Note

Lévy Meets Poisson: A Statistical Artifact May Lead to Erroneous Recategorization of Lévy Walk as Brownian Motion

Arild O. Gautestad*

Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway

abstract: The flow of GPS data on animal space is challenging old paradigms, such as the issue of the scale-free Lévy walk versus scale-specific Brownian motion. Since these movement classes often require different protocols with respect to ecological analyses, further theoretical development in this field is important. I describe central concepts such as scale-specific versus scale-free movement and the difference between mechanistic and statistical-mechanical levels of analysis. Next, I report how a specific sampling scheme may have produced much confusion: a Lévy walk may be wrongly categorized as Brownian motion if the duration of a move, or bout, is used as a proxy for step length and a move is subjectively defined. Hence, the categorization and recategorization of movement class compliance surrounding the Lévy walk controversy may have been based on a statistical artifact. This issue may be avoided by collecting relocations at a fixed rate at a temporal scale that minimizes over- and undersampling.

Keywords: Lévy walk, Lévy flight, Poisson process, animal foraging, animal movement.

Introduction

From the perspective of a biological journal, this note is starting from an unexpected location: a description of a moving robot (cybernetics) is connected to some basic principles of statistical mechanics (physics) before landing at the core message (biology). The motivation for this broadened approach is shared by an increasing number of ecologists who seek a better integration of physics and biology in analyses of animal movement (Gautestad and Mysterud 2005; Getz and Saltz 2008; Nathan et al. 2008; Struve et al. 2010; Petrovskii et al. 2011). For example, the Lévy flight foraging hypothesis (Viswanathan et al.

* E-mail: a.o.gautestad@bio.uio.no.

1999; Humphries et al. 2010, 2012; Sims et al. 2012) explicitly builds on adaptive switching between the physical models Brownian motion (BM) and Lévy walk (LW) under different environmental conditions. In the context of this note, LW and Lévy flight can be considered synonymous. In a resource-poor environment where food is randomly scattered and unpredictable, the occasional very long steps of LW are advantageous for food detection since a given total movement path covers a larger area than a BM path of similar accumulated length (BM, LW, and other concepts appearing in this outline will be defined in the next two sections). However, to what extent animals are actually performing LW is a controversial theme (Viswanathan et al. 2011), which will come into focus in the second part of this note.

Large GPS samples of individual locations, or fixes, coupled with high-resolution and multilevel GIS data, provide a rapidly expanding empirical database. However, what do the data provide us beyond descriptive analyses? What is the predictive power of the respective models for space-use dynamics? A wide range of sophisticated models are emerging (Fryxell et al. 2008; Gautestad and Mysterud 2010b), and old ones are subject to acid testing against the broader and better data material (Humphries et al. 2010; Sims et al. 2012). For example, biological models on animal space use, such as BM and diffusion, have been traditionally built on theory from physics of scale-specific statistical mechanics. But physicists may also be drawn to the recent series of GPS results indicating scale-free rather than scale-specific movement (see below), "particles" that move in a manner leading to complex but statistically consistent spatial patterns of space use, apparently stretching the theory of nonequilibrium statistical mechanics beyond its limits (Gautestad and Mysterud 2010a; Gautestad 2012b).

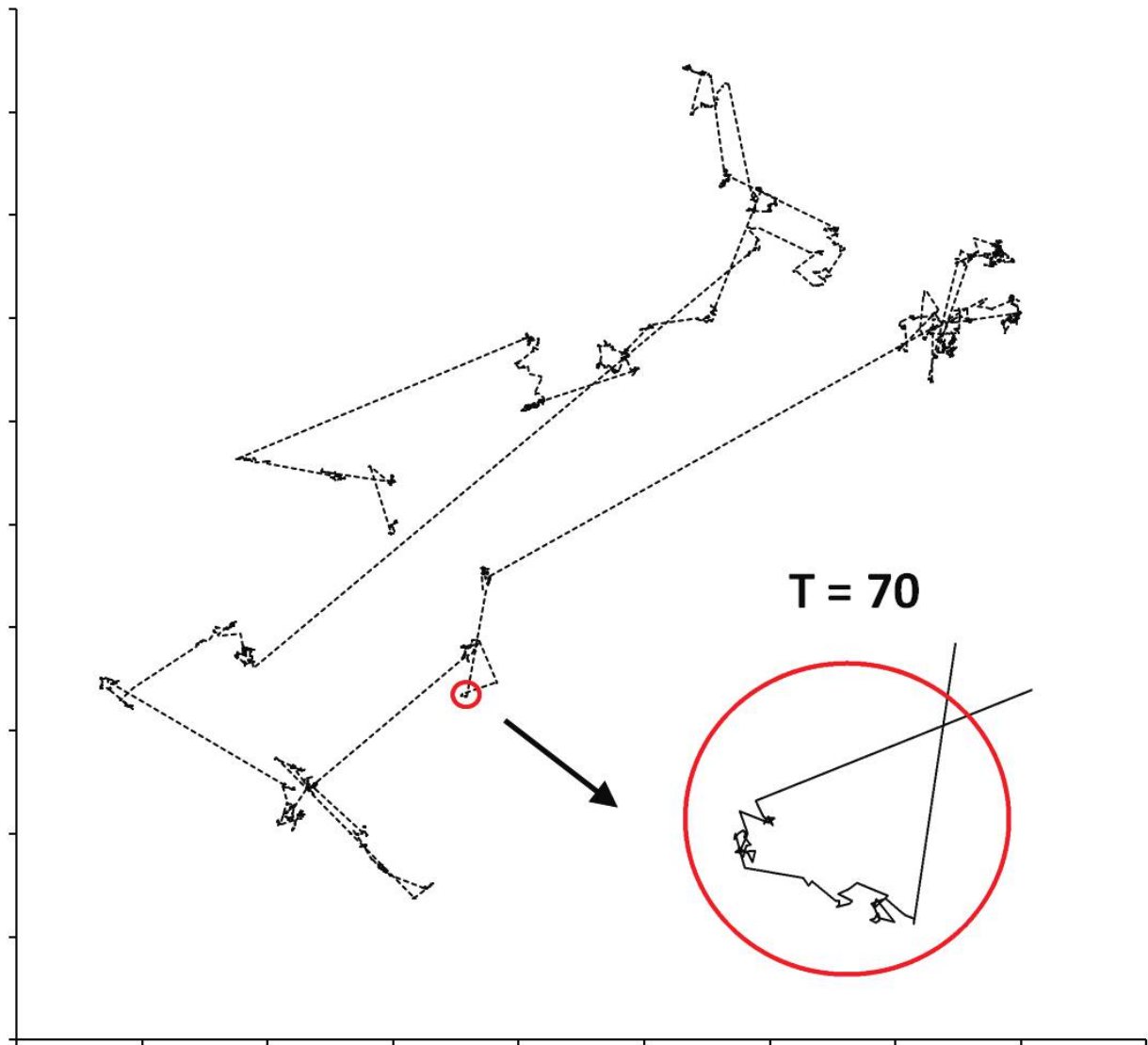To illustrate one particular challenge, figure 1 indicates

Figure 1: A simulated series of $N = 10^4$ spatial relocations of a Lévy walk, where the next move length $L_{LW} = \alpha(1 - \text{rnd})^{-(\beta-1)}$, with $\alpha = 1$ and $\beta = 2$ (rnd is a random number between 0 and 1). A maximum step length of $L_{max} = 40{,}000$ length units (identical in magnitude to the length scale of the area shown) was imposed, but this maximum length was not reached by any of the steps in the series. Successive relocations (representing fixes in GPS terminology) are connected by line segments. The segment circled in red represents an example of a period ($N = 70$) with apparently little movement from the perspective of the complete track but with microscale displacements at a fine spatial resolution (*inset*).

how scale-free movement will make it problematic to apply the local density of fixes as a proxy for local habitat preference. Density will vary in a self-similar (fractal) manner, leading to fix aggregations over a range of scales even in a completely homogeneous environment. The increased fix density variance from scale-free movement, relative to expectation based on standard BM-based diffusion, will require novel approaches to ecological inference based on analysis of GPS fixes. For example, Gautestad and Mysterud (2010*b*) proposed an index for local intensity of space use that adjusts for the scaling complexity by comparing density of fixes at two spatial resolutions. Two localities may have similar fix density, but the fixes may have different "clumping intensity."

Below I provide a brief summary of some central concepts related to scale-specific and scale-free habitat utilization and show how a specific method to test for Lévy walk (LW), an example of scale-free space use, may have

contributed to some of the confusion and controversy in statistical analyses of animal movement. In particular, LW may have been wrongly classified as BM.

Markov the Robot

Consider an animal, represented by a robot called Markov, moving unidirectionally by default but responding to environmental conditions in a deterministic and strictly rule-following manner. For example, when an obstacle is reached, Markov decides to move to the right or left, based on which direction seems to offer the optimal choice (e.g., Markov would move to the left if fewer obstacles were sensed in that direction). During some intervals and over some locations, the interrupts may be more frequent than during other intervals and over other places, implying environmental heterogeneity. Further consider that a sequence of this path is successively resampled by recording the location at constant time intervals t_{obs}, where t_{obs} is substantially greater than the mean time interval t' between direction-influencing events (this is often the case for GPS fixes of animals, which may have t_{obs} of hours rather than seconds or minutes). Next, study the step-length distribution by plotting the total sample of step lengths into respective size categories $L_1, L_2, L_3, ...$ where each L_j represents a unit interval called a "bin" (a larger j means a longer step length). Of particular interest is the shape and steepness of the large-step ("tail") part of the distribution $F(L_j)$, over the range of j where L_j is greater than the median step length. If t_{obs} and the sample size are both sufficiently large, the number of steps falling into a given bin L_j will tend to be, based on the rules given for Markov above, a given percentage smaller than the number in the preceding bin L_{j-1}. In other words, in the long run, the tail fits a Poisson distribution, characterized by a negative exponential curve, which is typical for a scale-specific process.

In this manner, a study of a sample of fixes would reveal a lot about Markov the robot's behavior. For example, the fact that Markov both perceives and responds to its environment within a narrow-scale range in time and space, characterizing a scale-specific kind of space use, would be revealed owing to the choice of a sufficiently large t_{obs}. Consequently, the focus would shift from the mechanistic to the statistical-mechanical level, bringing our study from the biological (behavior-characterized) microscales to the physical mesoscales. From the perspective of $t_{obs} \gg t'$, the successive lengths that appear from connecting line segments between fixes would no longer reflect successive behavioral decisions about if and where to move but would comply with a BM process. BM is statistical mechanical (and thus physical) by nature, not biological. In short, a given step length represents the resultant vector from a series of unknown intermediate move-related decisions,

leading to unsampled zigzagging in a more or less heterogeneous spatial "field" of Gaussian-dispersed path interrupts. This leads to an exponential variation of observed step lengths at the statistical-mechanical level t_{obs} (see "Statistical-Mechanical Aspects of GPS Data" in the appendix, available online).

In simulation examples to be shown below, I contrast BM with so-called scale-free movement, leading to different statistical-mechanical functions and parameters. This kind of physical-level information can be accessed only with great difficulty by analyzing the myriad behavioral events directly at biological microscales, where the individual actually interacts with its environment (Gautestad 2011; Petrovskii et al. 2011). I also propose how an explicit consideration of the statistical-mechanical properties of animal space use may contribute to resolving some of the controversy on scale-specific versus scale-free foraging bouts by individuals.

Scale-Specific Versus Scale-Free Movement: A Concept Walk-Through

The mechanistic rules that Markov the robot executes in a deterministic (nonstatistical) manner do not contain any rule for the exponential distribution of step lengths. On the contrary, there is no intrinsic rule for step termination at all; Markov moves till interrupted by an external obstacle. The average distance between interrupts, which may vary locally over many kinds of habitat, invokes one of nature's statistical laws: the central limit theorem. Exponential step-length distribution becomes an emergent property, resulting from the observer's choice to follow displacements at a scale t_{obs} that is larger than the interrupt "field," which in turn emerges as a result of environmental interactions on temporal scale t' on average. The Markovian algorithm for movement may be simple (as above) or very extensive, involving a large set of rules for various types of events. However, if each direction-influencing decision is independent of previous decisions, this menagerie of potential rules will lead to a qualitatively similar pattern at statistical-mechanical scales $t_{obs} \gg t'$, a negative exponential distribution of step lengths.

By purpose I defined Markov the robot's rules to be deterministic. The reason was to clarify a common misconception: when modeling animal movement by Brownian motion, this choice does not imply that the behavior behind the movement is assumed to be random and drunken walker–like. There may—or may not—be an element of stochasticity in all or some of the elements of the movement rules, but that is not crucial for the pattern that is observed at the statistical-mechanical level $t_{obs} \gg t'$. A BM model represents a simplification of scale-specific space-use dynamics at the expense of mechanistic details.

Interestingly, a BM path that is sampled at a larger t_{obs} is still a BM (Turchin 1998). The spatial pattern of fixes is self-similar (a statistical fractal; Mandelbrot 1983), despite the fact that the process as such is scale-specific owing to the characteristic disturbance scale t'.

In physics, the average length moved between direction-influencing events is called the mean free path, a central concept for statistical mechanics. In biology, this characteristic spatial scale and its temporal complement t' has an important meaning as well: an animal foraging in a resource-rich locality is expected to show a more strongly jagged path (Turchin 1998; Barraquand and Benhamou 2008) and, consequently, a smaller net displacement during an interval t_{obs} than in a more resource-sparse habitat.

Recall that the robot Markov was defined to move unidirectionally between environmentally invoked interrupts, and the BM appeared as a result of successive interactions with its environment at the scale of the mean free path. Then consider an alternative movement principle, Lévy walk, which is characterized by steps of length L that, on average, are taking place $1/L^{\beta}$ as often, with $1 < \beta < 3$. β is expressing how "steeply" the frequency of larger steps occur, relative to any chosen length L larger than the median length. For example, if we chose a bin representing step lengths in the interval 100–200 m (average 150 m) and compare the number of steps in this interval with those in the next bin comprising step lengths of 200–300 m (average 250 m), we expect $(150/250)^2 = 0.36$ as many steps in the larger bin if $\beta = 2$. Since this "ratio" relationship between two L_j is independent of which index j we choose to compare it with ($j + 1$, in our example), the movement is scale free over the range of L_j where β is constant.

LW is expressing a power-law tail of the distribution rather than an exponential tail: $F(L_j) = cL_j^{-\beta}$ and $1 < \beta < 3$ (where c is a scaling constant that is reflecting median step length). In logarithmic form, this becomes $\log[F(L_j)] = -\beta^* \log(L_j) + \log(c)$. Thus, the distribution's tail becomes linear under log transformation, with a slope $-\beta$. Both very short and very long steps become more predominant in comparison to the exponential distribution from a BM process. In spatial terms, the scale-specificity of a BM is expressed by λ in the exponential function $F(L_j) = \lambda e^{-\lambda L_j}$, where λ is inversely proportional to the average step length (a larger λ implies smaller steps). Under log transformation, this becomes $\log[F(L_j)] = -\lambda L_j + \log(\lambda)$. This kind of exponential tail is less "fat," or far less elongated, than a power-law tail. The inverse parameter, $1/\lambda$, represents the process' scale-specificity and is positively correlated with the mean free path. For example, while the LW step distribution is scale free owing to a constant ratio relation (divide one L_j with another and a pure number remains, without metrics such as m or km), a BM distribution changes relative to λL_j, which expresses a specific length scale such as m or km, when transformed to $\lambda' = 1/\lambda$.

Theoretically, the scale-free property of LW should be observable only at finer scales than the mean free path, since direction-influencing factors in the environment will tend to terminate long steps more prematurely the higher the spatial density of such factors (Reynolds and Rhodes 2009). In other words, when an LW path is sampled at coarser spatial scales than t', the more familiar exponential decay of step lengths in $F(L_j)$ that characterizes BM is expected. The principle is the same as described above for unidirectional (rather than LW) movement by Markov the robot when observed at $t_{obs} > t'$. Hence, LW may be observed over a limited temporal scale range, and the mean free path sets a limit to the bin range j where $F(L_j)$ is scale free. Hence, to expect a power-law distribution, t_{obs} should be larger than the microresolutions where Markov-compliant movement behavior (the mechanistic rules) may be studied in order to ensure a statistical-mechanical level of analysis. Further, t_{obs} should be smaller than the mean free path. This scale window means that LW becomes more complex to study than a scale-specific process like BM. As a consequence of this sampling scale sensitivity, the distribution of step lengths should reflect the following progression in the observed distribution of step lengths: LW (power-law tail for $t_{obs} \ll t'$ but larger than the Markov resolution), truncated LW with a power-law tail, but a tendency for cutoff in the form of an exponential tail toward the largest bins (when t_{obs} is somewhat smaller than t'), toward BM (pure exponential tail where $t_{obs} \gg t'$; Reynolds and Rhodes 2009; Gautestad 2012b).

However, LW has been observed in movement data from many species and taxa, over a broad range of scales of a magnitude of 100 times median step length or larger (Viswanathan et al. 2011). This fact supports the hypothesis that an individual may have some kind of cognitive capacity to switch between modes that lead to a power law of step lengths by ignoring potentially direction-interrupting events during the execution of long steps (Cole 1995; Bartumeus and Levin 2008; Gautestad and Mysterud 2010a). Markov the robot could, for example, have an additional "foraging" rule that made it ignorant of food patches for a power-law-distributed time span (many small intervals and some occasional large intervals) that was drawn randomly from one execution interval to the next (Benhamou 2007; Gautestad 2012a, 2012b). Other LW look-alike processes are summarized in "Power-Law Step-Length Distributions from Origins Other than Lévy Walk" in the appendix, available online.

Determining how to differentiate between various classes of movement based on, for example, distribution of step lengths has been chronically difficult. Below I report

one additional hurdle, which I describe by way of simulations and propose to resolve by use of a specific data collection practice. This aspect indicates that some of the controversy in the field of BM/LW studies may be rooted in a statistical artifact linked to an observer-introduced variant of the mean free path property described above.

Lévy Walk and Optimal Foraging: The Controversy

Since Cole's (1995) and Viswanathan et al.'s (1996) seminal papers on LW of the taxonomically distant fruit flies (*Drosophila melanogaster*) and wandering albatrosses (*Diomedea exulans*), mechanistic-stochastic[1] modeling of animal space use has gained increased focus, in particular in theoretical research on optimal foraging rules (Viswanathan et al. 1999; Bartumeus et al. 2005). However, some controversy has emerged as model predictions have been confronted with real data. Are the actual data showing LW or not? For example, the conclusion of LW compliance based on the original albatross movement series was based on serious flaws in the data analysis (Edwards et al. 2007), but in a ping-pong manner, weakness in this analysis has also been pointed out and LW in albatross movement resupported (Sims et al. 2012). Other data sets from a wide variety of species and taxa have also supported LW (see review in Viswanathan et al. [2011]).

The LW issue also extends to data collected at small scales, for example, insect movement studied by cameras or by other means. The movement of the black bean aphid (*Aphis fabae*) was, similarly to the albatross data, first classified as LW compliant and then reclassified as BM. While Mashanova et al. (2010) found evidence for movement in accordance to a truncated LW, Petrovskii et al. (2011) concluded that the apparent scale-free space-use pattern emerged from a population of fast and slow movers (represented by small and large λ', respectively), that is, an LW look-alike pattern from a composite ("mixed") BM-like distribution of move lengths at the population level. When the individual differences were accounted for by normalizing bout lengths in a given track relative to the mean track length, individual aphids seemed to move in close

agreement with an exponential function rather than a power law or truncated power law (Petrovskii et al. 2011).

So far the LW-BM controversy has focused mainly on statistical issues: what models to include in the test for movement-class compliance (power law, truncated power law where constant β is limited to a given range of L_j, exponential model, and other model variants) and what statistical method to apply to distinguish between them (Sims et al. 2007; Edwards 2011). For example, Boyer et al. (2008) questioned Edwards et al.'s (2007) reclassification of the albatross data as non-Lévy by showing how a truncated LW model (power law in the low- to mid-range of step lengths and exponential in the extreme tail) seemed to fit the data even after adjusting for the flaws reported by Edwards et al. (2007). Sims et al.'s (2012) analyses, both of original and additional data sets, also reaffirmed LW in albatross movement.

Confusion has also arisen after it has been shown how intermittent behavior (i.e., a mixture of fine- and coarser-grained scale-specific movement; a composite BM) may produce step-length distributions that appear power law–like and thus reflect LW in disguise (Benhamou 2007, 2008; Reynolds 2008). However, methods have been proposed to distinguish between a true scale-free process and a composite scale-specific process (BM with varying λ') by studying the effect from changing t_{obs}, in addition to characterizing the statistical pattern per se at a given t_{obs} (Plank and Codling 2009, 2011; Gautestad 2012a, 2012b).

In studies of the step-length distribution $F(L_j)$, the respective lengths (or time intervals; see below) are either calculated as successive distances between significant change of direction or collected from sampling successive spatial positions at constant time intervals (Sims et al. 2008, 2012; Reynolds and Rhodes 2009; Bartumeus et al. 2010; Humphries et al. 2010; Viswanathan et al. 2011). The fixed-sampling-interval method works out since an LW path is scale free (fractal like BM, but with a smaller fractal dimension) and thus looks the same from different temporal resolutions (Reynolds 2008). However, too high a frequency of data collection (implying smaller intervals) may lead to oversampling; many successive fixes on a relatively straight-line move sequence will influence the slope in the distribution $F(L_j)$ artificially over some range of L_j at these fine-grained resolutions (Turchin 1998; Dai et al. 2007; González et al. 2008).

Observational lag t_{obs} may, in fact, critically determine the shape of the observed step-length distribution and thus the degree of compliance with power-law or Poisson distribution, if the animal shows site fidelity driven by long-term memory of previously visited patches (Gautestad and Mysterud 2005; Gautestad 2011, 2012b). In this case, undersampling is the critical issue, in contrast to the issue of oversampling referred to above. An LW-like power-law

---

[1] Mechanistic modeling implies generation of a fine-grained movement path, based on a given algorithm for successive spatial displacements. If this algorithm involves one or more elements of stochastic rules, for example, some degree of random direction for the next move, the mechanism may be called mechanistic stochastic (as opposed to mechanistic deterministic). However, these two variants (on a continuum) are both mimicking movement at the detailed, behavior-explicit "micro" scale. In contrast, the meso- and macroscale level of statistical mechanics regards space-use pattern that emerges from an animal's successive displacements at microscale when successive locations are resampled at substantially larger intervals (lag). Hence, the pattern becomes statistical regardless of the degree of stochasticity/determinism in the behavioral algorithm at microscale.

distribution becomes masked due to influence from a mixture with non-power-law distribution of intermediate return events in the interval between successive relocations at scale t_{obs}.

In short, the BM-LW issue is extremely complex. However, much confusion is bound to surface if a given analysis has not taken into account the distinction among mechanistic scale ($t_{obs} < t'$), statistical-mechanical scale ($t_{obs} > t'$), and coupling between temporal and spatial scales. As a practical illustration, below I show how apparently "innocent" subjective rules of thumb for how to define a step length from a path that is sampled at high frequency (very small t_{obs}) may have contributed to the LW controversy.

Subjective Step Classification Rules May Corrupt a Power-Law Pattern

In the reclassification studies of wandering albatrosses and black bean aphids referred to above, the researchers did not study the respective step-length distributions directly. Instead, they calculated step durations (time intervals between successive moves) as a replacement for spatial lengths, under the apparently logical and widely accepted assumption that spatial move lengths and temporal intervals are proportional on average (Cole 1995; Johnson et al. 2002). Hence, a constant movement speed may be assumed, and long intervals (bout duration) should translate to proportionally long bout lengths in spatial terms ("bout" is jargon that may be translated as "step" or "move length," since it regards the issue of defining where successive steps have their start and stop points; see "The Step-Length Challenge" in the appendix, available online.

Unfortunately there is a glitch in this assumption if a specific kind of observer-induced (i.e., subjective) rule for bout termination is applied. For example, in the case of albatrosses (Edwards et al. 2007), flight duration was defined as the time interval when the apparatus (a saltwater-immersion logger) attached to one of the legs was dry for at least a defined minimum of time (30 s). The duration was determined terminated at the first instance of wet conditions. In addition to removing the shortest bouts, this procedure may have contributed to premature termination of long bouts. If the bird, during a relatively long and unidirectional stretch of movement, had swiftly landed at the surface to get a better perception of the local food condition, two intermediate-distance flight durations would have been recorded instead of one large interval (from the spatial perspective). With respect to the black bean aphids, bout duration was defined as movement of at least 3 s in which the speed exceeded 0.3 mm/s at every second (Mashanova et al. 2010; Petrovskii et al. 2011). Again, a subjective rule is imposed on the definition of a move length from the perspective of bout duration, as

opposed to an objectively defined temporal resolution (a fixed t_{obs}).

Exploring Subjective Bout Termination Rules

The consequences for the test of LW versus truncated LW or BM may be dire. For example, consider the simulated LW track in figure 1. The overall pattern of movement shows the typical mixture of many small and a few long steps, which, from the spatial perspective, adheres to a power-law distribution of L with exponent $\beta \approx 2$ (given by the simulation conditions). A complementary distribution of bout durations, where a bout is defined as the time interval from one uncorrelated redirection event to the next, under the assumption of a constant movement speed, would give the same result. However, consider replacing this system-specific (objective) definition of bout termination with a subjective bout termination rule, whereby a given bout is terminated if the average movement rate (speed) along the path falls below a critical minimum during a trailing time window of, for example, three consecutive high-frequency relocations. If the critical net displacement was set to 12 length units during 3^*t_{obs}, a sequence of three steps of length $5 + 5 + 5$ would trigger a bout termination if the resultant vector (sum of the three vectors of length 5 units each) had a length shorter than 12. This would happen, for example, if one of the steps was moving the individual backward relative to the other two driving it forward. From a practical perspective, this reduced speed may seem feasible as a definition of "resting," or practically stopping to move (similar to bout definition for the black bean aphid movement and equivalent to the data logger reporting that the albatross is getting its foot wet). One such event is marked in figure 1, and it lasts for about 70 time increments (0.7% of total track duration). However, when zooming in to this spatiotemporal window, it becomes obvious that, from a fine-grained perspective, the individual has continued exploring its local patch.

In statistical-mechanical terms, the respective bout termination rules for albatrosses and aphids mean that a "virtual" mean free path (i.e., the distance or time interval between successive interrupts of a move) may have been unintentionally invoked by the introduction of the bout termination rule, leading to a potentially premature interrupt of successive move intervals. While the mean free path in physical terms regards real interrupts such as collisions between gas molecules, the actual move termination rule defined here regards an observer-dependent kind of interrupt (on the observed pattern, not the underlying physics). However, in statistical-mechanical terms, the effect may be similar. Critically, if the observer-invoked mean free path has a finer "mesh" (resolution) than the

physical mean free path (i.e., if the frequency of rule-induced events from the virtual field is higher than the actual step-length truncation from environmental events), the interrupts may critically influence the model fitting of the distribution of bout durations. For example, if Markov the robot moves in a terrain that invokes the direction-changing rule every 10 m on average (i.e., $t' = 10$ s, if it moves 1 m/s), collecting fixes at intervals $t_{obs} > 10$ s will produce a negative exponential step-length function of observed fixes, as already described. However, consider an upgraded robot, where the movement algorithm allows for circumventing temporary obstacles in deciding which direction to move after scanning the environment within sight of its built-in camera. For example, a tree trunk or a hole in the ground may invoke a temporary zigzag while still holding the target active. Obviously, a subjective step definition rule that either fires a step termination event if the zigzag includes a sharp angle or if the time to target becomes larger than the defined limit (owing to zigzagging) would lead to a higher sample size of steps than if such a rule did not exist and a fixed t_{obs} were used instead. Small steps would have been inflated at the expense of medium and large steps, hence, a finer-grained mesh (finer mean free path) resulting from subjective rules.

In "Statistical-Mechanical Aspects of GPS Data" (fig. A3) in the appendix, available online, the LW path has been extended to a larger path, and the above-mentioned bout termination rule has been invoked in three variants of strength. The result for one of these conditions is seen in figure 2, showing distribution of bout duration. Three aspects stand out. First, the expected LW pattern (power law) is absent. Instead, a negative exponential distribution of bout durations is seen, demonstrating an apparent but false compliance with a BM process, if proportionality between bout duration and bout length is assumed. Second, this compliance with the negative exponential function becomes stronger (larger R^2) for the rule variant that produces the largest frequency of bout terminations (as expected, since interference from the "virtual" mean free path was stronger). Third, the rule that led to the fewest number of steps (and thus the largest step intervals on average) showed a somewhat elongated tail relative to expectation from a negative exponential function. Hence, a less intrusive step termination rule led to a tendency for a transition toward the true LW pattern, characterized by a power law rather than a negative exponential. This transition is expected, since less intrusive step termination conditions lead to step samples collected at larger time intervals on average. This also implied many intermediate "unobserved" steps, as required for a statistical-mechanical level of observation, and thus more closely resembles the true relationship of proportionality between t_{obs} and median step length for the underlying LW series.

In figure 3, the distribution of moves is displayed from the spatial perspective: net displacements of respective step lengths. In this case, an LW pattern is visible owing to the power-law compliance. A power law (linear function under double-log plotting) is seen for both the original LW series and a subsampled series 1 : 140 original size, whether the latter regards the first part of the original series ($t_{obs} = 1$ time unit) or a 1 : 140 subset where fixes are sampled uniformly (leading to a larger t_{obs} and thus a right-shifted plot; see below). Most interestingly, a power law of step lengths is also seen for the series resulting from the "strongest" subjective bout termination rule producing the largest set of steps (average step length of ca. 140 spatial units, and average time interval 122 units), despite this condition's best fit to an exponential distribution of time intervals (fig. 2). By applying the parallel shift method to test for true scale-free movement (Gautestad 2012b), the underlying LW process is additionally supported: the regression line for an approximately equal sample size of moves (1 : 122 of full series) right shifts in accordance with what should be expected from proportionality between net displacement length and the fixed or average time interval for observing the displacements. A composite BM process would have right shifted the distribution of similar-sized samples of steps proportionally with the square root of this difference in t_{obs} between the 1 : 140 sample from the original series and the 1 : 122 sample from the subjective condition 3 series in figure 2 (i.e., half the length shown by the dashed PS line in figure 3 owing to log-transformed scales). Thus, LW-characteristic superdiffusion rather than BM-characteristic classical diffusion is verified when studying step-length distribution directly, rather than assuming proportionality between step duration and step length, even when a subjective bout definition rule is applied.

With reference to Petrovskii et al.'s (2011) reclassification of Mashanova et al.'s (2010) black bean aphid movement as being BM-like rather than LW-like, the power-law patterns in figure 3 do not result from the lumping together of a population of BM-compatible track intervals of great and small characteristic movement speed (these LW look-alike variants are distinguishable by the parallel shift method; in fig. 3, the dashed PS line would have been half as long). Due to the property of the path of true self-similarity, splitting an LW path into smaller sections and rescaling each section according to the overall average bout length (sensu fig. 1 in Petrovskii et al. [2011]) will not influence double-log linearity and the estimate of β significantly. In contrast, the subjective bout duration rule that was simulated here, which is qualitatively similar to the protocol proposed by Petrovskii et al. (2011), leads erroneously to a BM-like pattern with respect to the distribution of bout durations. A spatial analysis of net spatial
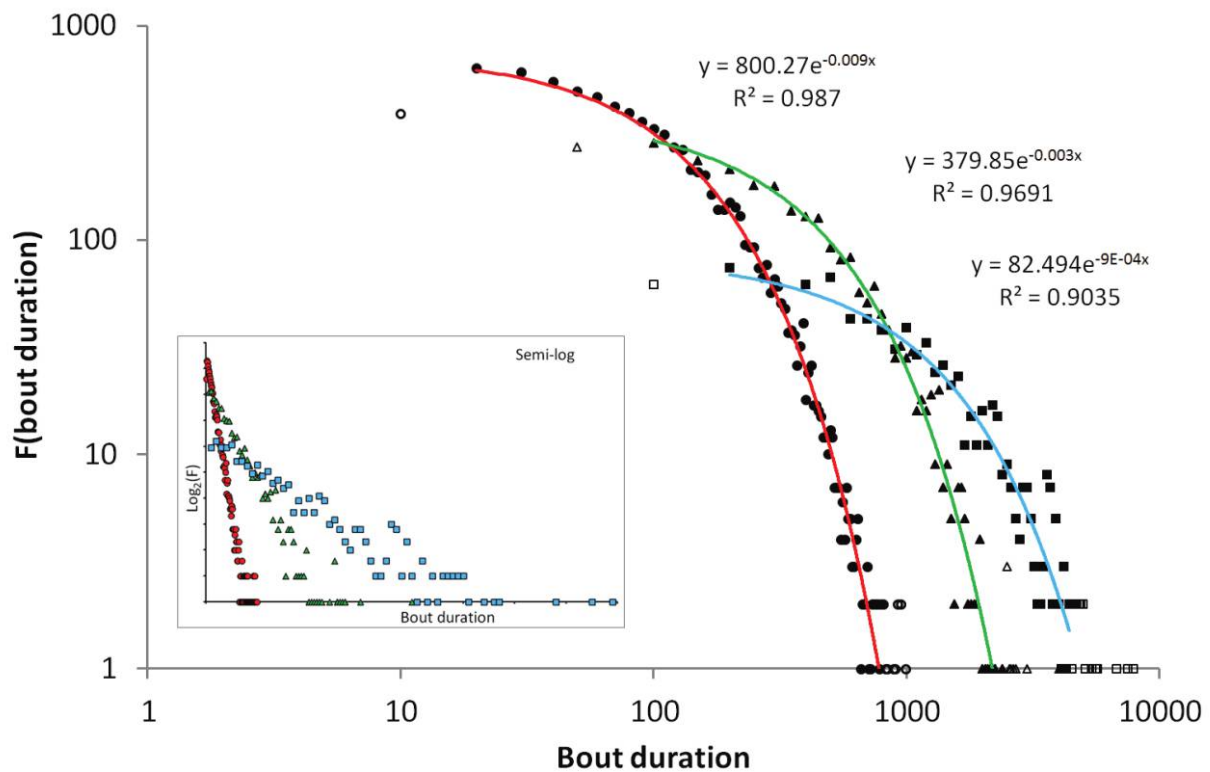
Figure 2: Under the same boundary conditions set in figure 1, a "virtual" mean free path owing to subjectively defined move-length interrupts, based on a critical minimum movement rate (speed) over the last three steps, was added in a subsequent simulation series of length 10^6 steps. If the net displacement was below the defined minimum, the step series was terminated. Bout duration was defined as the interval (in number of time increments) from the starting point at the previous termination point. The three conditions were 3.2, 3.3, and 3.5 length units per three time increments (conditions 1, 2, and 3, respectively). Condition 3 imposed a higher frequency of bout terminations (8,255 bouts in total), leading to shorter bout durations and, hence, shorter distances moved during a given bout, than conditions 1 and 2 (885 and 2,543 bouts, respectively). Bouts of 5 step lengths or fewer were excluded from the analysis. The distribution of bout durations was compliant with a Poisson process (negative exponential function), as shown by the blue (condition 1), green (condition 2), and red (condition 3) exponential regression lines. The three conditions show a transition from clear exponential form (condition 3) toward some elongation of the tail under condition 1. Observe the double-log-transformed axes. Power-law compliance would have shown a linear regression fit under double-log transformation. An exponential function produces linear fit on semilog plotting (*inset*; logarithms on *Y*-axis only).

displacements (fig. 3) was necessary to reveal the true LW pattern, which was additionally strengthened by the parallel shift test.

Discussion

One of the main messages of this note is the importance of making a clear distinction between an individual's interactions with its environment at microscales (via a high-frequency sampling of fixes), in contrast to how these processes appear at physical mesoscales (a lower-frequency sampling). The BM-LW continuum belongs to the latter level of observation. If one tunes an FM radio to a frequency between two stations, one may experience a mixed

bag of conflicting signals and messages. In the present context of space use, in order to properly decide if a given animal has related to its environment in a BM or LW manner, or whether BM is observed as a consequence of studying a true LW, but this is hidden by choosing $t_{obs} > t'$, one should make sure that t_{obs} is varied sufficiently to reveal such mean free path–influenced transitions. Unfortunately, the present example of choosing subjective move termination rules for step-length collection illustrates the common choice to study the path close to $t_{obs} = t'$, where t' represents an observer's subjectively introduced mean free path. This "artificial" disturbance field on long step lengths may mask the true mean free path that is experienced by the individual.
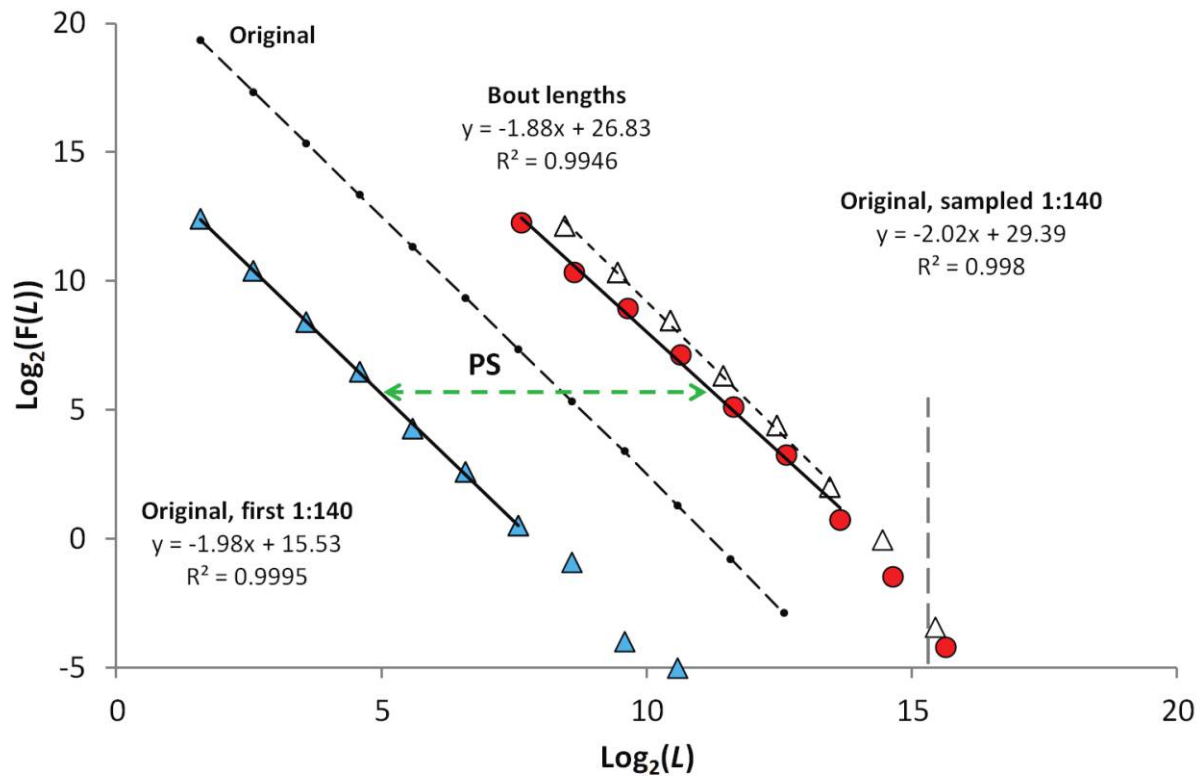
Figure 3: In the spatial domain (net bout lengths rather than complementary bout duration), power-law compliance of step-length distribution is characterized for the original series ($N = 10^6$ steps; dashed line, black circles; $\beta \approx 2$), the distribution of step lengths of the first $1 : 140$ part of the total series (blue triangles; $t_{obs} = 1$), and a similarly sized sample $1 : 140$ of the original series (uniformly sampled; open triangles; $t_{obs} = 140$). The two latter samples are included to show the expected parallel shift of the fitted regression line of magnitude 140 length units when median step length increases as a consequence of a 140-times-larger t_{obs}. Sample size is kept constant on magnitude $10^6/140 = 7{,}143$ between the two sampling variants to avoid sample-size issues of power-law distributions. The parallel shift is marked by the dashed, green line labeled "PS." The observed shift verifies superdiffusion of similar rate, that is, that bout length increases approximately proportionally with bout duration. A parallel shift of similar magnitude is seen in the step-length distribution from the subjective bout definition under condition 3 (red circles), which resulted in a median net step length of $139.2 \approx 140$ length units. The largest bins were moderately influenced by the intrinsic step-length truncation (see fig. 1 legend; L_{max} is marked by a vertical, gray dashed line). Close to this limit a somewhat steeper slope is observed. Bins were geometrically scaled and respective frequencies width-adjusted (normalized), in accordance with Sims et al. (2007).

As shown by simulation experiments on correlated random walks and related variants (Plank and Codling 2009; Codling and Plank 2011), subjective rules to define step lengths in a manner that indirectly mimics mean free path influence may even fool sophisticated statistical protocols for LW tests, such as the maximum likelihood estimation method (Edwards et al. 2007). Hence, in a complementary manner to this analysis, where LW may be wrongly classified as BM, the theoretical study of Codling and Plank (2011) shows how BM-originating paths may wrongly be classified as LW. Both issues are connected to the physical concept of mean free path (in this case, artificially introduced by subjective step-length rules). Applying temporal bout duration to represent spatial step length in an LW-BM model-fitting context is thus problematic.

Variants of rules have been proposed, whereby a move is terminated on the basis of directional autocorrelation along the fine-resolution movement path (Turchin 1998; Reynolds and Rhodes 2009). However, this approach still implies a subjective definition of the rule "strength" (based on degree of autocorrelation and spatial trailing length over which the movement angle is measured). Hence, a third approach, more in compliance with a statistical-mechanical framework, may be more representative of the underlying process: using a fixed lag to sample successive displacements (Johnson et al. 2002; Mårell et al. 2002; Morales et al. 2004; Gautestad and Mysterud 2005). This approach creates a more coherent and physical link between the spatial and temporal domain, since distance moved per time unit translates to movement rate. In the

case of LW, this rate scales self-similarly over a range of t_{obs} (Gautestad 2012*b*) and thus maintains the power-law property of the data at different resolutions. With reference to the scale-free nature of LW, observing a given trail at a sufficiently coarse temporal resolution to avoid oversampling but also to avoid undersampling (both situations lead to predictable qualitative changes in the distribution and are thus testable), an optimal distribution of step lengths for an LW-BM test may be achieved.

In some instances, subjectively defined move termination rules may have been adopted because the methods applied for tracking movement are themselves not error free owing to the resolution power of the positioning instruments. One may then be forced to apply such rules as a means to avoid "false movement," in which case an individual did not, in fact, move. However, the method proposed here, using fixed t_{obs} instead of collecting subjectively defined step lengths, is less prone to such measurement error. While positioning noise may trigger false steps under subjective rule conditions, the fixed t_{obs} method only adds a specific variance to the respective interfix distances. For the smallest steps, this superimposed variance may be substantial (but normally negligible for the larger ones), but it will not inflate the number of steps considered in the analysis. Contrary to the condition of subjective rules, this number is given by the product of t_{obs} and the total sampling period. Hence, if measurement noise is less than the spatial scale for the smallest bin L_j for $j = 1$, the result is not influenced. When studying the step-length distribution $F(L_j)$, it is the right-end tail that is under consideration. L_1 is thus normally set somewhat larger than the magnitude of the median step length (or the analysis starts from these larger scales). Implicitly, measurement error should not be an issue at these scales.

The explicit consideration of subjective mean path introduction and observer-defined lag for data collection illustrates how a statistical-mechanical approach may provide a constructive direction forward (Gautestad and Mysterud 2010*a*; Petrovskii et al. 2011; Gautestad 2012*b*) in a field that currently seems to be spinning deeper and deeper into endless discussions about statistical patterns and problematic sampling protocols. Statistical mechanics provides a more coherent and explicit link between a statistical pattern and the dynamics of the underlying process at finer spatiotemporal resolutions than the level at which data are collected and analyzed.

Acknowledgments

Literature Cited

Barraquand, F., and S. Benhamou. 2008. Animal movements in heterogeneous landscapes identifying profitable places and homogeneous movement bouts. Ecology 89:3336–3348.

Bartumeus, F., M. G. E. da Luz, G. M. Viswanathan, and J. Catalan. 2005. Animal search strategies: a quantitative random-walk analysis. Ecology 86:3078–3087.

Bartumeus, F., L. Giuggioli, M. Louzao, V. Bretagnolle, D. Oro, and S. A. Levin. 2010. Fishery discards impact on seabird movement patterns at regional scales. Current Biology 20:215–222.

Bartumeus, F., and S. A. Levin. 2008. Fractal reorientation clocks: linking animal behavior to statistical patterns of search. Proceedings of the National Academy of Sciences of the USA 105:19072–19077.

Benhamou, S. 2007. How many animals really do the Lévy walk? Ecology 88:1962–1969.

———. 2008. How many animals really do the Lévy walk? reply. Ecology 89:2351–2352.

Boyer, D., O. Miramontes, and G. Ramos-Fernández. 2008. Evidence for biological Lévy flights stands. Complexity Digest, arXiv0802.1762.

Codling, E. A., and M. J. Plank. 2011. Turn designation, sampling rate and the misidentification of power laws in movement path data using maximum likelihood estimates. Theoretical Ecology 4:397–406.

Cole, B. J. 1995. Fractal time in animal behaviour: the moment activity of *Drosophila*. Animal Behaviour 50:1317–1324.

Dai, X., G. Shannon, R. Slotow, B. Page, and K. J. Duffy. 2007. Short-duration daytime movements of a cow herd of African elephants. Journal of Mammalogy 88:151–157.

Edwards, A. M. 2011. Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. Ecology 92:1247–1257.

Edwards, A. M., R. A. Phillips, N. W. Watkins, M. P. Freeman, E. J. Murphy, V. Afanasyev, S. V. Buldyrev, et al. 2007. Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. Nature 449:1044–1049.

Fryxell, J. M., M. Hazell, L. Börger, B. D. Dalziel, D. T. Haydon, and J. M. Morales. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proceedings of the National Academy of Sciences of the USA 105:19114–19119.

Gautestad, A. O. 2011. Memory matters: influence from a cognitive map on animal space use. Journal of Theoretical Biology 287:26–36.

———. 2012*a*. Animal space use: distinguishing a two-level superposition of scale-specific walks from scale-free Lévy walk. Oikos, doi: 10.1111/j.1600-0706.2012.19998.x.

———. 2012*b*. Brownian motion or Lévy walk? stepping towards an extended statistical mechanics for animal locomotion. Journal of the Royal Society Interface 9:2332–2340.

Gautestad, A. O., and I. Mysterud. 2005. Intrinsic scaling complexity in animal dispersion and abundance. American Naturalist 165:44–55.

———. 2010*a*. The home range fractal: from random walk to memory dependent space use. Ecological Complexity 7:458–470.

———. 2010*b*. Spatial memory, habitat auto-facilitation and the emergence of fractal home range patterns. Ecological Modelling 221:2741–2750.

Getz, W. M., and D. Saltz. 2008. A framework for generating and analyzing movement paths on ecological landscapes. Proceedings of the National Academy of Sciences of the USA 105:19066–10971.

González, M. C., C. A. Hidalgo, and A.-L. Barabási. 2008. Understanding individual human mobility patterns. Nature 453:779–782.

Humphries, N. E., N. Queiroz, J. R. M. Dyer, N. G. Pade, M. K. Musyl, K. M. Schaefer, D. W. Fuller, et al. 2010. Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature 465:1066–1069.

Humphries, N. E., H. Weimerskirch, N. Queiroz, E. J. Southhall, and D. W. Sims. 2012. Foraging success of biological Lévy flights recorded in situ. Proceedings of the National Academy of Sciences of the USA 109:7169–7174.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225–235.

Mandelbrot, B. B. 1983. The fractal geometry of nature. W. H. Freeman, New York.

Mårell, A., J. P. Ball, and A. Hofgaard. 2002. Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. Canadian Journal of Zoology 80:854–865.

Mashanova, A., T. H. Oliver, and V. A. A. Jansen. 2010. Evidence for intermittency and a truncated power law from highly resolved aphid movement data. Journal of the Royal Society Interface 7:199–208.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85:2436–2445.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the USA 105:19052–19059.

Petrovskii, S., A. Mashanova, and V. A. A. Jansen. 2011. Variation in individual walking behavior creates the impression of a Lévy flight. Proceedings of the National Academy of Sciences of the USA 108:8704–8707.

Plank, M. J., and E. A. Codling. 2009. Sampling rate and misidentification of Lévy and non-Lévy movement paths. Ecology 90:3546–3553.

———. 2011. Sampling rate and misidentification of Lévy and non-Lévy movement paths: reply. Ecology 92:1701–1702.

Reynolds, A. 2008. How many animals really do the Lévy walk? comment. Ecology 89:2347–2351.

Reynolds, A. M., and C. J. Rhodes. 2009. The Lévy flight paradigm: random search patterns and mechanisms. Ecology 90:877–887.

Sims, D. W., N. E. Humphries, R. W. Bradford, and B. D. Bruce. 2012. Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. Journal of Animal Ecology 81:432–442.

Sims, D. W., D. Righton, and J. W. Pitchford. 2007. Minimizing errors in identifying Lévy flight behaviour of organisms. Journal of Animal Ecology 76:222–229.

Sims, D. W., E. J. Southall, N. E. Humphries, G. C. Hays, C. J. A. Bradshaw, J. W. Pitchford, A. James, et al. 2008. Scaling laws of marine predator search behaviour. Nature 451:1098–1103.

Struve, J., K. Lorenzen, J. Blanchard, L. Borger, N. Bunnefeld, C. Edwards, J. Hortal, et al. 2010. Lost in space? searching for directions in the spatial modelling of individuals, populations and species ranges. Biology Letters 6:575–578.

Turchin, P. 1998. Quantitative analysis of animal movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, MA.

Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. 1996. Lévy flight search patterns of wandering albatrosses. Nature 381:413–415.

Viswanathan, G. M., S. V. Buldyrev, S. Havlin, M. G. E. da Luz, E. P. Raposo, and H. E. Stanley. 1999. Optimizing the success of random searches. Nature 401:911–914.

Viswanathan, G. M., M. G. E. da Luz, E. P. Raposo, and H. E. Stanley. 2011. The physics of foraging: an introduction to random searches and biological encounters. Cambridge University Press, Cambridge.