu = 2$ Lévy walk (*open circle*) and ballistic (*filled square*) movement patterns. Prey are deleted once encountered. To maintain a constant density of prey, each deleted prey is replaced by a new prey placed at a randomly selected location within the search arena. Analogous results (not shown) have been obtained for prey at lower densities (square arena with size $1,000 \times 1,000$ arbitrary space units containing 5, 2 and 1 prey) and for searching within three-dimensions (cube arena with size $100 \times 100 \times 100$ arbitrary space units containing ten prey)

5 Some Closing Remarks and Some Open Questions

5.1 *Opening the Lévy Gates*

The research reported on here has shown that Lévy walks do not stand outside of the correlated random walk paradigm [104] but rather are natural consequences of

Fig. 8 Still fishing for answers. There is strong evidence for Lévy walks in the swimming patterns of the Magellanic penguin (Spheniscus magellanicus) and other marine predators [96] and these appear to be associated with foraging. The idealised Lévy walk searching model of [108] suggest that these movement patterns are an optimal foraging strategy. Much subsequent work paints a more complicated picture. Photo courtesy of Corbis

it and that the utility of Lévy walk models extends well beyond the description of search behaviours.

The apparent strangeness of Lévy walks was shown to be innocuous. After all, a pollen grain does both the Brownian and the Lévy walk. The seemingly peculiar fractal properties of Lévy walks are also seen in Brownian walks [77]. Power-law scaling, the hallmark of Lévy walks, is necessarily present in continuous-time correlated random walks that take explicit account of serial correlations [75]. And when correlated random walks represent accurately observed movement patterns, Lévy walks are the most conservative model of movements at larger scales [82]. This strand of research is also bridging between the separate disciplines of animal movement patterns and plant disease epidemiology. This is generating new perspectives and questions at the interface between these two disciplines and thereby contributing to the emergence of a new synthesis that transcends traditional boundaries. Other work [31,98] is bridging the gap between the separate disciplines of animal and human movement patterns.

The research has also extended the reach of Lévy walk search theory to encompass the predator–prey co-evolutionary arms race [86], dynamic adaption to conditions found along the search [72, 74, 78], and physiological constraints [58, 70]. Taken together this research suggests that $\mu \sim 2$ Lévy walk searches represent an evolutionarily stable strategy in changing or dynamic environments [97]. This warrants further investigation because it would reveal the extent of selection pressures for $\mu \sim 2$ Lévy walk movement patterns.

5.2 *Lévy Walks in Collective Motions: How the Blind Could Lead the Blind*

Collective movement behaviour is seen in almost every taxa and is arousing considerable amongst behavioural ecologists as well as physicists and mathematicians [5, 16, 19, 22, 23]. On focus of attention has been group decision making. In a seminal study, using idealised mathematical models, Couzin et al. [23] showed how information about the location of a food source or a migration route can be transferred within groups both without signalling and when group members do not which individuals, if any, have pertinent information. This work has demonstrated how a few individuals (approximately 5%) within honeybee swarms can guide the group to a new nest site [90] and how relatively few informed individuals within fish schools can influence the foraging behaviours of the group [69].

This leaves open the question of whether effective leadership and decision-making can arise when no individual in the group has pertinent information about the location of resources, i.e. the question of whether Lévy walks movement patterns can arise in groups from social interactions. Lévy walks patterns of movement in groups can, as in individuals, be advantageous in random search scenarios [88].

Preliminary considerations in this direction have shown that Lévy walks could be an emergent property of collective movements ranging from "swarming" where there is no parallel alignment among members, as in often seen in insects, particular the *Diptera*, through to the high parallel movements displayed in some fish shoals. This investigation has drawn also out further connections between Brownian and Lévy walks.

Consider an idealised model of collective movements in which there is one "leader" and a "follower". The leader moves in a straight line, changing its direction of travel only when one of the followers comes within its immediate vicinity (collision avoidance). The follower keeps pace with the leader but has small random (Brownian) movements in the two directions orthogonal to the leaders' direction of travel. It can be shown (unpublished report) that the leader and so the pair are following a $\mu = 3/2$ Lévy walk. Truncated Lévy walks result when the follower cannot meander to arbitrarily long distances from the leader but instead remains within a "zone of attraction" that enforces group cohesion. These findings are broadly consistent with telemetry data for midges (*Anarete pritchardi Kim)* flying within swarms [64]. Okubo and Chiang [64] reported that midge flights may be classified into two distinct patterns; one is a "wide" pattern, the other is a "tight" pattern. In a wide pattern, the insect exhibits a relatively long, straight or slightly curved path that might be regarded as a free flight. After a straight path the insect shifts its motion from one direction to another. In the tight pattern, insects exhibit a relatively short, zigzag flight that might be regarded as random motion. How these different patterns are related to the behaviour of swarming midges is still unknown.

Similarly Lévy walk movement patterns with $\mu = 1 + N/2$ are predicted to arise in highly parallel groups consisting of one leader and N followers that keep pace with the leader whilst making one-dimensional random movements (traverse to the current direction of travel of the leader). The finding may explain the presence of Lévy walk movement patterns in some fish that forage in shoals [96]. The empirical observations are recovered if leaders are responsive to just two of their followers. Here it is worth noting that leaders and followers have been identified in shoals [69].

Intrinsic variability in the mobility of individuals within a group may therefore have adaptive value and Lévy walk movement patterns could be an overlooked benefit of group living. This warrants further investigation.

5.3 Mathematical Challenges

A more formidable challenge is to develop an analytical theory of Lévy walk searching that is applicable for two- and three-dimensions. This would serve to validate numerical codes and facilitate an examination of searching in regimes that are currently inaccessible to computation, e.g. at the threshold of starvation where targets are in very dilute concentration and so detected very infrequently. It remains to seen whether "mean field theories" of the kind developed by Viswanathan et al. [108] for one-dimensional searches can reproduce faithfully simulation data for two- and three-dimension searches.

The employment of entropy maximization in movement patterns also warrants further investigation because it offers new unexplored means for quantifying the information content of correlated random walk and Lévy walk models, and for establishing new connections between these models. The simplest of correlated random walk models can, for instance, be construed as being the most conservative, maximally non-committal models of animal movement patterns given only the arithmetic mean move length. This is simply because maximisation of Shannon entropy yields an exponential distribution of move lengths [24]. The arithmetic move length is a potentially meaningful characteristic of a movement pattern if the move lengths do not show a tendency to grow during the time course of a movement pattern. When move lengths do tend to grow then the geometric (or logarithmic) average move length can be useful. The geometric average of a set of N moves with lengths $\{l_i\}$ is $\overline{l} = \left(\prod_{i=1}^{N} l_i\right)^{1/N} = \exp\left(\frac{1}{N}\sum_{i=1}^{N} \ln l_i\right) \equiv \exp\left(\langle \ln l \rangle\right)$ where $\langle \ln l \rangle$ is the logarithmic average. Maximisation of Shannon's entropy, subject to the condition that probabilities furnish the observed geometric average move length, gives a Pareto distribution of move lengths, $p(l) = (\mu - 1)a^{\mu-1}l^{-\mu}$ where $\mu = 1 - \frac{1}{\ln a - \langle \ln l \rangle}$ is the well known Hill's (maximum likelihood) estimate [36] for a power-law exponent [47]. Geometric constraints *per se* are not new [47] but until now had not appeared in movement ecology literature. Models utilizing move length distributions other than the Pareto or exponential distributions are less conservative if move lengths are characterized solely in terms of either the arithmetic or geometric average; a minimal requirement for any reasonable model of animal movement pattern. The Akaike information criterion which following [27] is now used widely to distinguish objectively between power-law and exponential distributions can, in this application, be interpreted as determining the relative appropriateness of the arithmetic and geometric averages as characterisations of the typical move length. This is because the Akaike weight for a power-law (i.e. weight of evidence in favour of a power-law) is determined by the logarithmic average whilst the Akaike weight for an exponential is determined by the arithmetic average. A bridge between the Lévy walk and correlated random walk models is formed if move lengths are simultaneously characterised in terms of arithmetic and geometric average move lengths (as would be the case if individuals occasionally switched between executing Lévy and correlated random walks or at the population level if Lévy walkers co-exist alongside correlated random walkers). In this case, maximisation of Shannon's entropy leads to a gamma distribution of length moves. This distribution has a power-law like core and an exponential tail, and was recently found to characterise accurately the flight patterns of the wandering albatross [27]. The wandering albatross may therefore bridge the apparent divide correlated random walks and Lévy walks. It seems that as with the humble pollen, Lévy walk research can still learn much from the wandering albatross.

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References

1. W. Alt, Modelling of motility in biological systems, in ed. by *ICIAM'87: Proceedings of the first international conference on industrial and applied mathematics,* J. McKenna, R. Temam. (SIAM, Philadelphia, 1988), pp 15–30
2. W. Alt, Correlation analysis of two-dimensional locomotion paths, in *'Biological Motion: Proceedings of a workshop held in Königswinter Germany'*, ed. by W. Alt, G. Hoffman. Lecture Notes in Biomathematics (Springer, Berlin, 1990), pp 254–268
3. M. Auger-Méthé, C. Cassady St. Clair, M.A. Lewis, A.E. Derocher, Sampling rate and misidentification of Lévy and non-Lévy movement patterns: comment. Ecology **92**, 1699–1701 (2011)
4. F.C.W. AusterlitzDick, C. Dutech, E.K. Klein, S. Oddou-Muratorio, P.E. Smouse, V.L. Sork, Using genetic markers to estimate the pollen dispersal curve. Mol. Ecol. **13**, 937–945 (2004)
5. M. Ballerini, N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini, M. Viale, V. Zdravkovic, Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. Proc. Natl. Acad. Sci. **105**, 1232–1237 (2008)
6. A.L. Barabasi, The origin of bursts and heavy tails in human dynamics. Nature **435**, 207–211 (2005)
7. F. Bartumeus, J. Catalan, U.L. Fulco, M.L. Lyra, G.M. Viswanathan, Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies. Phys. Rev. Lett. **88**, article 097901 (2002)
8. F. Bartumeus, M.G.E. da Luz, G.M. Viswanathan, J. Catalan, Animal search strategies: a quantitative random search analysis. Ecology **86**, 3078–3087 (2005)
9. F. Bartumeus, Lévy processes in animal movement: an evolutionary hypothesis. Fractals **15**, 151–162 (2007)
10. F. Bartumeus, P. Fernández, M.G.E. da Luz, J. Catalan, R.V. Solé, S.A. Levin, Superdiffusion and encounter rates in diluted, low dimensional worlds. Eur. Phys. J. Spec. Top. **157**, 157–166 (2008)
11. F. Bartumeus, Behavioral intermittence, Lévy patterns, and randomness in animal movement. Oikos **118**, 488–494 (2009)
12. F. Bartumeus, J. Catalan, Optimal search behavior and classic foraging theory. J. Phys. A **42**(article), 434002 (2009)
13. S. Benhamou, How many animals really do the Lévy walk? Ecology **88**, 518–528 (2007)
14. H.C. Berg, *Random Walks in Biology* (Princeton University Press, Princeton, New Jersey, 1983).

15. M.S. Blumberg, A.M.H. Seelje, S.B. Lowen, A.E. Karlson, Dynamics of sleep-wake cyclicity in developing rats. Proc. Natl. Acad. Sci. **102**, 14680–14864 (2005)
16. N.W. Bode, D.W. Franks, A.J. Woods, Limited interactions in flocks: relating model simulations to empirical data. R. Soc. Interface (2010). doi:10.1098/rsif.2010.0397
17. J.S. Brown, Vigilance, patch use and habitat selection: Foraging under predation risk. Evol. Ecol. Res. **1**, 49–71 (1999)
18. M. Buchanan, The mathematical mirror to animal nature. Nature **453**, 714–716 (2008)
19. J. Buhl, D.J.R. Sumpter, I.D. Couzin, J.J. Hale, E. Despland, E.R. Miller, S.J. Simpson, From disorder to order in marching locusts. Science **312**, 1402–1406 (2006)
20. O.V. Bychuk, B. O'Shaughnessy, Anomalous surface diffusion: A numerical study. J. Chem. Phys. **101**, 772–780 (1994)
21. S.A. Cannas, D.E. Marco, M.A. Montemurro, Long range dispersal and spatial pattern formation in biological invasions. Math. Biosci. **203**, 155–170 (2006)
22. I.D. Couzin, J. Krause, R. James, G.D. Ruxton, N.R. Franks, Collective memory and spatial sorting in animal groups. J. Theor. Biol. **218**, 1–11 (2002)
23. I.D. Couzin, J. Krause, N.R. Franks, S.A. Levin, Effective leadership and decision-making in animal groups on the move. Nature **433**, 513–516 (2005)
24. T.M. Cover, J.A. Thomas, *Elements of Information Theory* (Wiley, New York, 2006)
25. R. Dawkins, J.R. Krebs, Arms races between and within species. Proc. R. Soc. Lond. B **205**, 489–511 (1979)
26. G.A. Dunn, A.F. Brown, A unified approach to analyzing cell motility. J. Cell Sci. Suppl. **8**, 81–102 (1987)
27. A.M. Edwards, R.A. Phillips, N.W. Watkins, M.P. Freeman, E.J. Murphy, V. Afanasyev, S.V. Buldyrev, M.G.E. da Luz, E.P. Raposo, H.E. Stanley, G.M. Viswanathan, Revisiting Lévy walk search patterns of wandering albatrosses, bumblebees and deer. Nature **449**, 1044–1048 (2007)
28. A.M. Edwards, Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. Ecology **926**, 1247–1257 (2011)
29. A. Einstein, Über die von der molekularkinetischen Theorie der Wärme geforderte Bewegung von in ruhenden Flüssigkeiten suspendierten Teilchen. Ann. Phys. **17**, 549–506 (1905)
30. A. Einstein, Zur theorie der Brownschen bewegung. Ann. Phys. **19**, 549–560 (1906)
31. M.C. González, C.A. Hidalgo, A.L. Barabási, Understanding individual human mobility patterns. Nature **453**, 779–782 (2008)
32. E. Gurarie, R.D. Andrews, K.L. Laidre, A novel method for identifying behavioural changes in animal movement data. Ecol. Lett. **12**, 395–408 (2009)
33. B. Heinrich, Resource heterogeneity and patterns of movement of foraging bumblebees. Oecologia **40**, 235–245 (1979)
34. B. Heinrich, Do Bumblebees Forage Optimally, and Does It Matter? Am. Zool. **23**, 273–281 (1983)
35. A. Harnos, G. Horváth, A.B. Lawrence, G. Vattay, Scaling and intermittency in animal behaviour. Phys. A **286**, 312–320 (2000)
36. B.M. Hill, A simple general approach to inference about the tail of a distribution. Ann. Stat. **3**, 1163–1174 (1975)
37. N.E. Humphries, N. Queiroz, J.R.M. Dyer, N.G. Pade, M.K. Musyl, K.M. Schaefer, D.W. Fuller, J.M. Brunnschweiler, T.K. Doyle, J.D.R. Houghton, G.C. Hays, C.S. Jones, L.R. Noble, V.J. Wearmouth, E.J. Southall, D.W. Sims, Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature **465**, 1066–1069 (2010)
38. H. Isliker, I. Vlashos, Random walk through fractal environments. Phys. Rev. E **67**(article), 026413 (2003)
39. A. James, M.J. Planck, R. Brown, Optimizing the encounter rate in biological interactions: Ballistic versus Lévy versus Brownian strategies. Phys. Rev. E **78**(article), 051128 (2008)
40. A. James, M.J. Plank, A.M. Edwards, Assessing Lévy walks as models of animal foraging. J. R. Soc. Interface **8**, 1233–1247 (2011)
41. E.T. Jaynes, Information theory and statistical mechanics. Phys. Rev. **106**, 620–630 (1957a)

42. E.T. Jaynes, Information theory and statistical mechanics II. Phys. Rev. **108**, 171–190 (1957b)
43. E.T. Jaynes, in *Probability Theory: The Logic of Science*, ed. by Bretthorst, G.L. (Cambridge University Press, Cambridge, 2003)
44. R.P. Johnson, Scent marking in mammals. Anim. Behav. **21**, 521–535 (1973)
45. C.J. Johnson, K.L. Parker, D.C. Heard, M.P. Gillingham, Movement parameters of ungulates and scale-specific responses to the environment. J. Anim. Ecol. **71**, 225–235 (2002)
46. D.S. Johnson, J.M. London, M.A. Lea, J.W. Durban, The continuous-time correlated random walk model for animal telemetry data. Ecology **89**, 1208–1215 (2008)
47. J.N. Kapur, *Maximum-Entropy Models in Science and Engineering* (Wiley, New York, 1989)
48. P.M. Kareiva, Population dynamics in spatially complex environments: theory and data. Phil. Trans. R. Soc. Lond. B **330**, 175–190 (1990)
49. E. Korobkova, T. Emonet, J.M.G. Vilar, T.S. Shimizu, P. Cluzel, From molecular noise to behavioural variability in a single bacterium. Nature **428**, 574–578 (2004)
50. P. Knoppien, J. Reddingius, Predators with two modes of searching: a mathematical model. J. Theor. Biol. **114**, 273–301 (1985)
51. D.L. Kramer, R.L. McLaughlin, The behavioural ecology of intermittent locomotion. Am. Zool. **41**, 137–153 (2001)
52. S.A. Levin, The problem of pattern and scale in Ecology. Ecology **73**, 1943–1967 (1992)
53. C. Lett, H. Østergård, A stochastic model simulating the spatiotemporal dynamics of yellow rust on wheat. Acta Phytopathologica et Entomologica Hungarica **35**, 287–293 (2000)
54. P. Lévy, *Théorie de l'addition des Variables Aaléatoires* (Monographies des Probabilités, publiés sous la direction de E. Borel, no. 1.) (Guathier Villars, Paris, 1937)
55. S.L. Lima, P.A. Zollner, Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. **11**, 131–135 (1996)
56. C.C. Lo, L.A. Nunes Amaral, S. Havlin, P.C.h. Ivanov, T. Penzel, J.H. Peterand, H.E. Stanley, Dynamics of sleep-wake transitions during sleep. Europhys. Lett. **57**, 625–631 (2002)
57. C.C. Lo, T. Chou, T. Penzel, T.E. Scammell, R.E. Strecker, H.E. Stanley, P.C.h. Ivanov, Common scale-invariant pattern of sleep-wake transitions across mammalian species. Proc. Natl. Acad. Sci. **101**, 17545–17548 (2004)
58. M.A. Lomholt, K. Tal, R. Metzler, J. Klafter, Lévy strategies in intermittent search processes are advantageous. Proc. Natl. Acad. Sci. **105**, 11055–11059 (2008)
59. I. Lubashevsky, R. Friedrich, A. Heuer, Realization of Levy flights as continuous processes. Phys. Rev. E **79**(article), 011110 (2009)
60. J.R. Martin, A portrait of locomotor behaviour in Drosophila determined by a video-tracking paradigm. Behav. Process. **67**, 207–219 (2004)
61. J.M. Morales, S.P. Ellner, Scaling up animal movements in heterogeneous landscapes: the importance of behaviour. Ecology **83**, 2240–2247 (2002)
62. J.M. Morales, D.T. Haydon, J. Frair, K.E. Holsinger, J.M. Fryxell, Extracting more out of relocation data: Building movement models as mixtures of random walks. Ecology **85**, 2436–2445 (2004)
63. W.J. O'Brien, H.I. Browman, B.I. Evans, Search strategies of foraging animals. Am. Sci. **78**, 152–160 (1990)
64. A. Okubo, H.C. Chiang, An analysis of the kinematics of swarming behaviour of Anarete pritchardi Kim (Diptera: Cecidomyiidae). Res. Popul. Ecol. **16**, 1–42 (1974)
65. A. Okubo, *Diffusion and Ecological Problems: Mathematical Models* (Springer, Berlin, 1980)
66. O. Ovaskainen, Habitat specific movement parameters estimated using mark-recapture data and diffusion model. Ecology **85**, 242–257 (2004)
67. O. Ovaskainen, H. Rekola, E. Meyke, E. Arjas, Bayesian methods for analyzing movements in heterogeneous landscapes form mark-recapture data. Ecology **89**, 542–554 (2008)
68. M.J. Plank, A. James, Optimal foraging: Lévy pattern or process? R. Soc. Interface **5**, 1077–1086 (2008)
69. S.G. Reebs, Can a minority of informed leaders determine the foraging movements of a fish shoal? Anim. Behav. **59**, 403–409 (2000)

70. A.M. Reynolds, On the intermittent behaviour of foraging animals. Europhys. Lett. **75**, 517–520 (2006)
71. A.M. Reynolds, Deterministic walks with inverse-square power-law scaling are an emergent property of predators that use chemotaxis to located randomly distributed prey. Phys. Rev. E **78**(article), 011906 (2008a)
72. A.M. Reynolds, How many animals really do the Lévy walk? Comment. Ecology **89**, 2347–2351 (2008b)
73. A.M. Reynolds, Lévy flight patterns are predicted to be an emergent property of a bumblebee's foraging strategy. Behav. Ecol. Sociobiol. **64**, 19–23 (2009a)
74. A.M. Reynolds, Adaptive Lévy walks can outperform composite Brownian walks in non-destructive random searching scenarios. Phys. A **388**, 561–564 (2009b)
75. A.M. Reynolds, Bridging the gulf between correlated random walks and Lévy walks: Autocorrelation as a source of Lévy walk movement patterns. R. Soc. Interface **7**, 1753–1758 (2010a)
76. A.M. Reynolds, Can spontaneous cell movements be modelled as Lévy walks? Phys. A **389**, 273–277 (2010b)
77. A.M. Reynolds, Animals that randomly reorient at cues left by correlated random walkers do the Lévy walk. Am. Nat. **175**, 607–613 (2010c)
78. A.M. Reynolds, 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. Phys. A **389**, 4740–4746 (2010d)
79. A.M. Reynolds, Exponential and power-law contact distributions for windborne spores are representative of different atmospheric conditions. Phytopathology **101**, 1465–1470 (2011a)
80. A.M. Reynolds, Chemotaxis can provide biological organisms with good solutions to the travelling salesman problem. Phys. Rev. E **83**, 052901 (2011b)
81. A.M. Reynolds, On the origin of bursts and heavy tails in animal dynamics. Phys. A **390**, 245–249 (2011c)
82. A.M. Reynolds, Truncated Lévy walks are an expected outcome of correlated random walks models: Translating observations taken at small spatiotemporal scales into expected patterns at greater scales. J. R. Soc. Interface **9**, 528–534 (2012d)
83. A.M. Reynolds, A.D. Smith, R. Menzel, U. Greggers, D.R. Reynolds, J.R. Riley, Displaced honeybees perform optimal scale-free search flights. Ecology **88**, 1955–1961 (2007a)
84. A.M. Reynolds, A.D. Smith, D.R. Reynolds, N.L. Carreck, J.L. Osborne, Honeybees perform optimal scale-free searching flights when attempting to locate a food source. J. Exp. Biol. **210**, 3763–3770 (2007b)
85. A.M. Reynolds, C.J. Rhodes, The Lévy flight paradigm: random search patterns and mechanisms. Ecology **90**, 877–887 (2009)
86. A.M. Reynolds, F. Bartumeus, Optimising the success of random destructive searching: Lévy walks can outperform ballistic motions. J. Theor. Biol. **260**, 98–103 (2009)
87. A.M. Reynolds, J.L. Swain, A.D. Smith, A.P. Martin, J.L. Osborne, Honeybees use a Lévy flight search strategy and odour-mediated anemotaxis to relocate food sources. Behav. Sociobiol. **64**, 115–123 (2009)
88. M.C. Santos, E.P. Raposo, G.M. Viswanathan, M.G.E. da Luz, Can collective searches profit from Lévy walk strategies? J. Phys. A **42**(article), 4340174 (2009)
89. F.L. Schuster, M. Levandowsky, Chemosensory responses of *Acanthamoeba castellani*: Visual analysis of random movement and responses to chemical signals. J. Eukaryot. Microbiol. **43**, 150–158 (1996)
90. T.D. Seeley, *Honeybee Ecology: A Study of Adaptation in Social Life* (Princeton University Press, Princeton, 1985)
91. D. Selmeczi, S. Mosler, P.H. Hagedorn, N.B. Larsen, H. Flyvbjerg, Cell motility as persistent random motion: theories from experiments. Biophys. J **89**, 912–931 (2005)
92. M.W. Shaw, Simulation of population expansion and spatial pattern when individual dispersal distributions do not decline exponentially with distance. Proc. R. Soc. B **259**, 243–248 (1995)

93. M.W. Shaw, T.D. Harwood, M.J. Wilkinson, L. Elliott, Assembling spatially explicit landscape models of pollen and spore dispersal by wind for risk assessment. Proc. R. Soc. B **273**, 1705–1713 (2006)
94. M.F. Shlesinger, J. Klafter, Lévy walks versus Lévy flights. In *Growth and Form*, ed. by H.E. Stanley, N. Ostrowski (Martinus Nijhof Publishers, Amsterdam, 1986), pp 279–283
95. Shlesinger, M.F., Zaslavsky, G., Frisch, U. (eds). *Lévy Flights and Related Topics in Physics* (Springer, Berlin, 1995)
96. D.W. Sims, E.J. Southall, N.E. Humphries, G.C. Hays, C.J.A. Bradshaw, J.W. Pitchford, A. James, M.Z. Ahmed, A.S. Brierley, M.A. Hindell, D. Moritt, M.K. Musyl, D. Righton, E.L.C. Shepard, V.J. Wearmouth, R.P. Wilson, M.J. Witt, J.D. Metcalfe, Scaling laws of marine predator search behaviour. Nature **451**, 1098–1102 (2008)
97. J.M. Smith, G.R. Price, The logic of animal conflict. Nature **246**, 15–18 (1973)
98. C. Song, T. Koren, P. Wang, A.L. Barabási, Modelling the scaling properties of human mobility. Nat. Phys. **6**, 818-823 (2010)
99. E. Sparre Andersen, On the fluctuations of sums of random variables. Math. Scand. **1**, 263–285 (1953)
100. E. Sparre Andersen, On the fluctuations of sums of random variables II. Math. Scand. **2**, 195–223 (1954)
101. J. Travis, Ecology: do wandering albatrosses care about math? Science **318**, 742–743 (2007)
102. Y. Tu, G. Grinstein, How white noise generates power-law switching in bacterial flagellar motors. Phys. Rev. Lett. **94**, 208101. (2005)
103. P. Turchin, Fractal analyses of animal movements: a critique. Ecology **77**, 2086–2090 (1996)
104. P. Turchin, *Quantitative Analysis of Movement: Measuring and Modelling Population Redistribution in Animals and Plants* (Sinauer Associates, Sunderland, Massachusetts, 1998)
105. L. Van Valen, A new evolutionary law. Evol. Theor **1**, 1–30 (1973)
106. G.I. Vermeij, *Evolution and Escalation: An Ecological History of Life* (Princeton University Press, Princeton, 1987)
107. G.M. Viswanathan, V. Afanasyev, S.V. Buldyrev, E.J. Murphy, P.A. Prince, H.E. Stanley, Lévy flight search patterns of wandering albatrosses. Nature **381**, 413–415 (1996)
108. G.M. Viswanathan, S.V. Buldyrev, S. Havlin, M.G.E. da Luz, E.P. Raposo, H.E. Stanley, Optimizing the success of random searches. Nature **401**, 911–914 (1999)
109. A.W. Visser, T. Kiørboe, Plankton motility patterns and encounter rates. Oecologia **148**, 538–546 (2006)
110. E.P. White, B.J. Enquist, J.L. Green, On estimating the exponent of power-law frequency distributions. Ecology **89**, 905–912 (2008)
111. H. Wiemerskirsch, D. Pinaud, F. Pawloswski, C.A. Bost, Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. Am. Nat. **170**, 734–743 (2007)
112. L.U. Wingen, J.K.M. Brown, M.W. Shaw, The population genetic structure of clonal organisms generated by exponentially bounded and fat-tailed dispersal. Genetics **177**, 435–448 (2007)