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Understanding Movements of Organisms: It's Time to Abandon the Lévy Paradigm

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Abstract:	<p>1. Interest in Lévy walks within the context of movement of organisms has recently soared, with some now referring to this approach as the Lévy walk/ flight paradigm. The principal assumptions, taken from the world of physics, have been that organisms searching for food or some other resource adopt random walks, whereby the direction of each successive step in the walk is chosen at random from the complete circle and the length of each step, unless terminated through resource encounter, is chosen from a Lévy probability distribution with a particular exponent μ. The additional assumption that organisms forage optimally, such that μ maximises the rate of resource encounter, has led to the so-called Lévy foraging hypothesis, with many attempts to test it.</p> <p>2. However, the Lévy walk model is unrealistic, especially as it omits directionality between successive steps, a typical feature of movements of individual organisms at spatial scales relevant to their movement decisions. It also results in lower foraging efficiency than other more-realistic models and the evidence that organisms actually 'do the Lévy walk' is weak to non-existent, despite claims to the contrary. Early optimal foraging studies of movements of organisms and a new generation of movement models avoid these problems.</p> <p>3. It is therefore time to divorce the Lévy walk model from optimal foraging theory, revisit some of the early optimal foraging studies of movements, and pursue the new generation of movement models. However, the Lévy approach may still prove useful at relatively large spatial scales, in terms of both theory and observations, especially in relation to distribution, dispersal and other population-level phenomena, and in this way biology and physics may yet work well together.</p>

For Review Only

1 Understanding Movements of Organisms: It's Time to Abandon the Lévy Paradigm

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12

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3 soared, with some now referring to this approach as the Lévy walk/ flight paradigm.
4 The principal assumptions, taken from the world of physics, have been that organisms
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13 between successive steps, a typical feature of movements of individual organisms at
14 spatial scales relevant to their movement decisions. It also results in lower foraging
15 efficiency than other more-realistic models and the evidence that organisms actually
16 'do the Lévy walk' is weak to non-existent, despite claims to the contrary. Early
17 optimal foraging studies of movements of organisms and a new generation of
18 movement models avoid these problems.
- 19 3. It is therefore time to divorce the Lévy walk model from optimal foraging theory,
20 revisit some of the early optimal foraging studies of movements, and pursue the new
21 generation of movement models. However, the Lévy approach may still prove useful
22 at relatively large spatial scales, in terms of both theory and observations, especially
23 in relation to distribution, dispersal and other population-level phenomena, and in this
24 way biology, physics and mathematics may yet work well together.

25

1 Introduction

2 Interest in Lévy walks within the context of movement of organisms has soared (Codling &
3 Plank 2011; James, Plank & Edwards 2011; Reynolds 2012c), especially in the last few
4 years, and appears to be growing at an ever-increasing rate (Fig. 1), with some now referring
5 to this approach as the Lévy walk/ flight ‘paradigm’ (Reynolds & Rhodes 2009; Lundy *et al.*
6 2013). It is therefore timely to review this approach and, in the process, consider its basis in
7 terms of biological realism and logic, how useful it has so far been, and its likely future. I
8 shall attempt here to provide such a review.

9 My review will include the following components, considered in turn:

- 10 • movements of organisms from a biological perspective (in order to describe the
11 realistic context in which such movements occur)
- 12 • formulation of movement models (as these are essential for describing and
13 understanding movements)
- 14 • the role of evolution (as it is fundamental to the approach)
- 15 • the Lévy walk (as it defines the approach)
- 16 • optimal foraging (as it combines with the Lévy walk to generate the ‘Lévy
17 hypothesis’)
- 18 • potential problems with the Lévy ‘hypothesis’ (as some are immediately apparent)
- 19 • tests of the hypothesis (as these will determine how useful it is)
- 20 • development of the paradigm and its future; and closing with
- 21 • the potential future for the Lévy-walk approach in the context of organismal
22 movement.

23 Movements of Organisms: A Biological Perspective

24

1 Movement of individuals is an important biological process, exhibited by all organisms. All
2 organisms move at some stage in their lives, with consequences for individuals, populations,
3 species and biological communities (Jones 1977; Nathan *et al.* 2008). Through movement,
4 individual organisms may locate food, mates, shelter, a place in which to live, etc., or may
5 avoid predators or otherwise hazardous conditions (Jones 1977). Such factors affect the lives
6 of all kinds of organisms ranging from bacteria, viruses, and other such 'simple' organisms to
7 more complex multicellular organisms and to the wide variety of animal groups. The
8 movement of individual organisms may determine spatial distributions of populations and
9 species, and hence ultimately the spatial patterns exhibited by biological communities
10 consisting of co-occurring species (Hastings, Petrovskii & Morozov 2011; McLane *et al.*
11 2011; Mueller, Fagan & Grimm 2011; Kawai & Petrovskii 2012).

12 Movement may be active or passive, or a combination of both. Bacteria, for example,
13 propel themselves by rotating flagellar filaments (Berg 2000); animals exhibit an obvious
14 variety of means of locomotion; plants effectively move by growing in one direction or
15 another (Mommer *et al.* 2012). These are all active processes. On the other hand, movement
16 may sometimes be passive, brought about by currents of air or water, as may occur, for
17 example, in the case of pollen, seed and similar plant propagules, certain small invertebrates,
18 and larval stages of some animal groups. Of course, movements may sometimes involve both
19 active and passive processes. In this article, I shall focus on active movement by organisms.

20 Because active movement by individual organisms is such a prevalent and important
21 process, we need models for it, as bases for both description and predictive understanding,
22 and better still if the understanding has a theoretical foundation. For example, a very simple
23 movement model for an organism that is searching for food might consist of the following
24 rule: 'pick a direction at random, move in that direction until a food item is encountered (and
25 possibly consumed), then repeat the process'. Such a model might agree with the observed

1 movements of an organism and hence provide a description of that movement. It might also
2 provide some understanding of the movements, if it can predict how movements will change
3 as circumstances change. If the rule, or how it might change, can itself be predicted, perhaps
4 from a body of theory, then our understanding of the movements would be even more
5 profound. This is essentially what we are trying to achieve.

6 **Models of Organism Movement**

7 All organisms have ‘cognitive’ abilities, with regard to their movements and other
8 kinds of behaviour, as they use sensed information, past and present, about their surrounding
9 environment, to make behavioural choices (Nathan *et al.* 2008); they are hardly inert. Even
10 bacteria, that are generally regarded as relatively simple organisms, are known to respond, in
11 terms of their movements, to spatial and temporal variability in a variety of physical and
12 chemical factors, with such responses affected by previous experience and evolutionary
13 history (Segall, Block & Berg 1986; Hillesland, Velicer & Lenski 2009; Taylor & Stocker
14 2012). Of course, other organisms, especially those considered more complex, are known to
15 have similar, though often more sophisticated, capabilities. We should therefore expect that
16 models of organism movement would reflect such abilities, and would surely be surprised if
17 organisms none-the-less showed movement patterns similar to those exhibited by inert
18 molecules or gas particles, despite the obvious appeal of such a simple approach (Reynolds
19 2010; Gautestad 2011; Ferreira *et al.* 2012).

20 Movements of organisms exhibit variation in direction and speed, the fundamental
21 properties of movement, though it may sometimes be reasonable to assume constant speed.
22 Movement paths, sometimes described as ‘meandering’, obviously demonstrate changes in
23 direction over time (Bond 1980; Visser 2007). Velocities, calculated for a constant time
24 interval between successive ‘locations’ for a moving organism, typically exhibit a frequency

1 distribution over some range of variation (Vanduren & Videler 1995; Tuck & Hassall 2004).
2 Of course, this means that there will also be variation in 'step length' or distance between
3 successive locations when chosen on the basis of a constant time interval (Bovet &
4 Benhamou 1988). However, speed is often either omitted from consideration (Papastamatiou,
5 DeSalles & McCauley 2012) or assumed constant (Miramontes, Boyer & Bartumeus 2012),
6 both of which may be reasonable if variation in speed is small relative to variation in
7 direction, or if speed and direction are unrelated.

8 Movement models for organisms must also, in principle, consider body orientation,
9 because, put simply, all life has a front and rear end; but we can probably omit this
10 consideration in general. Even the 'simplest' organisms, such as bacteria and viruses, have
11 both internal and external structure resulting in an 'axis', with movement generally occurring
12 in a particular direction along this axis (Bovet & Benhamou 1988; Berg 2000). Of course, for
13 such relatively 'simple' organisms, as well as other kinds of organisms as well, the body axis
14 will generally be oriented in the same direction as overall movement (Berg 2000), and so
15 there may generally be no need to consider separately body orientation and movement
16 direction. It may also be reasonable, much of the time, simply to consider movements as
17 changes in spatial location of whole individuals (Nathan *et al.* 2008).

18 Movements of organisms involve changes in body orientation, direction and speed
19 that must be inherently continuous, without any real discontinuities (Bovet & Benhamou
20 1988; Reynolds & Rhodes 2009; Dray, Royer-Carenzi & Calenge 2010; Reynolds 2010;
21 Bazazi *et al.* 2012). Even a bee that has stopped at a flower to obtain nectar or pollen will
22 exhibit continuous changes in these three aspects of movement (Pyke & Cartar 1992). Hence,
23 so long as movements are considered at a spatial scale corresponding to about a body length,
24 or smaller, it is impossible for them to be anything other than continuous. Only if longer
25 spatial scales are considered and movements are divided into successive steps, can

1 movements appear and be modelled as having discontinuities (Bovet & Benhamou 1988;
2 Reynolds & Rhodes 2009; Bazazi *et al.* 2012; Papastamatiou, DeSalles & McCauley 2012).

3 Decisions of organisms, affecting their movements, should also be inherently
4 continuous. Organisms, while moving or doing anything else, continuously face alternative
5 actions and so are continuously able to alter what they are doing (McFarland 1977). Most
6 fundamentally, an organism can stop what it is doing at any instant in time and begin to do
7 something else (McFarland 1977). A bee, for example, can always choose to stop sucking
8 nectar from a flower and to begin to leave the flower, possibly heading to another flower
9 (Hodges & Wolf 1981; Zimmerman 1983). That organisms may respond to their surrounding
10 environment with changes in direction or speed (Noser & Byrne 2007; Papastamatiou,
11 DeSalles & McCauley 2012), indicates that they continuously choose a particular direction
12 and speed for their movement.

13 However, despite the inherently continuous nature of decision-making by organisms
14 and their consequent movements, we need to discretise movement paths and movement
15 decisions in order to describe and model them (Bovet & Benhamou 1988; Reynolds 2010).
16 Movement can be considered mathematically continuous if it is modelled as a diffusion
17 process, or combination of different diffusion processes (Blackwell 1997; Blackwell 2003).
18 Otherwise it varies from difficult to impossible to deal mathematically with continuous
19 movement, especially in real-world situations where there is more than one dimension
20 involved (Bovet & Benhamou 1988; Reynolds 2010; James, Plank & Edwards 2011; Kawai
21 & Petrovskii 2012; Lenz, Chechkin & Klages 2013). If, however, movements are considered
22 to consist of discrete and successive linear 'steps', then they can be described and modelled
23 as a Discrete Time Series process with each movement step being a change in positional
24 state for the process (Schick *et al.* 2008; Langrock *et al.* 2012). If it is additionally assumed
25 that changes in location depend only on current location and arrival direction, then

1 movements may be modelled as a Markov process (Bovet & Benhamou 1988; Reynolds
2 2010; Kawai & Petrovskii 2012; Langrock *et al.* 2012). Such discretisation of movements
3 also allows them to be simulated using Monte Carlo methods (Jones 1977), now made
4 relatively easy through modern computer technology (Bovet & Benhamou 1988; Nathan *et*
5 *al.* 2008). Discretisation of movements is therefore fundamental to both describing and
6 understanding them (Bovet & Benhamou 1988).

7 The spatial scale of fundamental relevance to an individual organism would generally
8 be about one body length, as this is the scale at which an organism senses and responds to its
9 environment. As mentioned above, all organisms, including the biologically simplest, have
10 internal and external structure, coupled with an axis of symmetry and movement, whereby
11 they sense and respond to their surrounds. A bacterium, for example, can detect and respond
12 to chemical changes in its surrounding environment over short time intervals as it moves
13 through it, with consequent effects on rotation of the flagellar filaments located at its rear end
14 (Berg 2000). Any attempt to understand the movements of organisms should therefore
15 include consideration of what happens at this small spatial scale.

16 Larger spatial scales may also be relevant to individual organisms because of their
17 perceptive abilities, memory and communication. If an organism detects things, such as food
18 or predators, at some distance, and responds through movement, then the spatial scale of such
19 perception would be relevant. A bee, for example, that is foraging for floral nectar may
20 generally see from one plant to another, so that a relevant spatial scale for both it, and anyone
21 observing its movements, might be that determined by the inter-plant distances. Organisms
22 may remember, or acquire through communication with others, information concerning
23 locations and their attributes outside of their range of perception, in which case such larger
24 spatial scales could also be relevant. A bee, for example, may have knowledge about

1 locations of food or its nest, and respond to such information through its movements. Of
2 course, for many organisms, the scale of perception will be many times a single body length.

3 The spatial scale at which movements of organisms are recorded may therefore be
4 natural, arbitrary, or limited by available technology. When organisms exhibit naturally
5 intermittent movement behaviour, then a natural spatial scale might be set by the spatial and
6 temporal intervals between ‘interruptions’ to movement (Bazazi *et al.* 2012). Animals, like
7 bees, that fly between flowers provide a good example, where the flower visits may be
8 considered interruptions to movement, and so it would be reasonable and natural to record
9 inter-flower movements as steps in recording of movements. For animals that exhibit bimodal
10 frequency distributions of movement speed, perhaps because they generally move relatively
11 quickly between locations where they feed or rest, a natural spatial scale might be that
12 determined by periods of fast movement being interrupted by periods of slow movement
13 (Benhamou 2007; Bartumeus & Levin 2008; Gautestad 2013a; Gautestad, Loe & Mysterud
14 2013). In situations where the location of an organism is recorded at a very high frequency, as
15 may arise through the use high-speed image-recording technology, and there is no apparent
16 natural spatial scale, any adopted spatial scale will be arbitrary. Obviously, the frequency
17 with which locations of organisms are recorded will determine the smallest possible spatial
18 scale, and this may be limited by technology. If, for example, locations are recorded via
19 attached transmitters and GPS technology, then the smallest possible spatial scale at which
20 movements may be considered will be determined by the frequency and accuracy of the
21 recording system.

22 It is therefore unsurprising that studies of the movements of organisms have been
23 carried out across a wide range of spatial scales. At one end of the spectrum, there are studies
24 that record locations at such a high rate that the average distance between location ‘fixes’
25 may be less than the average body length for the individuals involved. When, for example,

1 movements of bumblebees are recorded at high resolution, the average step length may be
2 less than half a body length (e.g., step length = time interval 0.02 sec x speed 0.275 m/sec =
3 0.55 cm \approx thorax width, 0.56 cm < half body length; Lenz, Chechkin & Klages 2013). At the
4 other end of the spectrum are studies where GPS technology is used and the large time
5 intervals between ‘fixes’ are such that the intervening distances travelled between them
6 would be very large in comparison with average body length. Albatrosses, for example,
7 whose movements have been recorded using attached transmitters and GPS technology
8 (Weimerskirch *et al.* 1993), typically fly at ground speeds of about 10 body lengths or more
9 per second (i.e., body lengths up to about 1m; flight speeds about 10 m/sec) (Wakefield *et al.*
10 2009), and so would cover distances about one thousand body lengths during intervals of 90 s
11 between location recordings (Weimerskirch *et al.* 1993). Female elk, whose movements were
12 recorded at roughly daily intervals, would have covered a similar number of body lengths in
13 moving between recorded locations, as they moved straight-line distances of 1.0 to 1.3 km/d,
14 would probably have covered considerably greater distances if followed continuously, and
15 have body lengths of about 2.1m (Feldhamer *et al.* 2003; Morales *et al.* 2004). In between
16 such extremes, there are studies, often based on natural movement intermittency, where the
17 ratio of step length to body length takes a moderate value. For example, when bumblebees
18 (*Bombus flavifrons* workers) were observed moving between inflorescences of *Aconitum*
19 *columbianum*, the average inter-inflorescence flight distance was about 40 cm (Pyke 1978b),
20 which is about 40 times the average body length for these bees.

21 Directionality of movement, which is the correlation between the directions of
22 successive movement steps (Levin, Kerster & Niedzlek 1971; Jones 1977; Pyke, Pulliam &
23 Charnov 1977; Kareiva & Shigesada 1983), is expected and observed to be a prominent
24 aspect of the movements of organisms, especially at small to moderate spatial scales. Because
25 all organisms move along an axis of symmetry with a front or leading end and a back or

1 trailing end and with ongoing momentum maintained through physical and chemical
2 processes, this correlation must necessarily be close to 1 when movements are considered at a
3 spatial scale of about one body length (Lenz *et al.* 2012). When movements have been
4 considered at spatial/ temporal scales dictated by natural intermittency, directions of
5 successive steps have generally, but not always, been significantly correlated (Zimmerman
6 1979; Pyke 1984). Directionality has sometimes been referred to as ‘directional persistence’
7 (Reynolds 2012d; Gautestad 2013a; Lenz, Chechkin & Klages 2013), and its converse as
8 ‘tortuosity’ (Dicke & Burrough 1988; Schick *et al.* 2008) and ‘sinuosity’ (Bovet &
9 Benhamou 1988; Bartumeus *et al.* 2008).

10 However, directionality will decline with increases in the adopted movement step
11 length or step duration, and so the adopted spatial/ temporal scale (hereafter referred to
12 simply as spatial scale) will profoundly affect the results of analyses of movements by
13 organisms (Kawai & Petrovskii 2012; Gautestad 2013a). Because organisms are likely to be
14 less affected by a previous movement direction with the passage of time and distance, the
15 correlation between successive movement directions should decrease with increasing step
16 duration, as has been observed (de Knegt *et al.* 2007; Lenz, Chechkin & Klages 2013).

17 However, studies at relatively large spatial scales provide little indication of the rate or extent
18 of decline in directionality, because they generally have not considered directionality (Lopez-
19 Lopez *et al.* 2013; Lundy *et al.* 2013; Schultheiss & Cheng 2013), and have obtained variable
20 levels of directionality when they have (Chapperon & Seuront 2013). As will be discussed
21 below, zero directionality is an important assumption in the Lévy walk paradigm.

22 In addition to correlations between successive movement directions, there may also be
23 higher order correlations, as well as correlations between directionality and other aspects of
24 movement (Dray, Royer-Carenzi & Calenge 2010; Bazazi *et al.* 2012). Organisms may, for
25 example, tend to alternate left and right ‘turns’, hence moving in a somewhat ‘zig-zag’

1 manner (Smith 1974a; Pyke 1978b; Visser 2007). There may be a correlation between the
2 change in direction between two successive movement steps and the length of the second
3 step, as can arise if organisms respond to food encounter through both decreased
4 directionality (i.e., turning more) and slower movement (Smith 1974b). Such responses to
5 food encounter are of widespread occurrence and are often referred to as ‘area-restricted
6 searching’ (Curio 1976; Benhamou & Bovet 1989; Mueller, Fagan & Grimm 2011). Other
7 movement correlations are possible, including between the velocities of successive
8 movements, but these and other possibilities have been little investigated (Lenz *et al.* 2012).
9 Like simple directionality, such correlations and responses to food encounter have been
10 omitted from the Lévy walk paradigm (see below).

11 To understand movements of organisms, it is therefore necessary to focus on the
12 movement decision-making processes, determining how they work and trying to predict them
13 (McFarland 1977). It follows from the above discussion that movement of organisms, at
14 spatial scales that are determined by body length, internal state, perceptive abilities and
15 knowledge otherwise acquired, and hence of direct relevance to them, should be viewed as
16 the result of decision-making processes whereby movement direction, distance and speed are
17 continuously adjusted in response to both past and present circumstances. How these
18 processes might be expected to evolve, and hence the adaptive nature of movements, can then
19 be considered, thus imbedding the study of organismal movements into a conceptual and
20 predictive framework.

21 **Evolution of Movement Behaviour**

22 Optimality models may help us to understand movements of organisms, because the
23 mechanisms by which organisms make movement-related decisions are likely to evolve
24 under natural selection, but biological context will always be important in determining the

1 appropriate currency of fitness (McFarland 1977; Pyke, Pulliam & Charnov 1977; Pyke
2 1983). In this case, the general hypothesis is that organisms adopt, as a result of evolution by
3 natural selection, decision-making processes that maximise individual biological fitness as
4 measured by some 'currency' associated with the movements (McFarland 1977; Pyke,
5 Pulliam & Charnov 1977; Pyke 1983). If, for example, the movements occur in the context of
6 foraging, the assumed currency could be some measure of foraging efficiency such as net rate
7 of energy intake (Pyke, Pulliam & Charnov 1977; Pyke 1983). If, however, an organism is
8 moving in order to avoid becoming someone else's meal, then the currency would be related
9 to predation risk, as well as or instead of other factors (Pyke, Pulliam & Charnov 1977; Pyke
10 1983). Context potentially makes a large difference in attempts to understand movements of
11 organisms (Pyke, Pulliam & Charnov 1977; Pyke 1983).

12 It is against the above background of descriptive and predictive models of movement
13 of organisms that the Lévy walk has entered the picture. To it, I now turn my attention.

14 **The Lévy and Other 'Random Walks'**

15 Discretisation leads naturally to organismal movements being described and modelled
16 as 'walks' based on sequences of linear steps, with successive steps determined by certain
17 'rules' of movement. Typically, each step is assumed to start at the end of the previous step,
18 with its direction, distance and speed resulting from the rules. Movement models may have
19 deterministic components as, for example, when step length or speed is assumed constant. On
20 the other hand, they may be stochastic or probabilistic when features of each step, such as
21 length and direction, have probability distributions, so that different outcomes occur with
22 different probabilities.

23 The Lévy walk, falls within a group of walks known as 'random walks', in which the
24 direction of each movement step is chosen 'at random' from all possible directions, the range

1 of which is assumed to be the complete circle. In all such walks, each step is assumed to
2 begin at the end of the preceding step. Within this group of walks, all possible directions for
3 these steps are equally probable, the frequency distribution of changes in direction is
4 therefore uniform, and there is zero correlation between the directions of successive
5 movements (Dray, Royer-Carenzi & Calenge 2010). Such walks contrast with those that
6 incorporate a correlation between successive directions and are generally known to as
7 ‘correlated random walks’ (Dray, Royer-Carenzi & Calenge 2010). Some refer to the former
8 as ‘simple’ or ‘mere’ random walks to distinguish them clearly from correlated random walks
9 (Benhamou 2007; Codling, Plank & Benhamou 2008). Obviously then, right from this initial
10 assumption, random walks depart in an obvious, and potentially significant, way from
11 observed movements of organisms, in which directionality plays a conspicuous and important
12 role.

13 The Lévy walk, here taken to be synonymous with Lévy flight (Reynolds & Rhodes
14 2009; Gautestad 2013b), differs from other random walks in that the length of each
15 movement step, unless terminated through resource encounter, is assumed to be chosen from
16 a Lévy probability distribution. In general a movement step is assumed to end if food, or
17 some other target resource, is encountered, at which point a new movement step is initiated
18 with a new and randomly-chosen direction. With a Lévy walk, in the absence of resource
19 encounter, different step lengths (ℓ) are assumed to occur with probabilities given by $P(\ell) =$
20 $a\ell^{-\mu}$ where the exponent μ lies within the range $1 < \mu \leq 3$ and a is a normalising constant
21 (Viswanathan *et al.* 1999). This probability distribution is sometimes referred to as Pareto,
22 Inverse Power Law or Pareto-Lévy (Edwards 2011; Scafetta 2011; Dagsvik *et al.* 2013). As
23 an alternative model, these step lengths might be generated from Poisson, Negative
24 Exponential, Gaussian or Gamma probability distributions (Gautestad 2011; Gautestad
25 2013b; Lundy *et al.* 2013). Other possibilities also exist.

1 The history of the Lévy-walk indicates a confluence of biology, mathematics and
2 physics. Paul Lévy (1886-1971) was a French mathematician who was interested in
3 probability distributions with certain properties, most notably that the probability distribution
4 for a sum of independent, identically-distributed random variables takes the same form as the
5 probability distribution for each component variable (Lévy 1937). His work found application
6 within physics, especially since about the early 1980s, when it was realized that various kinds
7 of random walk, considered to reflect certain physical processes, could lead to outcomes with
8 Lévy probability distributions (Hughes, Shlesinger & Montroll 1981; Khantha &
9 Balakrishnan 1983; Mukamel, Stern & Ronis 1983). In this context, the Lévy walk has
10 proven particularly useful in studies of processes involving ‘super diffusion’, where diffusion
11 occurs at a faster rate than the ‘normal diffusion’ resulting from Brownian motion (Eliazar &
12 Klafter 2011; Eliazar & Shlesinger 2013). From about the mid-1980s, physicists, with
13 interests in diffusion, have suggested that organisms should adopt Lévy walks when
14 searching for food because this would result in a higher rate of food gain than would result
15 from Brownian movement (Shlesinger & Klafter 1986; Shlesinger 2009), and at the same
16 time, observed that a Lévy probability distribution adequately describes the frequency
17 distribution of observed movement lengths for ants (Shlesinger & Klafter 1986).
18 Subsequently, it was reported that a variety of organisms exhibit similar Lévy walk patterns
19 (Klafter, White & Levandowsky 1990; Viswanathan *et al.* 1996) and suggested that the
20 optimal movement strategies for foraging organisms might be Lévy walks with a particular
21 value of 2 for the exponent μ (Viswanathan *et al.* 1999; Bartumeus *et al.* 2002) (see below).
22 Articles arising from this area of research have been, and continue to be, published in a wide
23 range of journals, representing the interests of both biologists and physicists (biology
24 journals: Carde, Carde & Girling 2012; Reynolds 2012a; Sims *et al.* 2012) (physics journals:
25 Ferreira *et al.* 2012; Lenz *et al.* 2012; Sotelo-Lopez *et al.* 2012).

1 **Optimal Foraging and the Lévy Hypothesis**

2 The Lévy hypothesis arose from a marriage between the Lévy walk model of
3 movements and the optimal foraging approach, leading initially to several predictions
4 depending on the density of the resource and how renewable it is (Viswanathan *et al.* 1999).
5 It had been shown previously that a Lévy walk strategy could be more effective at locating
6 randomly distributed targets than Brownian motion (Cole 1995). In the initial attempt to
7 determine the optimal foraging strategy, the resource targets in the foraging model were
8 assumed to be either ‘depleting’, such that once a target was encountered by the organism it
9 was removed (i.e., never renewed), or ‘non-depleting’ (i.e., instantly renewed), such that it
10 was unaffected by encounter (Viswanathan *et al.* 1999). A forager was assumed to adopt a
11 Lévy walk as a movement strategy and the value of the exponent μ in the associated Lévy
12 probability distribution was allowed to vary to the point that the overall rate of encounter
13 with targets was maximised, and this was then considered to be the optimal search strategy
14 for the organism, and therefore the one that the organism should theoretically adopt
15 (Viswanathan *et al.* 1999; Bartumeus *et al.* 2002; Ferreira *et al.* 2012). The environment
16 surrounding the organism was assumed featureless, conveying no information regarding
17 possible target locations, and the organism was assumed to have no memory concerning its
18 previous movements and resource encounters (Viswanathan *et al.* 1999). The foraging
19 organism was assumed to have some kind of internal mechanism whereby it could generate a
20 Lévy probability distribution of movement step lengths (Rhee *et al.* 2011).

21 It was found that the optimal exponent μ in the Lévy probability distribution, and
22 hence the predicted movement pattern, depended on whether resources were ‘depleting’ or
23 ‘non-depleting’, and on their density relative to the forager’s range of perception. When
24 targets are ‘depleting’, the optimal μ approaches 1, corresponding to ‘ballistic’ movement,
25 with almost no changes in direction at all (Viswanathan *et al.* 1999; Santos *et al.* 2004;

1 Ferreira *et al.* 2012; Yoda *et al.* 2012). On the other hand, if targets are ‘non-depleting’, the
2 optimal μ depends on target density; if target density is low, relative to perception range, then
3 the optimal μ is approximately 2, but if target density is high, then the optimal μ is
4 approximately 3, corresponding to Brownian movement (Viswanathan *et al.* 1999; Ferreira *et al.*
5 *et al.* 2012; Yoda *et al.* 2012). It has subsequently been shown, based on the same movement
6 model, that if target density is low and resource targets are ‘renewable’ after a time delay,
7 then the optimal μ lies somewhere between 1 and 2 (Raposo *et al.* 2009). Other variations of
8 the same movement model with renewable resource targets similarly lead to intermediate
9 values of optimal μ between 1 and 2 if resources are sparsely distributed and an optimal μ of
10 approximately 3 if resource density is high (Reynolds & Rhodes 2009; Ferreira *et al.* 2012).

11 These results in terms of movement theory have led to the so-called ‘Lévy walk/
12 flight/ foraging hypothesis’ (Reynolds & Rhodes 2009; Codling & Plank 2011; Lenz *et al.*
13 2012; Yoda *et al.* 2012; Chapperon & Seuront 2013), here referred to simply as the Lévy
14 hypothesis (Raposo *et al.* 2009), but it has taken a variety of forms. It was initially argued
15 that, in general, the food resources for which organisms are searching are ‘non-depleting’ and
16 occur at low density, such that foraging animals are expected to adopt a Lévy walk movement
17 strategy with an exponent μ of about 2 (Viswanathan *et al.* 1999). That organisms achieve
18 this, through some kind of internal ‘adaptive’ mechanism, has been the principal Lévy
19 hypothesis (Bartumeus 2007; Bartumeus 2009; Reynolds & Rhodes 2009; Reynolds 2012c;
20 Reynolds 2012b). Subsequently, a number of authors have omitted any caveats about the rate
21 at which food renewal occurs, hypothesising that organisms should adopt a Lévy walk
22 movement pattern when food is sparse and Brownian movement when it is abundant (de
23 Knegt *et al.* 2007; Humphries *et al.* 2010; Sueur 2011). A number of authors have
24 additionally omitted any caveats about food abundance, hypothesising that organisms should
25 exhibit a Lévy walk movement pattern because it is the optimal search strategy for randomly

1 distributed targets (Rhee *et al.* 2011). Others have hypothesised that organisms will exhibit
2 Lévy movement patterns, without specifying what the exponent should be (Reynolds 2012d).
3 Some have omitted all caveats, hypothesising simply that organisms should have generally
4 evolved to adopt Lévy search strategies with an exponent of 2 (Lopez-Lopez *et al.* 2013) or
5 to adopt Lévy search strategies without specifying an exponent (Schick *et al.* 2008;
6 Schultheiss & Cheng 2013).

7 **Immediate Problems with Lévy Walk Theory**

8 These different versions of the Lévy walk hypothesis, just like the model upon which
9 they are based, omit so much biological realism that the predictions seem unlikely to be
10 robust, when compared with other, more realistic models. Because the analyses assume that
11 organisms move in accordance with the Lévy model described above (Raposo *et al.* 2003),
12 they maintain the assumption that there is no correlation between directions of successive
13 movement steps, an assumption we know is invalid at spatial scales directly relevant to an
14 organism. Because they allow only for variation in the exponent μ of the Lévy distribution,
15 they restrict comparison to Lévy versus Brownian movement (Raposo *et al.* 2009; James,
16 Plank & Edwards 2011; Ferreira *et al.* 2012; Reynolds 2012b), and do not consider other
17 possible movement models (Hills, Kalff & Wiener 2013). Indeed, adopting more realistic
18 foraging models, especially including patchy food distributions and the possibility of ‘area
19 restricted search’, it has been shown that alternative search strategies can outperform the
20 Lévy walk (Plank & James 2008; James, Plank & Edwards 2011; Hills, Kalff & Wiener
21 2013).

22 It is possible, despite the issues discussed above, that the Lévy foraging theory
23 manages to capture sufficient realism to develop worthwhile and useful predictions. I
24 therefore now turn my attention to tests of the above Lévy hypothesis.

1 Testing the Lévy Hypothesis

2 The Lévy walk hypothesis has led, understandably, to investigations aimed at
3 determining the extent to which movements of organisms are well described by Lévy
4 movement models and how close the observed exponents are to the predicted values, with
5 many authors concluding positively on both counts, sometimes effusively so (Ferreira *et al.*
6 2012; Humphries *et al.* 2012; Reynolds 2012c; Reynolds 2012b; Sims *et al.* 2012; Sotelo-
7 Lopez *et al.* 2012). It has, for example, been suggested that we should expect to find Lévy
8 walks with exponent μ approximately 2 ‘widespread in the animal kingdom’ (Reynolds
9 2012a) and Lévy walks more generally in ‘almost all species’ (Sueur 2011). Many have
10 claimed, based on available evidence, that Lévy movements are exhibited by many species,
11 broadly in nature, and across a diverse taxonomic range (de Jager *et al.* 2011; Carde, Carde &
12 Girling 2012; Hanert 2012; Humphries *et al.* 2012). Some have suggested that this evidence
13 is extensive, growing and compelling (Reynolds 2012d; Reynolds 2012c; Reynolds 2012b;
14 Sims *et al.* 2012).

15 However, as I shall argue below, the empirical evidence supporting the Lévy
16 hypothesis is actually weak to non-existent, because investigations comparing Lévy walk
17 models and observed movement have generally been restrictive in ways strongly biased away
18 from conflicting observations and towards the confirmation or ‘discovery’ of Lévy patterns. I
19 shall discuss each issue in turn.

20 Fundamental to testing the Lévy hypothesis is the assumption that the organisms are
21 searching for food, or other resource, and yet this assumption is often unevaluated, at least
22 explicitly, and it is not always clear how valid it would be. It may sometimes be reasonably
23 clear, for example, when animals such as deer, bees and many others are observed over small
24 spatial scales, that they are indeed searching for food (Heinrich 1979; Focardi, Marcellini &

1 Montanaro 1996). In such situations, of course, it may be equally clear that the observed
2 organisms are not searching for anything, but are probably moving for some other reason,
3 possibly including movement between known locations (Sueur 2011). When locations of
4 organisms are recorded remotely, and over relatively large spatial scales, the extent to which
5 they are foraging may be far from obvious (Sims *et al.* 2008; Humphries *et al.* 2010; Sims *et*
6 *al.* 2012; Lundy *et al.* 2013). Of course, technological advances that permit remote recording
7 of internal body conditions of animals may help in this regard (Hoffmann *et al.* 2012). In any
8 case, the assumption should always be evaluated explicitly.

9 The spatial scales of theory and observations should be comparable, but tests of the
10 Lévy hypothesis have generally been biased towards relatively large spatial scales relative to
11 the body lengths of the organisms involved, leading to spatial scales, at which movement
12 observations have been recorded, being much greater than those at which organisms are
13 making relevant decisions affecting their movements, and hence unlikely to involve
14 behavioural strategies, Lévy or otherwise. In situations, for example, where locations of
15 organisms have been recorded remotely through attached transmitters and GPS technology,
16 as described above, the time intervals between location ‘fixes’ are typically long enough that
17 the organisms would travel large distances between them, possibly thousands of times greater
18 than their body length. A bias towards relatively large spatial scale also arises when
19 discretisation of movements is achieved through adopting a step length such that differences
20 in direction between successive steps exceed a substantial threshold (Bartumeus *et al.* 2003;
21 Rhee *et al.* 2011; Reynolds 2012d; Reynolds 2012a; Schultheiss & Cheng 2013), because
22 increases in step length and decreases in directionality occur together (Gautestad 2013a;
23 Gautestad, Loe & Mysterud 2013). There can be a similar bias when movements are defined
24 by periods of rapid movement separated by periods of slow movement, as such discretisation
25 may reflect large-scale movements, such as between habitats, and have no bearing on how an

1 organism searches for food (Yoda *et al.* 2012). Combining movement steps to form
2 composite steps, based on the first and last point in each sequence, will also enlarge the
3 spatial scale (Chappon & Seuront 2013). In general, the biological context should help to
4 determine whether or not the spatial scale is appropriate.

5 In testing the Lévy hypothesis, or any similar predictions concerning animal
6 behaviour, it is therefore essential to consider explicitly the relationship between the spatial
7 scales of movement decisions by organisms and records of observed movement, trying to
8 ensure that they are as comparable as possible; in many situations this should not be difficult
9 to do, yet apparently it has not so far happened. One way to achieve this would be through
10 consideration of the ratio of the average movement step length to the average body length of
11 the organisms involved. As discussed above, this would reveal ratios ranging from less than 1
12 up to thousands, with various values in between; a logarithmic scale might be warranted. A
13 second way would be to take the ratio of average observed step length to the estimated
14 distance limit of perception for the organisms. This would reveal that movements of bees
15 within and between flower-bearing plants typically occur at a spatial scale commensurate
16 with their abilities to perceive flowers at a distance (Pyke 1978b; Pyke 1979). It might
17 achieve a similar result for movements of birds, such as albatrosses, that can locate food at
18 considerable distances through sight and odour (Mardon *et al.* 2010). Of course, estimating
19 the distance limits of perception may be difficult for some organisms.

20 Testing the Lévy hypothesis requires evaluation of both the directionality of
21 movement, which is assumed zero, and the frequency distribution of movement step lengths,
22 which is predicted to take the form of a Lévy distribution, and yet studies claiming to support
23 the hypothesis have rarely considered directionality. In a recent study of foraging by a marine
24 gastropod it was found that the frequency distributions of angular changes in direction
25 between successive moves were mostly, but not always, uniform, as is required for

1 directionality to be zero (Chapperon & Seuront 2013). Most studies of movement patterns
2 generally find marked and significant directionality and that organisms vary the directionality
3 (or tortuosity) of their movements in response to circumstances (Papastamatiou, DeSalles &
4 McCauley 2012). However, directionality has rarely been included in testing the Lévy
5 hypothesis (Lopez-Lopez *et al.* 2013; Lundy *et al.* 2013; Schultheiss & Cheng 2013). The
6 Lévy hypothesis also assumes that there is no directional bias to movements, but this too has
7 been rarely evaluated (Chapperon & Seuront 2013). The major focus taken in testing the
8 Lévy hypothesis has been on the frequency distribution of movement step lengths
9 (Viswanathan *et al.* 1999).

10 A few investigations, including one seen as providing particularly strong support for
11 the Lévy hypothesis (Humphries *et al.* 2010), may be biased towards discovery of Lévy
12 movement patterns because they consider movements in just a single dimension, the vertical
13 (Sims *et al.* 2008; Sims *et al.* 2012). Consider, for example, a fish that is maintaining itself at
14 a particular depth, because that is where its food is located, and is otherwise moving
15 horizontally in search of such food. Suppose, additionally, that it occasionally shifts its depth
16 by a relatively large amount because it has moved into a region where the depth of its food
17 has changed or where variation in currents or underwater topography warrants a change in
18 swimming depth etc. Then its movements up and down might mostly be small, but with
19 occasional long vertical movements. Hence, an analysis based only on vertical movements,
20 with discretisation of movements determined by when changes in vertical movement
21 occurred (i.e., change from upwards to downwards movement, and vice versa) (Sims *et al.*
22 2008; Humphries *et al.* 2010; Sims *et al.* 2012) could result in a frequency distribution of
23 movement lengths with a 'fat tail' corresponding to the times when the fish shifts the depth at
24 which it is moving. In this way, the investigation may reveal a Lévy pattern, with respect to

1 vertical movements, that has nothing to do with the biology of the animal and is simply a
2 consequence of the analysis methods.

3 Testing the Lévy hypothesis should logically include a comparison between the
4 observed frequency distribution of movement step lengths and a Lévy distribution, but many
5 investigations are biased towards confirmation of Lévy movement patterns because they
6 consider just the part of the frequency distribution of observed step lengths ‘truncated’
7 between arbitrary minimum and maximum step lengths (Gautestad 2012) and hence focus on
8 the portion of the frequency distribution for which a Lévy pattern is observed or might be
9 expected. It is, for example, common practise to restrict analysis to the frequency distribution
10 of step lengths above some minimum threshold (Viswanathan *et al.* 1999; Yoda *et al.* 2012),
11 thus eliminating situations where the distribution of step lengths peaks at some value
12 distinctly greater than zero and generally restricting attention to the ‘tail’ of the distribution
13 (Rhee *et al.* 2011; Lopez-Lopez *et al.* 2013; Schultheiss & Cheng 2013). In some cases, the
14 value of the minimum step length is chosen so that agreement with a Lévy-like distribution is
15 maximised (Clauset, Shalizi & Newman 2009; Lopez-Lopez *et al.* 2013; Lundy *et al.* 2013).
16 Observed step length distributions commonly exhibit distinct non-zero peaks (Heinrich 1979;
17 Lundy *et al.* 2013; Schultheiss & Cheng 2013). In some cases, analysis has been restricted to
18 the portion of the step length distribution for step lengths less than some threshold, with the
19 distribution appearing Lévy-like below the threshold, but exhibiting distinct departures from
20 a Lévy distribution above the threshold (de Jager *et al.* 2011). In other words, analyses of step
21 length distributions have often focussed on those portions most closely resembling a Lévy
22 pattern, leading, probably inevitably, to the conclusion that organisms generally ‘do the Lévy
23 walk’.

24 Testing the Lévy hypothesis should focus on changes in direction that occur in the
25 *absence* of resource encounter and hence on distances between such changes, rather than on

1 distances between resource encounters, which have been considered in some studies. In the
2 Lévy movement model, as described above, the step lengths of a foraging animal are assumed
3 to follow a Lévy distribution *unless* movement is interrupted by resource encounter
4 (Viswanathan *et al.* 1999). Hence, it is necessary to separate movements related to resource
5 encounters from other movements, and only consider the latter, when attempting to test the
6 Lévy hypothesis (Miramontes, Boyer & Bartumeus 2012). In general, this would most likely
7 to be difficult and one study of settling behaviour of marine mussels has done so (de Jager *et*
8 *al.* 2014), but apparently no study of searching behaviour has attempted to do this and the
9 opposite has even been suggested (Edwards *et al.* 2007). Some studies have clearly taken the
10 alternative, and invalid, approach of focusing on movements between resource encounters.
11 For example, movement steps for bumblebees collecting nectar from flowers have been
12 defined as straight-line moves between successively visited flower-clusters, in other words as
13 movements between resource encounters (Heinrich 1979; Viswanathan *et al.* 1999).
14 Similarly, in studies of movements by marine birds, such as albatrosses, that rarely land on
15 the ocean surface except to capture food, the adopted step lengths have been the distances (or
16 times) between these landings (Humphries *et al.* 2012), once again corresponding to
17 movements between resource encounters. In general, the relationship between movements
18 and resource encounter has been unknown.

19 Furthermore, the comparisons, in terms of shape or ‘fit’, between the observed
20 frequency distribution of movement step lengths and various alternative distributions, have
21 not always assessed the ‘goodness of fit’ provided by the Lévy distribution and rarely
22 considered alternative distributions other than the exponential or Poisson, which is expected
23 with Brownian motion, thus creating a further bias towards the Lévy distribution (Clauset,
24 Shalizi & Newman 2009). For example, recent tests of the Lévy hypothesis have generally
25 been based on a comparison of Lévy and exponential distributions (Humphries *et al.* 2012;

1 Lopez-Lopez *et al.* 2013; Schultheiss & Cheng 2013), with Gaussian, Gamma and Log-
2 Normal distributions additionally included in a few cases (Lenz *et al.* 2012; Reyna-Hurtado *et*
3 *al.* 2012; Lundy *et al.* 2013), but no other distributions considered. I previously argued, from
4 an optimal foraging perspective, that the frequency distribution of movement step lengths d
5 might take the form $P(d) = ad \exp(-ad^2/2)$, which is a Rayleigh distribution and is positively
6 skewed (Pyke 1978b; Sun & Han 2010; Raqab 2013), perhaps similarly to a Lévy
7 distribution, but this possibility has not apparently been investigated, nor observed step length
8 distributions compared with a Rayleigh distribution. There are, of course, other possible
9 similarly-skewed distributions and it is possible that no candidate distribution will pass the
10 goodness of fit test.

11 Observations of Lévy movement ‘patterns’ at relatively large spatial scales may tell us
12 little or nothing about underlying movement ‘processes’, because a Lévy movement pattern
13 may be expected to emerge at such spatial scales, when movements either arise from a
14 combination of processes or are affected by spatial heterogeneity (Reynolds 2006; Codling &
15 Plank 2011; Reynolds 2012d), in other words most or all of the time. If, for example,
16 organisms respond to the generally patchy food distributions, as normally occur, with ‘area
17 restricted search’, whereby movement slows and/or becomes more tortuous following food
18 encounter, then the resultant frequency distribution of movement step lengths may resemble a
19 Lévy distribution (Benhamou 2007; Plank & James 2008; Hills, Kalff & Wiener 2013). If an
20 organism exhibits movement directionality that varies in response to environmental
21 heterogeneity and if its movements are discretised on the basis of ‘substantial changes in
22 direction of travel’ then the resulting frequency distribution of step lengths may resemble a
23 Lévy distribution with an exponent of 2 (Reynolds 2012d). These and other such studies have
24 shown that Lévy distributions of step lengths can arise from a variety of foraging scenarios
25 (Boyer *et al.* 2006; Reynolds 2006; Benhamou 2007; Santos *et al.* 2007; Reynolds 2012c;

1 Reynolds 2012b; Gautestad 2013a). Of course, non-Lévy distributions could also arise from a
2 variety of foraging scenarios and there may be general differences between foraging
3 scenarios that lead to Lévy versus non-Lévy step length distributions, which would be most
4 interesting as predicting and/or observing Lévy distributions at large spatial scales would
5 otherwise seem pretty trivial (Stumpf & Porter 2012).

6 It has been argued that signs of Lévy patterns exhibited by organisms, when placed in
7 ‘featureless’ laboratory environments, provide evidence that similar patterns observed under
8 more natural conditions must be mainly ‘internally shaped and governed’ and hence that
9 attempts to explain observed movement patterns should include such internally driven Lévy
10 variability (Cole 1995; Maye *et al.* 2007; Bazazi *et al.* 2012); however, this line of reasoning
11 suffers from the following difficulties. Organisms placed in such environments may respond
12 to features, possibly subtle, that remain, as it is no doubt impossible to create a truly
13 featureless environment. Furthermore, organisms live in heterogeneous worlds such that they
14 should evolve responses, in terms of their movements, to periods of time without encounter
15 with food or other stimuli, and they would therefore be expected to exhibit such responses
16 when placed in featureless lab environments. These responses could include changes,
17 occurring at relatively small spatial scale, to speed, directionality or directional bias, and such
18 responses might (or might not) lead to emergent Lévy-like patterns at larger spatial scales,
19 just as in the models discussed above. In either case, observing a particular movement pattern
20 does not necessitate that it resulted from a particular process (Codling, Plank & Benhamou
21 2008). In addition, as explained above, organisms are continuously making decisions, that
22 affect their movements, in response to changes in their environment, both internal and
23 external. Hence, understanding of movements by organisms will almost certainly arise from
24 consideration of such decision-making processes, and not from imagining that organisms
25 adopt Lévy walk movement strategies. In other words, the answer to the question, as to

1 'whether internal states or external stimuli drive behavioural variability' (Bazazi *et al.* 2012)
2 in regard to movement and other kinds of behaviour, has to be both, not one or the other.

3 It might be argued that strong and positive tests of the Lévy hypothesis have been
4 provided by studies that consider the predicted relationship between Lévy properties of
5 movements and food density (Chapperon & Seuront 2013; de Jager *et al.* 2014), but this
6 would not be valid, because it is not clear that observed differences in food density
7 correspond to those assumed in the Lévy model, assessments of food density have been
8 mostly qualitative and/or lacking supportive evidence, and quantitative tests have yielded
9 results that conflict with the hypothesis. The Lévy model equates low food density with a
10 high ratio of the average distance between food locations to the perceptive distance range of
11 the forager and high food density with situations in which this ratio is close to 1
12 (Viswanathan *et al.* 1999); no test of the Lévy hypothesis has so far considered this ratio.
13 Some tests of hypothesised relationships between food density and movement patterns have
14 been based on observed qualitative differences in food abundance from one area to another
15 (Papastamatiou, DeSalles & McCauley 2012); in most cases little or no supporting empirical
16 evidence has been presented (Humphries *et al.* 2010; Humphries *et al.* 2012; Miramontes,
17 Boyer & Bartumeus 2012; Sims *et al.* 2012; Chapperon & Seuront 2013). In some cases (e.g.,
18 Humphries *et al.* 2010; Sims *et al.* 2012; Chapperon & Seuront 2013), it is difficult to
19 determine whether there has been a genuine test of an a priori prediction or rather a post hoc
20 rationalisation, the latter making the argument essentially circular.

21 One study in which variation in food density has been quantified and patterns of
22 movement compared with expectations from the Lévy hypothesis (Bartumeus *et al.* 2003),
23 has yielded results that conflict with these expectations. In this study the predators were the
24 dinoflagellate *Oxyrrhis marina*, a very small animal, about 40 μm long and 15 μm wide
25 (Breckels *et al.* 2011; Roberts *et al.* 2011), and its prey were the even smaller algae

1 *Rhodomonas* sp, which are roughly spherical in shape with a diameter of about 8 μ m.
2 Assuming a chemical ‘phycosphere’ surrounding each *Rhodomonas* cell equal in width to up
3 to four times its radius, enabling detection by an *Oxyrrhis* when its path intersects this
4 phycosphere (Breckels *et al.* 2011), the effective radius of detection for *Oxyrrhis* searching
5 for *Rhodomonas* would be at most about 27.5 μ m (i.e., half *Oxyrrhis* width plus 5 times
6 *Rhodomonas* radius). At the highest prey density, which was reported to be in the range 10⁴
7 to 10⁵ per ml, the average distance from one prey item to its nearest neighbour would have
8 been about 215-464 μ m, some 8-17 times the above maximum likely perceptible range of the
9 predators. Other observed prey densities ranged down by a further four orders of magnitude
10 to just 10 per ml. Hence, from the Lévy hypothesis perspective, the observed prey densities
11 were all low to very low, and so Lévy rather than Brownian movements would be expected
12 all the time. Instead, however, Brownian movement was reported for the highest range of
13 prey densities (Bartumeus *et al.* 2003). In addition, since the predatory *Oxyrrhis* completely
14 consume their *Rhodomonas* prey (Hansen, Witte & Passarge 1996) which equates to
15 ‘destructive foraging’ (sensu Viswanathan *et al.* 1999), the frequency distribution of step
16 lengths is expected, according to the Lévy hypothesis, to resemble a Lévy distribution with
17 exponent close to 1 (i.e., near straight line or ballistic movement; Viswanathan *et al.* 1999;
18 Raposo *et al.* 2009), rather than the reported values that were near 2 (Bartumeus *et al.* 2003).

19 A second study (de Knegt *et al.* 2007), in which resource densities were high, also
20 produced results that conflict with the Lévy hypothesis. In this study, goats were observed
21 foraging by browsing on randomly scattered bushes and trees (referred to collectively as
22 ‘patches’), and grazing on a homogeneous grass layer in between. It was assumed, as might
23 be reasonable, that movement patterns were unaffected by grazing. The goats were observed
24 in two areas, with patch densities of 178 and 294 per ha, corresponding to average inter-patch
25 distances of about 7.5 and 5.8m respectively, which are similar to one another and

1 presumably relatively short relative to goat vision, such that the goats should be able to
2 constantly see a number of patches in both areas. Consequently, as the ratio of inter-patch
3 distance to perceptive range of the goats would thus have been less than 1 in both areas,
4 observed movements by the goats should have been Brownian in both areas, not Brownian in
5 the area with the higher patch density and Lévy in the other area, as was reported (de Knecht
6 *et al.* 2007). The authors rationalised their results by suggesting that goat vision was an
7 important component for foraging in the area with the higher patch density but negligible
8 when patch density was lower (de Knecht *et al.* 2007), a highly unlikely possibility. In
9 addition, since renewal of the plant material browsed, and hence consumed, by the goats,
10 would probably take a long time relative to the times that goats typically spend browsing in
11 any particular area, the expected exponent of the Lévy distribution would have been close to
12 1 and significantly less than the value of 2.1 reported for the area with the lower patch density
13 (de Knecht *et al.* 2007). Furthermore, in comparing observed and Lévy movement
14 distributions, the study restricts movement steps (referred to as ‘flights’) to combined
15 movements between points corresponding to relatively large departures from linear
16 movement (de Knecht *et al.* 2007), thus biasing results as described above.

17 Difficulties of a purely statistical nature have also been encountered in attempting to
18 determine whether observed step length distributions are best fit by Lévy or some other
19 distribution, leading to a somewhat separate area of research interest (Reynolds & Rhodes
20 2009). Initial statistical methods were shown to be fundamentally flawed (Edwards *et al.*
21 2007; Edwards 2011; Edwards *et al.* 2012). Subsequently, improved methods have been
22 developed and adopted (Sims *et al.* 2008; Reynolds *et al.* 2009). However, not surprisingly,
23 these new methods also have associated problems such as the requirement that sample sizes
24 must be large (Lomholt *et al.* 2008; Sims *et al.* 2012). In any case, given all the other
25 problems associated with the Lévy walk hypothesis, this concern about statistical

1 methodology in fitting distributions to step length frequencies might seem to be like the
2 proverbial ‘red herring’, and not something warranting much future attention (Gautestad
3 2013b; Gautestad, Loe & Mysterud 2013). On the other hand, any attempts to characterise
4 movement patterns, including considering possible Lévy-type distributions, should use
5 appropriate statistical techniques (Clauset, Shalizi & Newman 2009).

6 Evidence that organisms ‘do the Lévy walk’ in the manner predicted is therefore weak
7 to non-existent. As described above, studies purporting to test the Lévy hypothesis suffer
8 from many problems. All of the supposed tests of the hypothesis suffer from one or other of
9 these problems, most suffer from several combined problems, and no study currently exists
10 that is without such problems.

11 **Seeking a ‘Paradigm’ for Understanding Movements of Organisms**

12 Despite all the above issues and difficulties, the Lévy hypothesis has been labelled a
13 ‘paradigm’ (Plank & James 2008; Reynolds & Rhodes 2009; Reynolds 2010; Lundy *et al.*
14 2013), an apt description because this approach has been dictating the ways in which research
15 is carried out and results interpreted. Many studies have developed theoretical models of
16 searching for food or other targets based on the assumption that organisms move according to
17 the Lévy model (Viswanathan *et al.* 1999; Raposo *et al.* 2009; Ferreira *et al.* 2012; Reynolds
18 2013). The original model and optimality approach has been extended, while retaining its
19 essence, to allow for different spatial distributions of resources (Preston, Pitchford & Wood
20 2010), resource renewal (Raposo *et al.* 2003; Santos *et al.* 2004), moving targets (Bartumeus
21 *et al.* 2002; Viswanathan *et al.* 2002), variation in perceptive ability (Reynolds 2006), and
22 memory effects (Gautestad 2011; Ferreira *et al.* 2012). In one recent study, the movement
23 model has been modified to allow for movements that, rather than being Lévy walks, are
24 composite walks, consisting of Brownian random walks with different scaling parameters that

1 are adopted with certain probabilities; if the organism optimises these probabilities and
2 resources are non-depleting, then its frequency distribution of movement step lengths is
3 predicted to appear Lévy-like (Reynolds 2013). Following the realization that composite
4 Brownian motion movement could lead to Lévy-like movement patterns, the so-called ‘power
5 law in disguise’ paradox, further investigation focused on ways to distinguish between Lévy
6 and composite Brownian processes (Gautestad 2012; Gautestad 2013a), both of which
7 assume random directions of successive movements. Attempts have been made to determine
8 internal processes whereby organisms might generate Lévy-like patterns (Reynolds 2011;
9 Bazazi *et al.* 2012; Gautestad 2012). The theoretical studies have led to a large and rapid
10 increase in empirical studies, mostly seeking to discover or confirm Lévy patterns, and
11 sometimes attempting to relate changes in Lévy pattern to changes in food distribution
12 (Humphries *et al.* 2012). The Lévy approach has been extended to other kinds of search
13 situations including mate search through the location of odour trails (Carde, Carde & Girling
14 2012), mussels choosing a place to settle (de Jager *et al.* 2014), and location of a food source
15 on the basis of its approximate location (Reynolds *et al.* 2007; Reynolds 2008).

16 The proponents of the Lévy hypothesis seem largely determined to maintain the view
17 that it describes how organisms are expected and observed to move, despite all its faults. The
18 theoreticians modify their models, but the outcome remains essentially the same: organisms
19 are expected to exhibit Lévy-like movement patterns. The empiricists continue to look for,
20 and find, observations consistent with these expected Lévy patterns, while adopting
21 procedures that could hardly fail, and omitting or ignoring conflicting evidence. In some
22 cases, for example, movement has been recognised as being non-random in various respects,
23 but none-the-less analysed from the perspective of Lévy versus Brownian movement (Rhee *et*
24 *al.* 2011; Sueur 2011). Some have sought to determine internal mechanisms whereby an
25 individual organism might exhibit Lévy movements (Reynolds 2011; Bazazi *et al.* 2012).

1 Many have claimed that the hypothesis is well supported, both theoretically and empirically
2 (Reynolds 2011; Sims *et al.* 2012; Schultheiss & Cheng 2013). Literature relating directly to
3 the Lévy hypothesis has been relatively self-contained with reviews, and articles in general,
4 paying little apparent attention to articles from outside this area of research. That all of this
5 continues to occur despite the problems and issues discussed above, indicates a considerable
6 reluctance to move on from the Lévy paradigm, despite suggestions that this might now be
7 warranted (Reynolds 2012d).

8 It is time now to abandon the Lévy hypothesis as a paradigm of movements of
9 organisms. There is really little or no reason why organisms should be expected to possess
10 internal ‘processes’ that produce Lévy ‘patterns’, and good reason why they should adopt
11 very different processes (James, Plank & Edwards 2011). At spatial scales relevant to
12 individual organisms there is little or no evidence of Lévy walk patterns, and much evidence
13 of quite different movement patterns (see discussion above). At large spatial scale, Lévy
14 patterns may seemingly arise, as ‘emergent’ properties, from any realistic, and hence
15 complex, model of movement, and so any apparent observations of Lévy movement patterns
16 may tell us little or nothing about the underlying movement processes (Codling & Plank
17 2011; Reynolds 2012d). This view is reinforced by the observation that Lévy patterns may
18 also occur when movement is assumed to arise as a composite mixture of components as
19 simple as Brownian motion (Gautestad 2012; Gautestad 2013a), and would probably also
20 arise if the components included movement directionality. Of course, the ‘Lévy paradigm’
21 has arguably led to much worthwhile research (Reynolds 2012a); but it is surely time to let it
22 go and seek a replacement.

23 The original attempts to describe and understand forager movements via optimal
24 foraging theory embraced all the desirable attributes discussed above, and therefore provide
25 an alternative to the Lévy walk approach. Most fundamentally, the early studies of

1 movements of organisms acknowledged ‘directionality’ as an important aspect of such
2 movements (Siniff & Jessen 1969; Cody 1971; Smith 1974b) and hypothesised that
3 organisms would adopt movement decision processes resulting in maximal biological fitness
4 and/or foraging efficiency (Cody 1971; Smith 1974b; Pyke, Pulliam & Charnov 1977). They
5 also recognised that an organism would alter their movement patterns in response to
6 encounters with food and other resources, on account of patchy resource distributions (Smith
7 1974b; Curio 1976; Pyke 1984), and also by what it otherwise perceived and remembered,
8 about its environment and its previous movements (Smith 1974a; Jones 1977; Pyke, Pulliam
9 & Charnov 1977). They considered speed of movement from an optimal foraging perspective
10 (Ware 1975; Weihs 1975; Pyke, Pulliam & Charnov 1977; Pyke 1978b; Pyke 1981). Despite
11 the relatively limited nature of computer technology available at the time, they developed
12 computer-based simulation models of movements by foraging organisms (Siniff & Jessen
13 1969; Cody 1971; Jones 1977; Pyke 1978a). In short, these early studies had all the basic
14 ingredients (Pyke 1983).

15 Some authors have recently revisited such an approach, labelling their models
16 variously, but essentially synonymously, as ‘Artificial Neural Networks’ (i.e., ANN)
17 (Morales *et al.* 2005; Mueller, Fagan & Grimm 2011), ‘Individual Based Models’ (i.e., IBM)
18 (Stillman 2008; Giuggioli, Potts & Harris 2011) and ‘Agent Based Models’ (i.e., ABM)
19 (Nonaka & Holme 2007; McLane *et al.* 2011), or describing their approach as a new
20 ‘movement ecology’ paradigm (Nathan *et al.* 2008). In all cases, it is assumed that the
21 environment, through which an individual moves, can be represented by a two- or three-
22 dimensional grid of cells, such that spatial and temporal variation in relevant factors, biotic or
23 abiotic, are modelled through variation in these factors within and among cells. A patchy
24 food distribution, for example, may be setup through defining nearby cells to have similar
25 levels of food abundance (Stillman 2008; Mueller, Fagan & Grimm 2011). Movement is

1 assumed to be between grid cells and is modelled through rules that specify when the
2 individual will leave a particular cell and which cell it will move to next. Visits to cells may
3 change cell properties, as, for example, when food is encountered and consumed. Movement
4 rules may include information concerning the individual's internal state, as well as locations
5 and properties of visited cells, past and present, and of unvisited cells that it can perceive
6 from its current cell. Information concerning previously visited cells may be based on
7 relatively recent experience, such as might arise through previous visits to just one or a few
8 cells, long-term memory, or information that is passed from one individual to another through
9 communication or genetic transmission (Mueller, Fagan & Grimm 2011). Of course, these
10 possibilities exist as part of a continuum, and may occur in combination (Mueller, Fagan &
11 Grimm 2011). It is finally assumed that the movement rules will have evolved, based on
12 some currency of fitness such as net rate of energy intake, to the point that fitness is
13 maximised (Stillman 2008; McLane *et al.* 2011). The rule that maximises fitness may be
14 determined either directly or through a genetic algorithm that models the evolutionary
15 process (Mueller, Fagan & Grimm 2011); the outcomes seem likely to be the same. The end
16 result is the hypothesised 'optimal' movement rule, which can then be used as a basis for
17 comparison between observed and predicted patterns of movement. Of course, advancing
18 computer technology has facilitated the development of such simulation models (Nathan *et*
19 *al.* 2008).

20 In addition, Inferential Models have recently been developed for situations in which
21 movement data are collected remotely, without direct observations on animals, their food or
22 their predators, but often with broadscale information about the local environment, and
23 sometimes information about the state or behaviour of the animals involved (Schick *et al.*
24 2008; Hanks *et al.* 2011; McClintock *et al.* 2012). Through telemetry technology it is now
25 possible, for example, to track animal movements, sometimes over short time intervals, while

1 simultaneously recording changes indicative of various behaviours such as resting, feeding or
2 food ingestion, superimposed on spatial and temporal variation in habitat, topography or
3 other environmental variables (McClintock *et al.* 2012; Bestley *et al.* 2013). In such
4 situations, animal movement can be modelled as a mixture of specified processes (e.g.,
5 random walks), with unknown defining parameters and switch points, and then these
6 unknown variables can be estimated using Bayesian inferential statistics (Morales *et al.* 2004;
7 McClintock *et al.* 2012; McClintock *et al.* 2013). In some cases it may be reasonable to
8 assume that observations, though variable, are made with zero error (Morales *et al.* 2004); in
9 other cases, such as in so-called State-Space Models, it may be considered necessary to allow
10 for observational error (Patterson *et al.* 2008; Schick *et al.* 2008; Hanks *et al.* 2011).
11 Computer technology generally assists here as well, given the nature and extent of the
12 required statistical calculations (Patterson *et al.* 2008). The end result can be a model of
13 animal movement that accords with what is otherwise known about the biology of the
14 animals involved (Morales *et al.* 2004; Schick *et al.* 2013).

15 This approach might be further evaluated by comparing its output with the results of
16 direct observation, in situations where animals can be simultaneously tracked remotely *and*
17 observed directly, as they interact with other entities such as food, conspecifics and predators.
18 For example, it should now be possible to remotely follow and map the movements of nectar-
19 feeding animals, of bee-size or larger, while simultaneously and continuously observing their
20 behaviour along with the behaviour of other relevant organisms (Hagen, Wikelski & Kissling
21 2011; Osborne *et al.* 2013; Fischer *et al.* 2014). In this context, it should also be possible to
22 experimentally manipulate the local environment and to determine the consequences through
23 both inferential modelling and direct observation. One might hope or expect that an
24 inferential model, based on just a map and time-course of movements, outlines of the spatial

1 distributions of certain habitat features such as vegetation type, and the general biology of the
2 animals, would compare well with the results of direct observation.

3 In attempting to understand movements of organisms as they forage or search for
4 other resources, the time has therefore come to divorce the Lévy walk model from optimal
5 foraging theory (Reynolds 2012d), revisit some of the early optimal foraging studies of
6 movements, and pursue the new generations of movement models (i.e., ANN, IBM, ABM
7 and the like, as well as Inferential Models). At spatial scales relevant to individual organisms,
8 Lévy walks are neither optimal, and hence expected, nor observed. At larger spatial scales,
9 Lévy patterns may sometimes be both expected and observed, but simply as emergent
10 properties of movement complexity, and not informing anything about underlying biological
11 processes. Through their focus on spatial scales and movement processes relevant to the
12 movement of individual organisms, Individual-Based Models of foraging organisms, and
13 other similar new-age models, have much potential. Through developing an understanding of
14 animal movements when there has been limited or no direct observation, Inferential Models
15 may also contribute significantly. Further attempts should now be made to realise all of this
16 potential.

17 **Future Usefulness of Lévy Walk Approach**

18 Despite the need to abandon the so-called Lévy paradigm for understanding
19 movements of organisms, the random walk approach in general, and Lévy approach in
20 particular, may still prove useful at relatively large spatial scales, in terms of both theory and
21 observations (Gautestad 2011; McLane *et al.* 2011; Gautestad 2013a; Gautestad, Loe &
22 Mysterud 2013), and in this way biology, physics and mathematics may yet work well
23 together. It would, for example, be interesting and worthwhile to know the extent to which
24 Lévy patterns would be expected to occur as 'emergent properties' of large-scale movement

1 scenarios and to test such expectations empirically (Reynolds 2012d; Reynolds 2012a). Of
2 course, IBMs and the like, as discussed above, could be used as components of such
3 movement scenarios (Bonnell *et al.* 2013). It may turn out that analyses at the lowest spatial
4 scale, where organisms are making movement decisions, may be considered ‘mechanistic’ (or
5 biological), while those at large spatial scale are more ‘statistical mechanical’ in nature
6 (Gautestad 2013a; Gautestad, Loe & Mysterud 2013). The resulting understanding of
7 movements of organisms at large spatial scales could then be used in attempts to understand
8 other phenomena that occur at even larger spatial scales, such as dispersal and spread of
9 populations, and the resulting patterns of distribution (Levin 1992; Giuggioli & Bartumeus
10 2012; Hanert 2012). Such a process has been referred to as ‘scaling up’ by a number of
11 authors (Morales & Ellner 2002; Schick *et al.* 2008; Reynolds 2012d). Hence, through a joint
12 focus on phenomena occurring at relatively large spatial scale, biology, physics and
13 mathematics may work well together (Gautestad 2013b).

14 **Future Understanding of Movements and Distribution of Organisms**

15 To understand patterns of movement of organisms, they should be viewed, within an
16 evolutionary framework, as being the result of decision-making processes occurring at spatial
17 and temporal scales that are directly relevant to the organisms involved. Scale will then
18 depend primarily on body length, internal state, perceptive abilities and knowledge otherwise
19 acquired, and decisions made by organisms may result in continuous adjustment to direction,
20 distance and speed of movement. The optimality approach will likely provide a suitable
21 evolutionary framework, and discretization of the processes should help with their analysis
22 and modelling.

23 Unfortunately, the Lévy walk hypothesis and its associated paradigm, which arise
24 from a marriage between the Lévy walk model of movements and the optimal foraging

1 approach, fail to provide such an understanding of organismal movements, despite all the
2 enthusiasm that has been expressed about them. The Lévy model is biologically unrealistic,
3 especially as it omits 'directionality' of movements. Some tests have been invalid or
4 otherwise inadequate; others have been biased towards confirmation of Lévy patterns. No test
5 is so far without such problems, and quantitative tests provide results that clearly conflict
6 with expectations under Lévy walk hypothesis. The Lévy paradigm has encouraged
7 acceptance of the Lévy hypothesis, directed research towards its confirmation, and
8 discouraged consideration of alternative approaches.

9 Fortunately, however, there *are* worthwhile alternatives to the Lévy walk hypothesis
10 and its associated paradigm. One such alternative arises from modelling approaches that date
11 back to the early days of Optimal Foraging Theory and have been revamped as Individual-
12 Based Models and the like. Another alternative is to develop Inferential Models, especially in
13 situations where it has not been possible to directly observe encounters between organisms
14 and elements, such as food, that affect them.

15 It is also possible, especially at relatively large spatial scales, that Lévy and other
16 patterns will prove useful, thus continuing the confluence between biology, physics and
17 mathematics. The Lévy distribution may provide descriptions of movements at such scales,
18 and so be incorporated into investigations of distributions of organisms and other population-
19 level phenomena. Lévy distributions may also be expected under certain circumstances,
20 especially those analogous to diffusion, and similar processes, which have long-time been of
21 interest within the combined area of physics and mathematics.

22 The best path forward in terms of understanding movements and distribution of
23 organisms can therefore be simply stated: Abandon the Lévy movement paradigm for spatial
24 scales, generally relatively small to moderate, relevant to individual organisms; pursue other

1 modelling approaches such as the new generation of individual-based and inferential models;
2 continue, at larger spatial scales, to evaluate Lévy and other patterns as descriptions and
3 expectations for movement patterns, and as components affecting distribution and other
4 population-level phenomena; maintain the dialogue and collaboration between biology,
5 physics and mathematics.

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12 References

- 13 Bartumeus, F. (2007) Levy processes in animal movement: An evolutionary hypothesis. *Fractals-*
14 *Complex Geometry Patterns and Scaling in Nature and Society*, **15**, 151-162.
- 15 Bartumeus, F. (2009) Behavioral intermittence, Lévy patterns, and randomness in animal movement.
16 *Oikos*, **118**, 488-494.
- 17 Bartumeus, F., Catalan, J., Fulco, U.L., Lyra, M.L. & Viswanathan, G.M. (2002) Optimizing the
18 encounter rate in biological interactions: Lévy versus Brownian strategies. *Physical Review*
19 *Letters*, **88**.
- 20 Bartumeus, F., Catalan, J., Viswanathan, G.M., Raposo, E.P. & da Luz, M.G.E. (2008) The influence of
21 turning angles on the success of non-oriented animal searches. *Journal of Theoretical*
22 *Biology*, **252**, 43-55.
- 23 Bartumeus, F. & Levin, S.A. (2008) Fractal reorientation clocks: linking animal behavior to statistical
24 patterns of search. *Proceedings of the National Academy of Sciences*, **105**, 19072–19077.
- 25 Bartumeus, F., Peters, F., Pueyo, S., Marrase, C. & Catalan, J. (2003) Helical Lévy walks: Adjusting
26 searching statistics to resource availability in microzooplankton. *Proceedings of the National*
27 *Academy of Sciences of the United States of America*, **100**, 12771-12775.
- 28 Bazazi, S., Bartumeus, F., Hale, J.J. & Couzin, I.D. (2012) Intermittent Motion in Desert Locusts:
29 Behavioural Complexity in Simple Environments. *Plos Computational Biology*, **8**, e1002498.
- 30 Benhamou, S. (2007) How many animals really do the Levy walk? *Ecology*, **88**, 1962-1969.
- 31 Benhamou, S. & Bovet, P. (1989) How animals use their environment: a new look at kinesis. *Animal*
32 *Behaviour*, **38**, 375-383.
- 33 Berg, H.C. (2000) Motile Behavior of Bacteria. *Physics Today*, **53**, 24-29.
- 34 Bestley, S., Jonsen, I.D., Hindell, M.A., Guinet, C. & Charrassin, J.-B. (2013) Integrative modelling of
35 animal movement: incorporating in situ habitat and behavioural information for a migratory
36 marine predator. *Proceedings of the Royal Society B-Biological Sciences*, **280**.

- 1 Blackwell, P.G. (1997) Random diffusion models for animal movement. *Ecological Modelling*, **100**,
2 87-102.
- 3 Blackwell, P.G. (2003) Bayesian inference for Markov processes with diffusion and discrete
4 components. *Biometrika*, **90**, 613-627.
- 5 Bond, A.B. (1980) Optimal Foraging in a Uniform Habitat the Search Mechanism of the Green
6 Lacewing *Chrysopa carnea*. *Animal Behaviour*, **28**, 10-19.
- 7 Bonnell, T.R., Dutilleul, P., Chapman, C.A., Reyna-Hurtado, R., Uriel Hernandez-Sarabia, R. &
8 Sengupta, R. (2013) Analysing small-scale aggregation in animal visits in space and time: the
9 ST-BBD method. *Animal Behaviour*, **85**, 483-492.
- 10 Bovet, P. & Benhamou, S. (1988) Spatial analysis of animals' movements using a correlated random
11 walk model. *Journal of Theoretical Biology*, **131**, 419-433.
- 12 Boyer, D., Ramos-Fernández, G., Miramontes, O., Mateos, J.L., Cocho, G., Larralede, H., Ramos, H. &
13 Rojas, F. (2006) Scale-free foraging by primates emerges from their inter-action with a
14 complex environment. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1743-
15 1750 &/or 1595.
- 16 Breckels, M.N., Roberts, E.C., Archer, S.D., Malin, G. & Steinke, M. (2011) The role of dissolved
17 infochemicals in mediating predator-prey interactions in the heterotrophic dinoflagellate
18 *Oxyrrhis marina*. *Journal of Plankton Research*, **33**, 629-639.
- 19 Carde, R.T., Carde, A.M. & Girling, R.D. (2012) Observations on the flight paths of the day-flying moth
20 *Virbia lamae* during periods of mate location: do males have a strategy for contacting the
21 pheromone plume? *Journal of Animal Ecology*, **81**, 268-276.
- 22 Chapperon, C. & Seuront, L. (2013) Temporal shifts in motion behaviour and habitat use in an
23 intertidal gastropod. *Journal of the Marine Biological Association of the United Kingdom*, **93**,
24 1025-1034.
- 25 Clauset, A., Shalizi, C.R. & Newman, M.E.J. (2009) Power-law distributions in empirical data. *SIAM*
26 *Review*, **51**, 661-703.
- 27 Codling, E.A. & Plank, M.J. (2011) Turn designation, sampling rate and the misidentification of power
28 laws in movement path data using maximum likelihood estimates. *Theoretical Ecology*, **4**,
29 397-406.
- 30 Codling, E.A., Plank, M.J. & Benhamou, S. (2008) Random walk models in biology. *Journal of the*
31 *Royal Society Interface*, **5**, 813-834.
- 32 Cody, M.L. (1971) Finch flocks in the Mohave Desert. *Theoretical Population Biology*, **2**, 142-158.
- 33 Cole, B.J. (1995) Fractal time in animal behaviour: the movement activity of *Drosophila*. *Animal*
34 *Behaviour*, **50**, 1317-1324.
- 35 Curio, E. (1976) *The ethology of predation*. Springer, Berlin/Heidelberg/New York.
- 36 Dagsvik, J.K., Jia, Z., Vatne, B.H. & Zhu, W. (2013) Is the Pareto-Lévy law a good representation of
37 income distributions? *Empirical Economics*, **44**, 719-737.
- 38 de Jager, M., Bartumeus, F., Kolzsch, A., Weissing, F.J., Hengeveld, G.M., Nolet, B.A., Herman, P.M.J.
39 & de Koppel, J.v. (2014) How superdiffusion gets arrested: ecological encounters explain
40 shift from Levy to Brownian movement. *Proceedings of the Royal Society B-Biological*
41 *Sciences*, **281**.
- 42 de Jager, M., Weissing, F.J., Herman, P.M.J., Nolet, B.A. & van de Koppel, J. (2011) Levy Walks Evolve
43 Through Interaction Between Movement and Environmental Complexity. *Science*, **332**, 1551-
44 1553.
- 45 de Knegt, H.J., Hengeveld, G.M., van Langevelde, F., de Boer, W.F. & Kirkman, K.P. (2007) Patch
46 density determines movement patterns and foraging efficiency of large herbivores.
47 *Behavioral Ecology*, **18**, 1065-1072.
- 48 Dicke, M. & Burrough, A.P. (1988) Using fractal dimensions for characterizing the tortuosity of
49 animal trails. *Physiological Entomology*, **13**, 393-398.
- 50 Dray, S., Royer-Carenzi, M. & Calenge, C. (2010) The exploratory analysis of auto correlation in
51 animal-movement studies. *Ecological Research*, **25**, 673-681.

- 1 Edwards, A.M. (2011) Overturning conclusions of Levy flight movement patterns by fishing boats and
2 foraging animals. *Ecology*, **92**, 1247-1257.
- 3 Edwards, A.M., Freeman, M.P., Breed, G.A. & Jonsen, I.D. (2012) Incorrect Likelihood Methods Were
4 Used to Infer Scaling Laws of Marine Predator Search Behaviour. *PLoS ONE*, **7**.
- 5 Edwards, A.M., Phillips, R.A., Watkins, N.W., Freeman, M.P., Murphy, E.J., Afanasyev, V., Buldyrev,
6 S.V., da Luz, M.G.E., Raposo, E.P., Stanley, H.E. & Viswanathan, G.M. (2007) Revisiting Lévy
7 flight search patterns of wandering albatrosses, bumblebees and deer. *Nature*, **449**, 1044-
8 1048.
- 9 Eliazar, I. & Klafter, J. (2011) Anomalous is ubiquitous. *Annals of Physics*, **326**, 2517-2531.
- 10 Eliazar, I.I. & Shlesinger, M.F. (2013) Fractional motions. *Physics Reports-Review Section of Physics
11 Letters*, **527**, 101-129.
- 12 Feldhamer, G.A., Thompson, B.C., Chapman, J.A., Feldhamer, G.A., Thompson, B.C. & Chapman, J.A.
13 (2003) *Wild mammals of North America: biology, management, and conservation. Second
14 edition.*
- 15 Ferreira, A.S., Raposo, E.P., Viswanathan, G.M. & da Luz, M.G.E. (2012) The influence of the
16 environment on Levy random search efficiency: Fractality and memory effects. *Physica a-
17 Statistical Mechanics and Its Applications*, **391**, 3234-3246.
- 18 Fischer, J., Mueller, T., Spatz, A.-K., Greggers, U., Gruenewald, B. & Menzel, R. (2014) Neonicotinoids
19 Interfere with Specific Components of Navigation in Honeybees. *PLoS One*, **9**.
- 20 Focardi, S., Marcellini, P. & Montanaro, P. (1996) Do ungulates exhibit a food density threshold? A
21 field study of optimal foraging and movement patterns. *Journal of Animal Ecology*, **65**, 606-
22 620.
- 23 Gautestad, A.O. (2011) Memory matters: influence from a cognitive map on animal space use.
24 *Journal of Theoretical Biology*, **287**, 26-36.
- 25 Gautestad, A.O. (2012) Brownian motion or Lévy walk? stepping towards an extended statistical
26 mechanics for animal locomotion. *Journal of the Royal Society Interface*, **9**, 2332-2340.
- 27 Gautestad, A.O. (2013a) Animal space use: distinguishing a two-level superposition of scale-specific
28 walks from scale-free Levy walk. *Oikos*, **122**, 612-620.
- 29 Gautestad, A.O. (2013b) Levy Meets Poisson: A Statistical Artifact May Lead to Erroneous
30 Recategorization of Levy Walk as Brownian Motion. *American Naturalist*, **181**, 440-450.
- 31 Gautestad, A.O., Loe, L.E. & Mysterud, A. (2013) Inferring spatial memory and spatiotemporal scaling
32 from GPS data: comparing red deer *Cervus elaphus* movements with simulation models.
33 *Journal of Animal Ecology*, **82**, 572-586.
- 34 Giuggioli, L. & Bartumeus, F. (2012) Linking animal movement to site fidelity. *Journal of
35 Mathematical Biology*, **64**, 647-656.
- 36 Giuggioli, L., Potts, J.R. & Harris, S. (2011) Animal interaction and the emergence of territoriality.
37 *PLoS Comput Biol*, **7**, e1002008.
- 38 Hagen, M., Wikelski, M. & Kissling, W.D. (2011) Space Use of Bumblebees (*Bombus* spp.) Revealed by
39 Radio-Tracking. *PLoS One*, **6**.
- 40 Hanert, E. (2012) Front dynamics in a two-species competition model driven by Levy flights. *Journal
41 of Theoretical Biology*, **300**, 134-142.
- 42 Hanks, E.M., Hooten, M.B., Johnson, D.S. & Sterling, J.T. (2011) Velocity-based movement modeling
43 for individual and population level inference. *PLoS One*, **6**.
- 44 Hansen, F.C., Witte, H.J. & Passarge, J. (1996) Grazing in the heterotrophic dinoflagellate *Oxyrrhis
45 marina*: Size selectivity and preference for calcified *Emiliania huxleyi* cells. *Aquatic Microbial
46 Ecology*, **10**, 307-313.
- 47 Hastings, A., Petrovskii, S. & Morozov, A. (2011) Spatial ecology across scales. *Biology Letters*, **7**, 163-
48 165.
- 49 Heinrich, B. (1979) Resource heterogeneity and patterns of movement in foraging bumblebees.
50 *Oecologia*, **40**, 235-245.

- 1 Hillesland, K.L., Velicer, G.J. & Lenski, R.E. (2009) Experimental evolution of a microbial predator's
2 ability to find prey. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 459-467.
- 3 Hills, T.T., Kalff, C. & Wiener, J.M. (2013) Adaptive Levy processes and area-restricted search in
4 human foraging. *PLoS ONE*, **8**, e60488-e60488.
- 5 Hodges, C.M. & Wolf, L.L. (1981) Optimal foraging in bumblebees: why is nectar left behind in
6 flowers? *Behavioral Ecology and Sociobiology*, **9**, 41-44.
- 7 Hoffmann, K., Coolen, A., Schlumbohm, C., Meerlo, P. & Fuchs, E. (2012) Remote long-term
8 registrations of sleep-wake rhythms, core body temperature and activity in marmoset
9 monkeys. *Behavioural Brain Research*, **235**, 113-123.
- 10 Hughes, B.D., Shlesinger, M.F. & Montroll, E.W. (1981) Random walks with self-similar clusters.
11 *Proceedings of the National Academy of Sciences of the United States of America*, **78**, 3287-
12 3291.
- 13 Humphries, N.E., Queiroz, N., Dyer, J.R.M., Pade1, N.G., Musy, M.K., Schaefer, K.M., D.W., F.,
14 Brunnschweiler, J.M., Doyle, T.K., Houghton, J.D.R., Hays, G.C., Jones, C.S., Noble, L.R.,
15 Wearmouth, V.J., Southall, E.J. & Sims, D.W. (2010) Environmental context explains Lévy and
16 Brownian movement patterns of marine predators. *Nature*, **465**, 1066–1069.
- 17 Humphries, N.E., Weimerskirch, H., Queiroz, N., Southall, E.J. & Sims, D.W. (2012) Foraging success
18 of biological Levy flights recorded in situ. *Proceedings of the National Academy of Sciences of
19 the United States of America*, **109**, 7169-7174.
- 20 James, A., Plank, M.J. & Edwards, A.M. (2011) Assessing Levy walks as models of animal foraging.
21 *Journal of the Royal Society Interface*, **8**, 1233-1247.
- 22 Jones, R. (1977) Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal
23 Ecology*, **46**, 195-212.
- 24 Kareiva, P.M. & Shigesada, N. (1983) Analyzing insect movement as a correlated random walk.
25 *Oecologia*, **56**, 234–238.
- 26 Kawai, R. & Petrovskii, S. (2012) Multi-scale properties of random walk models of animal movement:
27 lessons from statistical inference. *Proceedings of the Royal Society a-Mathematical Physical
28 and Engineering Sciences*, **468**, 1428-1451.
- 29 Khantha, M. & Balakrishnan, V. (1983) First passage time distributions for finite one-dimensional
30 random walks. *Pramana*, **21**, 111-122.
- 31 Klafter, J., White, B.S. & Levandowsky, M. (1990) Micro-zooplankton feeding behavior and the Levy
32 walk. *Biological motion* (eds W. Alt & G. Hoffmann), pp. 281-293. Springer-Verlag, Berlin,
33 Germany.
- 34 Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D. & Morales, J.M. (2012) Flexible and
35 practical modeling of animal telemetry data: hidden Markov models and extensions.
36 *Ecology*, **93**, 2336-2342.
- 37 Lenz, F., Chechkin, A.V. & Klages, R. (2013) Constructing a Stochastic Model of Bumblebee Flights
38 from Experimental Data. *PLoS ONE*, **8**.
- 39 Lenz, F., Ings, T.C., Chittka, L., Chechkin, A.V. & Klages, R. (2012) Spatiotemporal Dynamics of
40 Bumblebees Foraging under Predation Risk. *Physical Review Letters*, **108**.
- 41 Levin, D.A., Kerster, H.W. & Niedzlek, M. (1971) Pollinator flight directionality and its effect on pollen
42 flow. *Evolution*, **25**, 113-118.
- 43 Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943-1967.
- 44 Lévy, P. (1937) *Theorie de l'Addition des Variables Aleatoires*. Gauthier-Villiers, Paris.
- 45 Lomholt, M.A., Koren, T., Metzler, R. & Klafter, J. (2008) Lévy strategies in intermittent search
46 processes are advantageous. *Proceedings of the National Academy of Sciences*, **105**, 11055–
47 11059.
- 48 Lopez-Lopez, P., Benavent-Corai, J., Garcia-Ripolles, C. & Urios, V. (2013) Scavengers on the Move:
49 Behavioural Changes in Foraging Search Patterns during the Annual Cycle. *PLoS One*, **8**.

- 1 Lundy, M.G., Harrison, A., Buckley, D.J., Boston, E.S., Scott, D.D., Teeling, E.C., Montgomery, W.I. &
2 Houghton, J.D.R. (2013) Prey field switching based on preferential behaviour can induce Levy
3 flights. *Journal of the Royal Society Interface*, **10**.
- 4 Mardon, J., Nesterova, A.P., Traugott, J., Saunders, S.M. & Bonadonna, F. (2010) Insight of scent:
5 experimental evidence of olfactory capabilities in the wandering albatross (*Diomedea*
6 *exulans*). *Journal of Experimental Biology*, **213**, 558-563.
- 7 Maye, A., Hsieh, C.H., Sugihara, G. & Brembs, B. (2007) Order in spontaneous behavior. *PLoS ONE*, **2**,
8 e443.
- 9 McClintock, B.T., King, R., Thomas, L., Matthiopoulos, J., McConnell, B.J. & Morales, J.M. (2012) A
10 general discrete-time modeling framework for animal movement using multistate random
11 walks. *Ecological Monographs*, **82**, 335-349.
- 12 McClintock, B.T., Russell, D.J.F., Jason, M. & King, R. (2013) Combining individual animal movement
13 and ancillary biotelemetry data to investigate population-level activity budgets. *Ecology*, **94**,
14 838-849.
- 15 McFarland, D.J. (1977) Decision making in animals. *Nature*, **269**, 15- 21.
- 16 McLane, A.J., Semeniuk, C., McDermid, G.J. & Marceau, D.J. (2011) The role of agent-based models
17 in wildlife ecology and management. *Ecological Modelling*, **222**, 1544-1556.
- 18 Miramontes, O., Boyer, D. & Bartumeus, F. (2012) The Effects of Spatially Heterogeneous Prey
19 Distributions on Detection Patterns in Foraging Seabirds. *PLoS One*, **7**.
- 20 Mommer, L., van Ruijven, J., Jansen, C., van de Steeg, H.M. & de Kroon, H. (2012) Interactive effects
21 of nutrient heterogeneity and competition: implications for root foraging theory? *Functional*
22 *Ecology*, **26**, 66-73.
- 23 Morales, J.M. & Ellner, S.P. (2002) Scaling up animal movements in heterogeneous landscapes: the
24 importance of behavior. *Ecology*, **83**, 2240-2247.
- 25 Morales, J.M., Fortin, D., Frair, J.L. & Merrill, E.H. (2005) Adaptive models for large herbivore
26 movements in heterogeneous landscapes. *Landscape Ecology*, **20**, 301-316.
- 27 Morales, J.M., Haydon, D.T., Frair, J., Holsiner, K.E. & Fryxell, J.M. (2004) Extracting more out of
28 relocation data: Building movement models as mixtures of random walks. *Ecology*, **85**, 2436-
29 2445.
- 30 Mueller, T., Fagan, W.F. & Grimm, V. (2011) Integrating individual search and navigation behaviors in
31 mechanistic movement models. *Theoretical Ecology*, **4**, 341-355.
- 32 Mukamel, S., Stern, P.S. & Ronis, D. (1983) Universality in the critical broadening of spectral lines in
33 simple fluids. *Physical Review Letters*, **50**, 590-594.
- 34 Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A
35 movement ecology paradigm for unifying organismal movement research. *Proceedings of*
36 *the National Academy of Sciences*, **105**, 19052-19059.
- 37 Nonaka, E. & Holme, P. (2007) Agent-based model approach to optimal foraging in heterogeneous
38 landscapes: effects of patch clumpiness. *Ecography*, **30**, 777-788.
- 39 Noser, R. & Byrne, R.W. (2007) Travel routes and planning of visits to out-of-sight resources in wild
40 chacma baboons, *Papio ursinus*. *Animal Behaviour*, **73**, 257-266.
- 41 Osborne, J.L., Smith, A., Clark, S.J., Reynolds, D.R., Barron, M.C., Lim, K.S. & Reynolds, A.M. (2013)
42 The Ontogeny of Bumblebee Flight Trajectories: From Naive Explorers to Experienced
43 Foragers. *PLoS One*, **8**.
- 44 Papastamatiou, Y.P., DeSalles, P.A. & McCauley, D.J. (2012) Area-restricted searching by manta rays
45 and their response to spatial scale in lagoon habitats. *Marine Ecology Progress Series*, **456**,
46 233-244.
- 47 Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008) State-space
48 models of individual animal movement. *Trends in Ecology & Evolution*, **23**, 87-94.
- 49 Plank, M.J. & James, A. (2008) Optimal foraging: Levy pattern or process? *Journal of the Royal*
50 *Society Interface*, **5**, 1077-1086.

- 1 Preston, M.D., Pitchford, J.W. & Wood, A.J. (2010) Evolutionary optimality in stochastic search
2 problems. *Journal of the Royal Society Interface*, **7**, 1301-1310.
- 3 Pyke, G.H. (1978a) Are animals efficient harvesters? *Animal Behaviour*, **26**, 241-250.
- 4 Pyke, G.H. (1978b) Optimal foraging: Movement patterns of bumblebees between inflorescences.
5 *Theoretical Population Biology*, **13**, 72-98.
- 6 Pyke, G.H. (1979) Optimal foraging in bumblebees: Rule of movement between flowers within
7 inflorescences. *Animal Behaviour*, **27**, 1167-1181.
- 8 Pyke, G.H. (1981) Optimal Travel Speeds of Animals. *American Naturalist*, **118**, 475-487.
- 9 Pyke, G.H. (1983) Animal movements: An optimal foraging approach. *The Ecology of Animal*
10 *Movement* (eds J.R. Swingland & G. P.J.), pp. 7-31. Oxford University Press, Oxford.
- 11 Pyke, G.H. (1984) Optimal Foraging Theory a Critical Review. *Annual Review of Ecology and*
12 *Systematics*, **15**, 523-575.
- 13 Pyke, G.H. & Cartar, R.V. (1992) The flight directionality of bumblebees: Do they remember where
14 they came from? *Oikos*, **65**, 321-327.
- 15 Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal Foraging a Selective Review of Theory and
16 Tests. *Quarterly Review of Biology*, **52**, 137-154.
- 17 Raposo, E.P., Buldyrev, S.V., da Luz, M.G.E., Santos, M.C., Stanley, H.E. & Viswanathan, G.M. (2003)
18 Dynamical robustness of Lévy search strategies. *Physical Review Letters*, **91**, e240601.
- 19 Raposo, E.P., Buldyrev, S.V., da Luz, M.G.E., Viswanathan, G.M. & Stanley, H.E. (2009) Lévy flights
20 and random searches. *Journal of Physics A: Mathematical and Theoretical*, **42**.
- 21 Raqab, M.Z. (2013) Discriminating between the generalized Rayleigh and Weibull distributions.
22 *Journal of Applied Statistics*, **40**, 1480-1493.
- 23 Reyna-Hurtado, R., Chapman, C.A., Calme, S. & Pedersen, E.J. (2012) Searching in heterogeneous and
24 limiting environments: foraging strategies of white-lipped peccaries (*Tayassu pecari*). *Journal*
25 *of Mammalogy*, **93**, 124-133.
- 26 Reynolds, A.M. (2006) On the intermittent behaviour of foraging animals. *Europhysics Letters*, **75**,
27 517-520.
- 28 Reynolds, A.M. (2008) Optimal random Lévy-loop searching: new insights into the searching
29 behaviours of central-place foragers. *European Physics Letters*, **82**.
- 30 Reynolds, A.M. (2010) Bridging the gulf between correlated random walks and Lévy walks:
31 autocorrelation as a source of Lévy walk movement patterns. *Journal of the Royal Society*
32 *Interface*, **7**, 1753-1758.
- 33 Reynolds, A.M. (2011) On the origin of bursts and heavy tails in animal dynamics. *Physica a-*
34 *Statistical Mechanics and Its Applications*, **390**, 245-249.
- 35 Reynolds, A.M. (2012a) Distinguishing between Levy walks and strong alternative models. *Ecology*,
36 **93**, 1228-1233.
- 37 Reynolds, A.M. (2012b) Fitness-maximizing foragers can use information about patch quality to
38 decide how to search for and within patches: optimal Levy walk searching patterns from
39 optimal foraging theory. *Journal of the Royal Society Interface*, **9**, 1568-1575.
- 40 Reynolds, A.M. (2012c) Olfactory search behaviour in the wandering albatross is predicted to give
41 rise to Levy flight movement patterns. *Animal Behaviour*, **83**, 1225-1229.
- 42 Reynolds, A.M. (2012d) Truncated Levy walks are expected beyond the scale of data collection when
43 correlated random walks embody observed movement patterns. *Journal of the Royal Society*
44 *Interface*, **9**, 528-534.
- 45 Reynolds, A.M. (2013) Selection pressures give composite correlated random walks Levy walk
46 characteristics. *Journal of Theoretical Biology*, **332**, 117-122.
- 47 Reynolds, A.M. & Rhodes, C.J. (2009) The Lévy flight paradigm: random search patterns and
48 mechanisms. *Ecology*, **90**, 877-887.
- 49 Reynolds, A.M., Smith, A.D., Reynolds, D.R., Carreck, N.L. & Osborne, J.L. (2007) Honeybees perform
50 optimal scale-free searching flights when attempting to locate a food source. *Journal of*
51 *Experimental Biology*, **210**, 3763-3770.

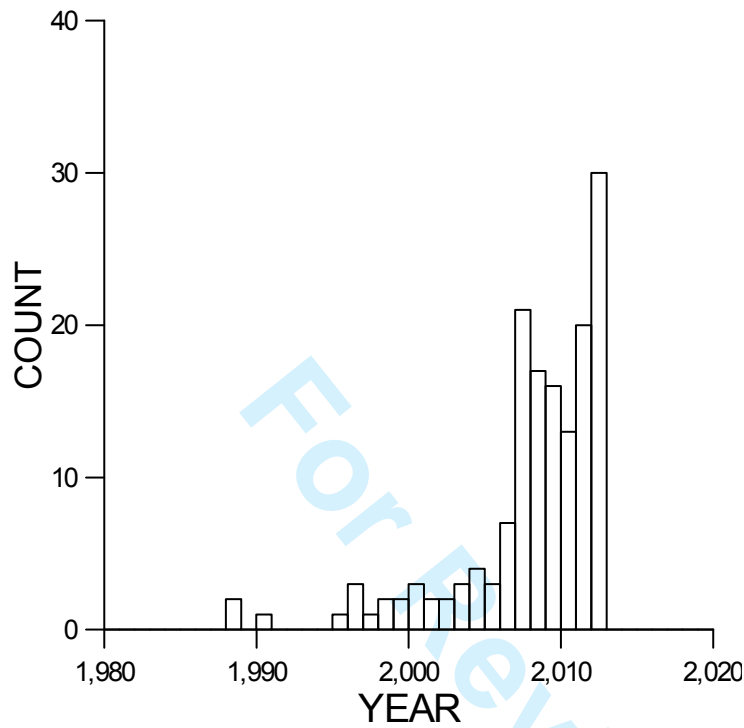
- 1 Reynolds, A.M., Swain, J.L., Smith, A.D., Martin, A.P. & Osborne, J.L. (2009) Honeybees use a Lévy
2 flight search strategy and odour-mediated anemotaxis to relocate food sources. *Behavioral*
3 *Ecology & Sociobiology*, **64**, 115–123.
- 4 Rhee, I., Shin, M., Hong, S., Lee, K., Kim, S.J. & Chong, S. (2011) On the Levy-Walk Nature of Human
5 Mobility. *Ieee-Acm Transactions on Networking*, **19**, 630-643.
- 6 Roberts, E.C., Wootton, E.C., Davidson, K., Jeong, H.J., Lowe, C.D. & Montagnes, D.J.S. (2011) Feeding
7 in the dinoflagellate *Oxyrrhis marina*: linking behaviour with mechanisms. *Journal of*
8 *Plankton Research*, **33**, 603-614.
- 9 Santos, M.C., Boyer, D., Miramontes, O., Viswanathan, G.M., Raposo, E.P., Mateos, J.L. & da Luz,
10 M.G.E. (2007) Origin of power-law distributions in deterministic walks: the influence of
11 landscape geometry. *Physical Review E*, **75**, 061114.
- 12 Santos, M.C., Raposo, E.P., Viswanathan, G.M. & da Luz, M.G.E. (2004) Optimal random searches of
13 revisitable targets: crossover from superdiffusive to ballistic random walks. *Europhysics*
14 *Letters*, **67**, 734–740.
- 15 Scafetta, N. (2011) Understanding the complexity of the Levy-walk nature of human mobility with a
16 multi-scale cost/benefit model. *Chaos*, **21**.
- 17 Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N.,
18 McClellan, C.M. & Clark, J.S. (2008) Understanding movement data and movement
19 processes: current and emerging directions. *Ecology Letters*, **11**, 1338-1350.
- 20 Schick, R.S., Roberts, J.J., Eckert, S.A., Halpin, P.N., Bailey, H., Chai, F., Shi, L. & Clark, J.S. (2013)
21 Pelagic movements of pacific leatherback turtles (*Dermochelys coriacea*) reveal the complex
22 role of prey and ocean currents. *Movement Ecology*, **1**, 11.
- 23 Schultheiss, P. & Cheng, K. (2013) Finding food: outbound searching behavior in the Australian
24 desert ant *Melophorus bagoti*. *Behavioral Ecology*, **24**, 128-135.
- 25 Segall, J.E., Block, S.M. & Berg, H.C. (1986) Temporal Comparisons in Bacterial Chemotaxis.
26 *Proceedings of the National Academy of Sciences of the United States of America*, **83**, 8987–
27 8991.
- 28 Shlesinger, M.F. (2009) Random searching. *Journal of Physics A: Mathematical and Theoretical*, **42**.
- 29 Shlesinger, M.F. & Klafter, J. (1986) Lévy walks versus Lévy flights. *On growth and form* (eds H.E.
30 Stanley & N. Ostrowsky), pp. 279–283. Nijhoff, Dordrecht, The Netherlands.
- 31 Sims, D.W., Humphries, N.E., Bradford, R.W. & Bruce, B.D. (2012) Levy flight and Brownian search
32 patterns of a free-ranging predator reflect different prey field characteristics. *Journal of*
33 *Animal Ecology*, **81**, 432-442.
- 34 Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W., James, A.,
35 Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton, D., Shepard,
36 E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J. & Metcalfe, J.D. (2008) Scaling laws of
37 marine predator search behaviour. *Nature*, **451**, 1098-1102.
- 38 Siniff, D.B. & Jessen, C.R. (1969) A simulation model of animal movement patterns. *Advances in*
39 *Ecological Research*, **6**, 185-219.
- 40 Smith, J.N.M. (1974a) The food searching behavior of two European thrushes. I. Description and
41 analyses of the search paths. *Behaviour*, **48**, 276-302.
- 42 Smith, J.N.M. (1974b) The food searching behavior of two European thrushes. II. The adaptiveness of
43 the search patterns. *Behaviour*, **49**, 1-61.
- 44 Sotelo-Lopez, S.A., Santos, M.C., Raposo, E.P., Viswanathan, G.M. & da Luz, M.G.E. (2012) Conditions
45 under which a superdiffusive random-search strategy is necessary. *Physical Review E*, **86**,
46 031133.
- 47 Stillman, R.A. (2008) MORPH—an individual-based model to predict the effect of environmental
48 change on foraging animal populations. *Ecological Modelling*, **216**, 265–276.
- 49 Stumpf, M.P.H. & Porter, M.A. (2012) Critical truths about power laws. *Science*, **335**, 665-666.
- 50 Sueur, C. (2011) A non-Lévy random walk in chacma baboons: What does it mean? *PLoS ONE*, **6**,
51 e16,131.

- 1 Sun, Z.-G. & Han, C.-Z. (2010) Modeling high-resolution synthetic aperture radar images with heavy-
2 tailed distributions. *Acta Physica Sinica*, **59**, 998-1008.
- 3 Taylor, J.R. & Stocker, R. (2012) Trade-Offs of Chemotactic Foraging in Turbulent Water. *Science*,
4 **338**, 675-679.
- 5 Tuck, J.M. & Hassall, M. (2004) Foraging behaviour of *Armadillidium vulgare* (Isopoda:Oniscidea) in
6 heterogeneous environments. *Behaviour*, **141**, 233-244.
- 7 Vanduren, L.A. & Videler, J.J. (1995) Swimming Behavior of Developmental Stages of the Calanoid
8 Copepod *Temora longicornis* at Different Food Concentrations. *Marine Ecology Progress
9 Series*, **126**, 153-161.
- 10 Visser, A.W. (2007) Motility of zooplankton: fitness, foraging and predation. *Journal of Plankton
11 Research*, **29**, 447-461.
- 12 Viswanathan, G.M., Afanasyev, V., Buldyrev, S.V., Murphy, E.J., Prince, P.A. & Stanley, H.E. (1996)
13 Lévy flight search patterns of wandering albatrosses. *Nature*, **381**, 413.
- 14 Viswanathan, G.M., Bartumeus, F., Buldyrev, S.V., Catalan, J., Fulco, U.L., Havlin, S., da Luz, M.G.E.,
15 Lyra, M.L., Raposo, E.P. & Stanley, H.E. (2002) Lévy flight random searches in biological
16 phenomena. *Physica A*, **314**, 208-213.
- 17 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., da Luz, M.C.E., Raposo, E.P. & Stanley, H.E. (1999)
18 Optimizing the success of random searches. *Nature*, **401**, 911-914.
- 19 Wakefield, E.D., Phillips, R.A., Matthiopoulos, J., Fukuda, A., Higuchi, H., Marshall, G.J. & Trathan,
20 P.N. (2009) Wind field and sex constrain the flight speeds of central-place foraging
21 albatrosses. *Ecological Monographs*, **79**, 663-679.
- 22 Ware, D.M. (1975) Growth, metabolism and optimal swimming speed in a pelagic fish. *Journal of the
23 Fisheries Research Board of Canada*, **32**, 33-41.
- 24 Weihs, D. (1975) An optimum swimming speed of fish based on feeding efficiency. *Israel Journal of
25 Technology*, **13**, 163-169.
- 26 Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. (1993) Foraging strategy of wandering
27 albatrosses through the breeding season: A study using satellite telemetry. *Auk*, **110**, 325-
28 342.
- 29 Yoda, K., Tomita, N., Mizutani, Y., Narita, A. & Niizuma, Y. (2012) Spatio-temporal responses of black-
30 tailed gulls to natural and anthropogenic food resources. *Marine Ecology Progress Series*,
31 **466**, 249-259.
- 32 Zimmerman, M. (1979) Optimal Foraging a Case for Random Movement. *Oecologia*, **43**, 261-268.
- 33 Zimmerman, M. (1983) Calculating Nectar Production Rates Residual Nectar and Optimal Foraging.
34 *Oecologia*, **58**, 258-259.

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3 Figure 1: Numbers of published articles per year (through 2012) that consider Lévy walks
4 and movements by organisms (Obtained by using Web of Knowledge to search for published
5 articles re Lévy walks/ flights/ foraging and then selecting those that relate to movements by
6 organisms)

7