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

Abstract:

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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.

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

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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, physics and mathematics may yet work well together.
Introduction

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

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

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

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

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

Because active movement by individual organisms is such a prevalent and important process, we need models for it, as bases for both description and predictive understanding, and better still if the understanding has a theoretical foundation. For example, a very simple movement model for an organism that is searching for food might consist of the following rule: ‘pick a direction at random, move in that direction until a food item is encountered (and possibly consumed), then repeat the process’. Such a model might agree with the observed
movements of an organism and hence provide a description of that movement. It might also
provide some understanding of the movements, if it can predict how movements will change
as circumstances change. If the rule, or how it might change, can itself be predicted, perhaps
from a body of theory, then our understanding of the movements would be even more
profound. This is essentially what we are trying to achieve.

Models of Organism Movement

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

Movements of organisms exhibit variation in direction and speed, the fundamental
properties of movement, though it may sometimes be reasonable to assume constant speed.
Movement paths, sometimes described as ‘meandering’, obviously demonstrate changes in
direction over time (Bond 1980; Visser 2007). Velocities, calculated for a constant time
interval between successive ‘locations’ for a moving organism, typically exhibit a frequency
distribution over some range of variation (Vanduren & Videler 1995; Tuck & Hassall 2004).
Of course, this means that there will also be variation in ‘step length’ or distance between
successive locations when chosen on the basis of a constant time interval (Bovet &
Benhamou 1988). However, speed is often either omitted from consideration (Papastamatiou,
DeSalles & McCauley 2012) or assumed constant (Miramontes, Boyer & Bartumeus 2012),
both of which may be reasonable if variation in speed is small relative to variation in
direction, or if speed and direction are unrelated.

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

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

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

However, despite the inherently continuous nature of decision-making by organisms and their consequent movements, we need to discretise movement paths and movement decisions in order to describe and model them (Bovet & Benhamou 1988; Reynolds 2010). Movement can be considered mathematically continuous if it is modelled as a diffusion process, or combination of different diffusion processes (Blackwell 1997; Blackwell 2003). Otherwise it varies from difficult to impossible to deal mathematically with continuous movement, especially in real-world situations where there is more than one dimension involved (Bovet & Benhamou 1988; Reynolds 2010; James, Plank & Edwards 2011; Kawai & Petrovskii 2012; Lenz, Chechkin & Klages 2013). If, however, movements are considered to consist of discrete and successive linear ‘steps’, then they can be described and modelled as a Discrete Time Series process with each movement step being a change in positional state for the process (Schick et al. 2008; Langrock et al. 2012). If it is additionally assumed that changes in location depend only on current location and arrival direction, then
movements may be modelled as a Markov process (Bovet & Benhamou 1988; Reynolds 2010; Kawai & Petrovskii 2012; Langrock et al. 2012). Such discretisation of movements also allows them to be simulated using Monte Carlo methods (Jones 1977), now made relatively easy through modern computer technology (Bovet & Benhamou 1988; Nathan et al. 2008). Discretisation of movements is therefore fundamental to both describing and understanding them (Bovet & Benhamou 1988).

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

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

course, for many organisms, the scale of perception will be many times a single body length.

The spatial scale at which movements of organisms are recorded may therefore be

natural, arbitrary, or limited by available technology. When organisms exhibit naturally

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

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

Directionality of movement, which is the correlation between the directions of
successive movement steps (Levin, Kerster & Niedzlek 1971; Jones 1977; Pyke, Pulliam &
Charnov 1977; Kareiva & Shigesada 1983), is expected and observed to be a prominent
aspect of the movements of organisms, especially at small to moderate spatial scales. Because
all organisms move along an axis of symmetry with a front or leading end and a back or
trailing end and with ongoing momentum maintained through physical and chemical
processes, this correlation must necessarily be close to 1 when movements are considered at a
spatial scale of about one body length (Lenz et al. 2012). When movements have been
considered at spatial/temporal scales dictated by natural intermittency, directions of
successive steps have generally, but not always, been significantly correlated (Zimmerman
1979; Pyke 1984). Directionality has sometimes been referred to as ‘directional persistence’
(Reynolds 2012d; Gautestad 2013a; Lenz, Chechkin & Klages 2013), and its converse as
‘tortuosity’ (Dicke & Burrough 1988; Schick et al. 2008) and ‘sinuosity’ (Bovet &
Benhamou 1988; Bartumeus et al. 2008).

However, directionality will decline with increases in the adopted movement step
length or step duration, and so the adopted spatial/temporal scale (hereafter referred to
simply as spatial scale) will profoundly affect the results of analyses of movements by
organisms (Kawai & Petrovskii 2012; Gautestad 2013a). Because organisms are likely to be
less affected by a previous movement direction with the passage of time and distance, the
 correlation between successive movement directions should decrease with increasing step
duration, as has been observed (de Knegt et al. 2007; Lenz, Chechkin & Klages 2013).
However, studies at relatively large spatial scales provide little indication of the rate or extent
of decline in directionality, because they generally have not considered directionality (Lopez-
Lopez et al. 2013; Lundy et al. 2013; Schultheiss & Cheng 2013), and have obtained variable
levels of directionality when they have (Chapperon & Seuront 2013). As will be discussed
below, zero directionality is an important assumption in the Lévy walk paradigm.

In addition to correlations between successive movement directions, there may also be
higher order correlations, as well as correlations between directionality and other aspects of
movement (Dray, Royer-Carenzi & Calenge 2010; Bazazi et al. 2012). Organisms may, for
example, tend to alternate left and right ‘turns’, hence moving in a somewhat ‘zig-zag’
manner (Smith 1974a; Pyke 1978b; Visser 2007). There may be a correlation between the change in direction between two successive movement steps and the length of the second step, as can arise if organisms respond to food encounter through both decreased directionality (i.e., turning more) and slower movement (Smith 1974b). Such responses to food encounter are of widespread occurrence and are often referred to as ‘area-restricted searching’ (Curio 1976; Benhamou & Bovet 1989; Mueller, Fagan & Grimm 2011). Other movement correlations are possible, including between the velocities of successive movements, but these and other possibilities have been little investigated (Lenz et al. 2012).

Like simple directionality, such correlations and responses to food encounter have been omitted from the Lévy walk paradigm (see below).

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

**Evolution of Movement Behaviour**

Optimality models may help us to understand movements of organisms, because the mechanisms by which organisms make movement-related decisions are likely to evolve under natural selection, but biological context will always be important in determining the
appropriate currency of fitness (McFarland 1977; Pyke, Pulliam & Charnov 1977; Pyke
1983). In this case, the general hypothesis is that organisms adopt, as a result of evolution by
natural selection, decision-making processes that maximise individual biological fitness as
measured by some ‘currency’ associated with the movements (McFarland 1977; Pyke,
Pulliam & Charnov 1977; Pyke 1983). If, for example, the movements occur in the context of
foraging, the assumed currency could be some measure of foraging efficiency such as net rate
of energy intake (Pyke, Pulliam & Charnov 1977; Pyke 1983). If, however, an organism is
moving in order to avoid becoming someone else’s meal, then the currency would be related
to predation risk, as well as or instead of other factors (Pyke, Pulliam & Charnov 1977; Pyke
1983). Context potentially makes a large difference in attempts to understand movements of
organisms (Pyke, Pulliam & Charnov 1977; Pyke 1983).

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

**The Lévy and Other ‘Random Walks’**

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

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

The Lévy walk, here taken to be synonymous with Lévy flight (Reynolds & Rhodes
2009; Gautestad 2013b), differs from other random walks in that the length of each
movement step, unless terminated through resource encounter, is assumed to be chosen from
a Lévy probability distribution. In general a movement step is assumed to end if food, or
some other target resource, is encountered, at which point a new movement step is initiated
with a new and randomly-chosen direction. With a Lévy walk, in the absence of resource
encounter, different step lengths (ℓ) are assumed to occur with probabilities given by P(ℓ) =
aℓ⁻µ where the exponent µ lies within the range 1<µ≤3 and a is a normalising constant
(Viswanathan et al. 1999). This probability distribution is sometimes referred to as Pareto,
Inverse Power Law or Pareto-Lévy (Edwards 2011; Scafetta 2011; Dagsvik et al. 2013). As
an alternative model, these step lengths might be generated from Poisson, Negative
Exponential, Gaussian or Gamma probability distributions (Gautestad 2011; Gautestad
2013b; Lundy et al. 2013). Other possibilities also exist.
The history of the Lévy-walk indicates a confluence of biology, mathematics and physics. Paul Lévy (1886-1971) was a French mathematician who was interested in probability distributions with certain properties, most notably that the probability distribution for a sum of independent, identically-distributed random variables takes the same form as the probability distribution for each component variable (Lévy 1937). His work found application within physics, especially since about the early 1980s, when it was realized that various kinds of random walk, considered to reflect certain physical processes, could lead to outcomes with Lévy probability distributions (Hughes, Shlesinger & Montroll 1981; Khantha & Balakrishnan 1983; Mukamel, Stern & Ronis 1983). In this context, the Lévy walk has proven particularly useful in studies of processes involving ‘super diffusion’, where diffusion occurs at a faster rate than the ‘normal diffusion’ resulting from Brownian motion (Eliazar & Klafter 2011; Eliazar & Shlesinger 2013). From about the mid-1980s, physicists, with interests in diffusion, have suggested that organisms should adopt Lévy walks when searching for food because this would result in a higher rate of food gain than would result from Brownian movement (Shlesinger & Klafter 1986; Shlesinger 2009), and at the same time, observed that a Lévy probability distribution adequately describes the frequency distribution of observed movement lengths for ants (Shlesinger & Klafter 1986). Subsequently, it was reported that a variety of organisms exhibit similar Lévy walk patterns (Klafter, White & Levandowsky 1990; Viswanathan et al. 1996) and suggested that the optimal movement strategies for foraging organisms might be Lévy walks with a particular value of 2 for the exponent $\mu$ (Viswanathan et al. 1999; Bartumeus et al. 2002) (see below). Articles arising from this area of research have been, and continue to be, published in a wide range of journals, representing the interests of both biologists and physicists (biology journals: Carde, Carde & Girling 2012; Reynolds 2012a; Sims et al. 2012) (physics journals: Ferreira et al. 2012; Lenz et al. 2012; Sotelo-Lopez et al. 2012).
Optimal Foraging and the Lévy Hypothesis

The Lévy hypothesis arose from a marriage between the Lévy walk model of movements and the optimal foraging approach, leading initially to several predictions depending on the density of the resource and how renewable it is (Viswanathan et al. 1999).

It had been shown previously that a Lévy walk strategy could be more effective at locating randomly distributed targets than Brownian motion (Cole 1995). In the initial attempt to determine the optimal foraging strategy, the resource targets in the foraging model were assumed to be either ‘depleting’, such that once a target was encountered by the organism it was removed (i.e., never renewed), or ‘non-depleting’ (i.e., instantly renewed), such that it was unaffected by encounter (Viswanathan et al. 1999). A forager was assumed to adopt a Lévy walk as a movement strategy and the value of the exponent \( \mu \) in the associated Lévy probability distribution was allowed to vary to the point that the overall rate of encounter with targets was maximised, and this was then considered to be the optimal search strategy for the organism, and therefore the one that the organism should theoretically adopt (Viswanathan et al. 1999; Bartumeus et al. 2002; Ferreira et al. 2012). The environment surrounding the organism was assumed featureless, conveying no information regarding possible target locations, and the organism was assumed to have no memory concerning its previous movements and resource encounters (Viswanathan et al. 1999). The foraging organism was assumed to have some kind of internal mechanism whereby it could generate a Lévy probability distribution of movement step lengths (Rhee et al. 2011).

It was found that the optimal exponent \( \mu \) in the Lévy probability distribution, and hence the predicted movement pattern, depended on whether resources were ‘depleting’ or ‘non-depleting’, and on their density relative to the forager’s range of perception. When targets are ‘depleting’, the optimal \( \mu \) approaches 1, corresponding to ‘ballistic’ movement, with almost no changes in direction at all (Viswanathan et al. 1999; Santos et al. 2004;
Ferreira et al. 2012; Yoda et al. 2012). On the other hand, if targets are ‘non-depleting’, the optimal $\mu$ depends on target density; if target density is low, relative to perception range, then the optimal $\mu$ is approximately 2, but if target density is high, then the optimal $\mu$ is approximately 3, corresponding to Brownian movement (Viswanathan et al. 1999; Ferreira et al. 2012; Yoda et al. 2012). It has subsequently been shown, based on the same movement model, that if target density is low and resource targets are ‘renewable’ after a time delay, then the optimal $\mu$ lies somewhere between 1 and 2 (Raposo et al. 2009). Other variations of the same movement model with renewable resource targets similarly lead to intermediate values of optimal $\mu$ between 1 and 2 if resources are sparsely distributed and an optimal $\mu$ of approximately 3 if resource density is high (Reynolds & Rhodes 2009; Ferreira et al. 2012).

These results in terms of movement theory have led to the so-called ‘Lévy walk/flight/foraging hypothesis’ (Reynolds & Rhodes 2009; Codling & Plank 2011; Lenz et al. 2012; Yoda et al. 2012; Chapperon & Seuront 2013), here referred to simply as the Lévy hypothesis (Raposo et al. 2009), but it has taken a variety of forms. It was initially argued that, in general, the food resources for which organisms are searching are ‘non-depleting’ and occur at low density, such that foraging animals are expected to adopt a Lévy walk movement strategy with an exponent $\mu$ of about 2 (Viswanathan et al. 1999). That organisms achieve this, through some kind of internal ‘adaptive’ mechanism, has been the principal Lévy hypothesis (Bartumeus 2007; Bartumeus 2009; Reynolds & Rhodes 2009; Reynolds 2012c; Reynolds 2012b). Subsequently, a number of authors have omitted any caveats about the rate at which food renewal occurs, hypothesising that organisms should adopt a Lévy walk movement pattern when food is sparse and Brownian movement when it is abundant (de Knegt et al. 2007; Humphries et al. 2010; Sueur 2011). A number of authors have additionally omitted any caveats about food abundance, hypothesising that organisms should exhibit a Lévy walk movement pattern because it is the optimal search strategy for randomly
distributed targets (Rhee et al. 2011). Others have hypothesised that organisms will exhibit
Lévy movement patterns, without specifying what the exponent should be (Reynolds 2012d).
Some have omitted all caveats, hypothesising simply that organisms should have generally
evolved to adopt Lévy search strategies with an exponent of 2 (Lopez-Lopez et al. 2013) or
to adopt Lévy search strategies without specifying an exponent (Schick et al. 2008;
Schultheiss & Cheng 2013).

Immediate Problems with Lévy Walk Theory

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

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

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

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

Fundamental to testing the Lévy hypothesis is the assumption that the organisms are searching for food, or other resource, and yet this assumption is often unevaluated, at least explicitly, and it is not always clear how valid it would be. It may sometimes be reasonably clear, for example, when animals such as deer, bees and many others are observed over small spatial scales, that they are indeed searching for food (Heinrich 1979; Focardi, Marcellini &
Montanaro 1996). In such situations, of course, it may be equally clear that the observed organisms are not searching for anything, but are probably moving for some other reason, possibly including movement between known locations (Sueur 2011). When locations of organisms are recorded remotely, and over relatively large spatial scales, the extent to which they are foraging may be far from obvious (Sims et al. 2008; Humphries et al. 2010; Sims et al. 2012; Lundy et al. 2013). Of course, technological advances that permit remote recording of internal body conditions of animals may help in this regard (Hoffmann et al. 2012). In any case, the assumption should always be evaluated explicitly.

The spatial scales of theory and observations should be comparable, but tests of the Lévy hypothesis have generally been biased towards relatively large spatial scales relative to the body lengths of the organisms involved, leading to spatial scales, at which movement observations have been recorded, being much greater than those at which organisms are making relevant decisions affecting their movements, and hence unlikely to involve behavioural strategies, Lévy or otherwise. In situations, for example, where locations of organisms have been recorded remotely through attached transmitters and GPS technology, as described above, the time intervals between location ‘fixes’ are typically long enough that the organisms would travel large distances between them, possibly thousands of times greater than their body length. A bias towards relatively large spatial scale also arises when discretisation of movements is achieved through adopting a step length such that differences in direction between successive steps exceed a substantial threshold (Bartumeus et al. 2003; Rhee et al. 2011; Reynolds 2012d; Reynolds 2012a; Schultheiss & Cheng 2013), because increases in step length and decreases in directionality occur together (Gautestad 2013a; Gautestad, Loe & Mysterud 2013). There can be a similar bias when movements are defined by periods of rapid movement separated by periods of slow movement, as such discretisation may reflect large-scale movements, such as between habitats, and have no bearing on how an
organism searches for food (Yoda et al. 2012). Combining movement steps to form composite steps, based on the first and last point in each sequence, will also enlarge the spatial scale (Chapperon & Seuront 2013). In general, the biological context should help to determine whether or not the spatial scale is appropriate.

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

Testing the Lévy hypothesis requires evaluation of both the directionality of movement, which is assumed zero, and the frequency distribution of movement step lengths, which is predicted to take the form of a Lévy distribution, and yet studies claiming to support the hypothesis have rarely considered directionality. In a recent study of foraging by a marine gastropod it was found that the frequency distributions of angular changes in direction between successive moves were mostly, but not always, uniform, as is required for
directionality to be zero (Chapperon & Seuront 2013). Most studies of movement patterns generally find marked and significant directionality and that organisms vary the directionality (or tortuosity) of their movements in response to circumstances (Papastamatiou, DeSalles & McCauley 2012). However, directionality has rarely been included in testing the Lévy hypothesis (Lopez-Lopez et al. 2013; Lundy et al. 2013; Schultheiss & Cheng 2013). The Lévy hypothesis also assumes that there is no directional bias to movements, but this too has been rarely evaluated (Chapperon & Seuront 2013). The major focus taken in testing the Lévy hypothesis has been on the frequency distribution of movement step lengths (Viswanathan et al. 1999).

A few investigations, including one seen as providing particularly strong support for the Lévy hypothesis (Humphries et al. 2010), may be biased towards discovery of Lévy movement patterns because they consider movements in just a single dimension, the vertical (Sims et al. 2008; Sims et al. 2012). Consider, for example, a fish that is maintaining itself at a particular depth, because that is where its food is located, and is otherwise moving horizontally in search of such food. Suppose, additionally, that it occasionally shifts its depth by a relatively large amount because it has moved into a region where the depth of its food has changed or where variation in currents or underwater topography warrants a change in swimming depth etc. Then its movements up and down might mostly be small, but with occasional long vertical movements. Hence, an analysis based only on vertical movements, with discretisation of movements determined by when changes in vertical movement occurred (i.e., change from upwards to downwards movement, and vice versa) (Sims et al. 2008; Humphries et al. 2010; Sims et al. 2012) could result in a frequency distribution of movement lengths with a ‘fat tail’ corresponding to the times when the fish shifts the depth at which it is moving. In this way, the investigation may reveal a Lévy pattern, with respect to
vertical movements, that has nothing to do with the biology of the animal and is simply a consequence of the analysis methods.

Testing the Lévy hypothesis should logically include a comparison between the observed frequency distribution of movement step lengths and a Lévy distribution, but many investigations are biased towards confirmation of Lévy movement patterns because they consider just the part of the frequency distribution of observed step lengths ‘truncated’ between arbitrary minimum and maximum step lengths (Gautestad 2012) and hence focus on the portion of the frequency distribution for which a Lévy pattern is observed or might be expected. It is, for example, common practice to restrict analysis to the frequency distribution of step lengths above some minimum threshold (Viswanathan et al. 1999; Yoda et al. 2012), thus eliminating situations where the distribution of step lengths peaks at some value distinctly greater than zero and generally restricting attention to the ‘tail’ of the distribution (Rhee et al. 2011; Lopez-Lopez et al. 2013; Schultheiss & Cheng 2013). In some cases, the value of the minimum step length is chosen so that agreement with a Lévy-like distribution is maximised (Clauset, Shalizi & Newman 2009; Lopez-Lopez et al. 2013; Lundy et al. 2013).

Observed step length distributions commonly exhibit distinct non-zero peaks (Heinrich 1979; Lundy et al. 2013; Schultheiss & Cheng 2013). In some cases, analysis has been restricted to the portion of the step length distribution for step lengths less than some threshold, with the distribution appearing Lévy-like below the threshold, but exhibiting distinct departures from a Lévy distribution above the threshold (de Jager et al. 2011). In other words, analyses of step length distributions have often focussed on those portions most closely resembling a Lévy pattern, leading, probably inevitably, to the conclusion that organisms generally ‘do the Lévy walk’.

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

Furthermore, the comparisons, in terms of shape or ‘fit’, between the observed
frequency distribution of movement step lengths and various alternative distributions, have
not always assessed the ‘goodness of fit’ provided by the Lévy distribution and rarely
considered alternative distributions other than the exponential or Poisson, which is expected
with Brownian motion, thus creating a further bias towards the Lévy distribution (Clauset,
Shalizi & Newman 2009). For example, recent tests of the Lévy hypothesis have generally
been based on a comparison of Lévy and exponential distributions (Humphries et al. 2012;
Lopez-Lopez et al. 2013; Schultheiss & Cheng 2013), with Gaussian, Gamma and Log-
Normal distributions additionally included in a few cases (Lenz et al. 2012; Reyna-Hurtado et al. 2012; Lundy et al. 2013), but no other distributions considered. I previously argued, from an optimal foraging perspective, that the frequency distribution of movement step lengths $d$ might take the form $P(d)= ad \exp (-ad^2/2)$, which is a Rayleigh distribution and is positively skewed (Pyke 1978b; Sun & Han 2010; Raqab 2013), perhaps similarly to a Lévy distribution, but this possibility has not apparently been investigated, nor observed step length distributions compared with a Rayleigh distribution. There are, of course, other possible similarly-skewed distributions and it is possible that no candidate distribution will pass the goodness of fit test.

Observations of Lévy movement ‘patterns’ at relatively large spatial scales may tell us little or nothing about underlying movement ‘processes’, because a Lévy movement pattern may be expected to emerge at such spatial scales, when movements either arise from a combination of processes or are affected by spatial heterogeneity (Reynolds 2006; Codling & Plank 2011; Reynolds 2012d), in other words most or all of the time. If, for example, organisms respond to the generally patchy food distributions, as normally occur, with ‘area restricted search’, whereby movement slows and/or becomes more tortuous following food encounter, then the resultant frequency distribution of movement step lengths may resemble a Lévy distribution (Benhamou 2007; Plank & James 2008; Hills, Kalff & Wiener 2013). If an organism exhibits movement directionality that varies in response to environmental heterogeneity and if its movements are discretised on the basis of ‘substantial changes in direction of travel’ then the resulting frequency distribution of step lengths may resemble a Lévy distribution with an exponent of 2 (Reynolds 2012d). These and other such studies have shown that Lévy distributions of step lengths can arise from a variety of foraging scenarios (Boyer et al. 2006; Reynolds 2006; Benhamou 2007; Santos et al. 2007; Reynolds 2012c;
Of course, non-Lévy distributions could also arise from a variety of foraging scenarios and there may be general differences between foraging scenarios that lead to Lévy versus non-Lévy step length distributions, which would be most interesting as predicting and/or observing Lévy distributions at large spatial scales would otherwise seem pretty trivial (Stumpf & Porter 2012).

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

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

One study in which variation in food density has been quantified and patterns of movement compared with expectations from the Lévy hypothesis (Bartumeus et al. 2003), has yielded results that conflict with these expectations. In this study the predators were the dinoflagellate *Oxyrrhis marina*, a very small animal, about 40 µm long and 15 µm wide (Breckels et al. 2011; Roberts et al. 2011), and its prey were the even smaller algae
Rhodomonas sp, which are roughly spherical in shape with a diameter of about 8µm.

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

A second study (de Knegt et al. 2007), in which resource densities were high, also produced results that conflict with the Lévy hypothesis. In this study, goats were observed foraging by browsing on randomly scattered bushes and trees (referred to collectively as ‘patches’), and grazing on a homogeneous grass layer in between. It was assumed, as might be reasonable, that movement patterns were unaffected by grazing. The goats were observed in two areas, with patch densities of 178 and 294 per ha, corresponding to average inter-patch distances of about 7.5 and 5.8m respectively, which are similar to one another and
presumably relatively short relative to goat vision, such that the goats should been able to
constantly see a number of patches in both areas. Consequently, as the ratio of inter-patch
distance to perceptive range of the goats would thus have been less than 1 in both areas,
observed movements by the goats should have been Brownian in both areas, not Brownian in
the area with the higher patch density and Lévy in the other area, as was reported (de Knegt
et al. 2007). The authors rationalised their results by suggesting that goat vision was an
important component for foraging in the area with the higher patch density but negligible
when patch density was lower (de Knegt et al. 2007), a highly unlikely possibility. In
addition, since renewal of the plant material browsed, and hence consumed, by the goats,
would probably take a long time relative to the times that goats typically spend browsing in
any particular area, the expected exponent of the Lévy distribution would have been close to
1 and significantly less than the value of 2.1 reported for the area with the lower patch density
(de Knegt et al. 2007). Furthermore, in comparing observed and Lévy movement
distributions, the study restricts movement steps (referred to as ‘flights’) to combined
movements between points corresponding to relatively large departures from linear
movement (de Knegt et al. 2007), thus biasing results as described above.

Difficulties of a purely statistical nature have also been encountered in attempting to
determine whether observed step length distributions are best fit by Lévy or some other
distribution, leading to a somewhat separate area of research interest (Reynolds & Rhodes
2009). Initial statistical methods were shown to be fundamentally flawed (Edwards et al.
2007; Edwards 2011; Edwards et al. 2012). Subsequently, improved methods have been
developed and adopted (Sims et al. 2008; Reynolds et al. 2009). However, not surprisingly,
these new methods also have associated problems such as the requirement that sample sizes
must be large (Lomholt et al. 2008; Sims et al. 2012). In any case, given all the other
problems associated with the Lévy walk hypothesis, this concern about statistical
methodology in fitting distributions to step length frequencies might seem to be like the proverbial ‘red herring’, and not something warranting much future attention (Gautestad 2013b; Gautestad, Loe & Mysterud 2013). On the other hand, any attempts to characterise movement patterns, including considering possible Lévy-type distributions, should use appropriate statistical techniques (Clauset, Shalizi & Newman 2009).

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

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

Despite all the above issues and difficulties, the Lévy hypothesis has been labelled a ‘paradigm’ (Plank & James 2008; Reynolds & Rhodes 2009; Reynolds 2010; Lundy et al. 2013), an apt description because this approach has been dictating the ways in which research is carried out and results interpreted. Many studies have developed theoretical models of searching for food or other targets based on the assumption that organisms move according to the Lévy model (Viswanathan et al. 1999; Raposo et al. 2009; Ferreira et al. 2012; Reynolds 2013). The original model and optimality approach has been extended, while retaining its essence, to allow for different spatial distributions of resources (Preston, Pitchford & Wood 2010), resource renewal (Raposo et al. 2003; Santos et al. 2004), moving targets (Bartumeus et al. 2002; Viswanathan et al. 2002), variation in perceptive ability (Reynolds 2006), and memory effects (Gautestad 2011; Ferreira et al. 2012). In one recent study, the movement model has been modified to allow for movements that, rather than being Lévy walks, are composite walks, consisting of Brownian random walks with different scaling parameters that...
are adopted with certain probabilities; if the organism optimises these probabilities and
resources are non-depleting, then its frequency distribution of movement step lengths is
predicted to appear Lévy-like (Reynolds 2013). Following the realization that composite
Brownian motion movement could lead to Lévy-like movement patterns, the so-called ‘power
law in disguise’ paradox, further investigation focused on ways to distinguish between Lévy
and composite Brownian processes (Gautestad 2012; Gautestad 2013a), both of which
assume random directions of successive movements. Attempts have been made to determine
internal processes whereby organisms might generate Lévy-like patterns (Reynolds 2011;
Bazazi et al. 2012; Gautestad 2012). The theoretical studies have led to a large and rapid
increase in empirical studies, mostly seeking to discover or confirm Lévy patterns, and
sometimes attempting to relate changes in Lévy pattern to changes in food distribution
(Humphries et al. 2012). The Lévy approach has been extended to other kinds of search
situations including mate search through the location of odour trails (Carde, Carde & Girling
2012), mussels choosing a place to settle (de Jager et al. 2014), and location of a food source
on the basis of its approximate location (Reynolds et al. 2007; Reynolds 2008).

The proponents of the Lévy hypothesis seem largely determined to maintain the view
that it describes how organisms are expected and observed to move, despite all its faults. The
theoreticians modify their models, but the outcome remains essentially the same: organisms
are expected to exhibit Lévy-like movement patterns. The empiricists continue to look for,
and find, observations consistent with these expected Lévy patterns, while adopting
procedures that could hardly fail, and omitting or ignoring conflicting evidence. In some
cases, for example, movement has been recognised as being non-random in various respects,
but none-the-less analysed from the perspective of Lévy versus Brownian movement (Rhee et
al. 2011; Sueur 2011). Some have sought to determine internal mechanisms whereby an
individual organism might exhibit Lévy movements (Reynolds 2011; Bazazi et al. 2012).
Many have claimed that the hypothesis is well supported, both theoretically and empirically (Reynolds 2011; Sims et al. 2012; Schultheiss & Cheng 2013). Literature relating directly to the Lévy hypothesis has been relatively self-contained with reviews, and articles in general, paying little apparent attention to articles from outside this area of research. That all of this continues to occur despite the problems and issues discussed above, indicates a considerable reluctance to move on from the Lévy paradigm, despite suggestions that this might now be warranted (Reynolds 2012d).

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

The original attempts to describe and understand forager movements via optimal foraging theory embraced all the desirable attributes discussed above, and therefore provide an alternative to the Lévy walk approach. Most fundamentally, the early studies of
movements of organisms acknowledged ‘directionality’ as an important aspect of such
movements (Siniff & Jessen 1969; Cody 1971; Smith 1974b) and hypothesised that
organisms would adopt movement decision processes resulting in maximal biological fitness
and/or foraging efficiency (Cody 1971; Smith 1974b; Pyke, Pulliam & Charnov 1977). They
also recognised that an organism would alter their movement patterns in response to
encounters with food and other resources, on account of patchy resource distributions (Smith
1974b; Curio 1976; Pyke 1984), and also by what it otherwise perceived and remembered,
about its environment and its previous movements (Smith 1974a; Jones 1977; Pyke, Pulliam
& Charnov 1977). They considered speed of movement from an optimal foraging perspective
(Ware 1975; Weihs 1975; Pyke, Pulliam & Charnov 1977; Pyke 1978b; Pyke 1981). Despite
the relatively limited nature of computer technology available at the time, they developed
computer-based simulation models of movements by foraging organisms (Siniff & Jessen
1969; Cody 1971; Jones 1977; Pyke 1978a). In short, these early studies had all the basic
ingredients (Pyke 1983).

Some authors have recently revisited such an approach, labelling their models
variously, but essentially synonymously, as ‘Artificial Neural Networks’ (i.e., ANN)
(Morales et al. 2005; Mueller, Fagan & Grimm 2011), ‘Individual Based Models’ (i.e., IBM)
(Stillman 2008; Giuggioli, Potts & Harris 2011) and ‘Agent Based Models’ (i.e., ABM)
(Nonaka & Holme 2007; McLane et al. 2011), or describing their approach as a new
‘movement ecology’ paradigm (Nathan et al. 2008). In all cases, it is assumed that the
environment, through which an individual moves, can be represented by a two- or three-
dimensional grid of cells, such that spatial and temporal variation in relevant factors, biotic or
abiotic, are modelled through variation in these factors within and among cells. A patchy
food distribution, for example, may be setup through defining nearby cells to have similar
levels of food abundance (Stillman 2008; Mueller, Fagan & Grimm 2011). Movement is
assumed to be between grid cells and is modelled through rules that specify when the
individual will leave a particular cell and which cell it will move to next. Visits to cells may
change cell properties, as, for example, when food is encountered and consumed. Movement
rules may include information concerning the individual’s internal state, as well as locations
and properties of visited cells, past and present, and of unvisited cells that it can perceive
from its current cell. Information concerning previously visited cells may be based on
relatively recent experience, such as might arise through previous visits to just one or a few
cells, long-term memory, or information that is passed from one individual to another through
communication or genetic transmission (Mueller, Fagan & Grimm 2011). Of course, these
possibilities exist as part of a continuum, and may occur in combination (Mueller, Fagan &
Grimm 2011). It is finally assumed that the movement rules will have evolved, based on
some currency of fitness such as net rate of energy intake, to the point that fitness is
maximised (Stillman 2008; McLane et al. 2011). The rule that maximises fitness may be
determined either directly or through a genetic algorithm that models the evolutionary
process (Mueller, Fagan & Grimm 2011); the outcomes seem likely to be the same. The end
result is the hypothesised ‘optimal’ movement rule, which can then be used as a basis for
comparison between observed and predicted patterns of movement. Of course, advancing
computer technology has facilitated the development of such simulation models (Nathan et
al. 2008).

In addition, Inferential Models have recently been developed for situations in which
movement data are collected remotely, without direct observations on animals, their food or
their predators, but often with broadscale information about the local environment, and
sometimes information about the state or behaviour of the animals involved (Schick et al.
2008; Hanks et al. 2011; McClintock et al. 2012). Through telemetry technology it is now
possible, for example, to track animal movements, sometimes over short time intervals, while
simultaneously recording changes indicative of various behaviours such as resting, feeding or food ingestion, superimposed on spatial and temporal variation in habitat, topography or other environmental variables (McClintock et al. 2012; Bestley et al. 2013). In such situations, animal movement can be modelled as a mixture of specified processes (e.g., random walks), with unknown defining parameters and switch points, and then these unknown variables can be estimated using Bayesian inferential statistics (Morales et al. 2004; McClintock et al. 2012; McClintock et al. 2013). In some cases it may be reasonable to assume that observations, though variable, are made with zero error (Morales et al. 2004); in other cases, such as in so-called State-Space Models, it may be considered necessary to allow for observational error (Patterson et al. 2008; Schick et al. 2008; Hanks et al. 2011).

Computer technology generally assists here as well, given the nature and extent of the required statistical calculations (Patterson et al. 2008). The end result can be a model of animal movement that accords with what is otherwise known about the biology of the animals involved (Morales et al. 2004; Schick et al. 2013).

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

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

**Future Usefulness of Lévy Walk Approach**

Despite the need to abandon the so-called Lévy paradigm for understanding movements of organisms, the random walk approach in general, and Lévy approach in particular, may still prove useful at relatively large spatial scales, in terms of both theory and observations (Gautestad 2011; McLane et al. 2011; Gautestad 2013a; Gautestad, Loe & Mysterud 2013), and in this way biology, physics and mathematics may yet work well together. It would, for example, be interesting and worthwhile to know the extent to which Lévy patterns would be expected to occur as ‘emergent properties’ of large-scale movement
scenarios and to test such expectations empirically (Reynolds 2012d; Reynolds 2012a). Of course, IBM's and the like, as discussed above, could be used as components of such movement scenarios (Bonnell et al. 2013). It may turn out that analyses at the lowest spatial scale, where organisms are making movement decisions, may be considered ‘mechanistic’ (or biological), while those at large spatial scale are more ‘statistical mechanical’ in nature (Gautestad 2013a; Gautestad, Loe & Mysterud 2013). The resulting understanding of movements of organisms at large spatial scales could then be used in attempts to understand other phenomena that occur at even larger spatial scales, such as dispersal and spread of populations, and the resulting patterns of distribution (Levin 1992; Giuggioli & Bartumeus 2012; Hanert 2012). Such a process has been referred to as ‘scaling up’ by a number of authors (Morales & Ellner 2002; Schick et al. 2008; Reynolds 2012d). Hence, through a joint focus on phenomena occurring at relatively large spatial scale, biology, physics and mathematics may work well together (Gautestad 2013b).

Future Understanding of Movements and Distribution of Organisms

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

Unfortunately, the Lévy walk hypothesis and its associated paradigm, which arise from a marriage between the Lévy walk model of movements and the optimal foraging
approach, fail to provide such an understanding of organismal movements, despite all the
enthusiasm that has been expressed about them. The Lévy model is biologically unrealistic,
especially as it omits ‘directionality’ of movements. Some tests have been invalid or
otherwise inadequate; others have been biased towards confirmation of Lévy patterns. No test
is so far without such problems, and quantitative tests provide results that clearly conflict
with expectations under Lévy walk hypothesis. The Lévy paradigm has encouraged
acceptance of the Lévy hypothesis, directed research towards its confirmation, and
discouraged consideration of alternative approaches.

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

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

The best path forward in terms of understanding movements and distribution of
organisms can therefore be simply stated: Abandon the Lévy movement paradigm for spatial
scales, generally relatively small to moderate, relevant to individual organisms; pursue other
modelling approaches such as the new generation of individual-based and inferential models; continue, at larger spatial scales, to evaluate Lévy and other patterns as descriptions and expectations for movement patterns, and as components affecting distribution and other population-level phenomena; maintain the dialogue and collaboration between biology, physics and mathematics.

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