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Brownian motion or Lévy walk? Stepping towards an extended statistical mechanics for animal locomotion

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Animals moving under the influence of spatio-temporal scaling and long-term memory generate a kind of space-use pattern that has proved difficult to model within a coherent theoretical framework. An extended kind of statistical mechanics is needed, accounting for both the effects of spatial memory and scale-free space use, and put into a context of ecological conditions. Simulations illustrating the distinction between scale-specific and scale-free locomotion are presented. The results show how observational scale (time lag between relocations of an individual) may critically influence the interpretation of the underlying process. In this respect, a novel protocol is proposed as a method to distinguish between some main movement classes. For example, the 'power law in disguise' paradox—from a composite Brownian motion consisting of a superposition of independent movement processes at different scales—may be resolved by shifting the focus from pattern analysis at one particular temporal resolution towards a more process-oriented approach involving several scales of observation. A more explicit consideration of system complexity within a statistical mechanical framework, supplementing the more traditional mechanistic modelling approach, is advocated.

Keywords: Lévy walk; Brownian motion; multi-scaled random walk; animal space use; statistical mechanics

1. INTRODUCTION

Consider the movement path of a foraging mammal. After bouncing back and forth on a relatively local scale for a while, the animal suddenly takes a more directional and long-lasting displacement, bringing it to a relatively distant location within a few time increments. What has happened? From the perspective of small time increments, an observer will typically look for local causes: was the food patch depleted to a critical level, *sensu* the marginal value theorem [1]? Or had a predator suddenly emerged in the neighbourhood? From a coarser temporal perspective, was the individual just performing one of its more strategic moves (from the finer-scaled point of view), which just 'waited to happen'—with no clear local causation whatsoever? However, the causation might have been easier to reveal from a coarser spatio-temporal level of analysis, where the finer-grained myriad of interactions could be averaged out as background noise. On the other hand, fine-grained mechanics also generate seeds for coarser-grained behaviour. Hence, the real challenge for a coherent theory regards this kind of multiple-scale complexity where processes at various scales interact in a dual-directional manner.

Below, this challenge is approached in three steps. First, contemporary issues related to modelling of animal movement are summarized, with a focus on challenges relating to scaling and memory. It is argued that a realistic implementation of these aspects in models requires an extension of the classical statistical mechanical framework. Second, simulation results illustrate the qualitative difference between (i) apparently scale-free space use owing to habitat utilization at different scales in an inter-independent manner (memory-less composite random walk) and (ii) true scale-free space use emerging from an intrinsically scale-free space-use process. The latter covers a memory-less to memory-influenced continuum between Lévy walk (LW) and multi-scaled random walk (MRW) (to be described below). Third, a novel statistical protocol is described to distinguish between (i) and (ii) from a set of animal relocations such as series of GPS fixes.

Many animals relate to their habitat over a range of spatio-temporal scales, commonly conceptualized as a nested hierarchy of landscape elements [2]. Hence, habitat heterogeneity generates a tension between fine- and coarse-scale weighing with respect to what goal to follow for the next move. In an apparent adaptation to cope with habitat heterogeneity, many species have

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developed a cognitive capacity to use past experiences in a spatially explicit manner. This implies strategic movement, including homing—guided by a memory map [3–8]. However, transforming the interplay between scaling and memory into actual simulations under a coherent theoretical framework has proved difficult and contains many challenges [9–11].

A variety of statistical mechanical models such as correlated random walk and LW have been explored in the context of scale-free versus scale-specific movement, in particular in relation to optimal foraging, as reviewed by, e.g. Reynolds & Rhodes [12] and Viswanathan *et al.* [13]. However, it has been argued that theoretical progress in the context of vertebrate space use also depends on a realistic implementation of the memory aspect of movement [9–11], including a statistical mechanical system description in this regard [14–16]. Thus, on the one hand, the scaling property observed in real GPS data over some scale range [13,17,18]—even if the power-law fit has been questioned for some of the datasets [19,20]—requires a deeper understanding of the processes behind the emergence of scale-free movement. A statistical description of scaling is given in the context of vertebrate movement is given below, followed by a description of how observed scaling may reflect a process involving long-term memory.

A power-law pattern is indicative of an intrinsically driven scale-free process [21]. In the present context of movement, the long step tail part of a histogram of distances L between successive spatial relocations (e.g. GPS fixes) of an individual at a given observer time lag t_{obs} often fits a power law [13,22]; i.e. a k times larger step length appearing with a frequency of $1/k^{\beta}$ over a scale range from L_{min} to L_{max}. The power-law distribution can then be described by a so-called truncated LW:

$$F(L) = aL^{-\beta}|1 < \beta < 3, L_{\mathrm{min}} < L < L_{\mathrm{max}}, \qquad (1.1)$$

where $F(L)$ represents number of displacements falling within a given bin (range of step length), a is a parameter for unit bin for the power-law compliance and β represents the 'steepness' of the right-tail part of the distribution. L_{min} is larger than the median step length, whereas L_{max} defines a transition towards a steeper cut-off (truncation zone; i.e. typically a negative exponential form of the distribution for the largest bin intervals). The truncation could—for example—be due to maximum movement distance during the observation interval t_{obs}, environmental constraint or other factors interfering with large step lengths. Without the truncation aspect, equation (1.1) is expressing a so-called Lévy flight, which is characterized by successive abrupt displacements, rather than a movement with a mean displacement rate per unit time and a power-law distribution of steps lengths between random directional turns. Hence, the phrase LW is used here owing to its closer physical compliance with animal movement, but the two phrases are often used synonymously in the biological literature [12]. However, synonymy in the case of LW requires that t_{obs} is sufficiently large to allow for observation of large step lengths (rather than cutting them into pieces owing to too frequent fix sampling). Otherwise, the scale-free interval, $L_{\mathrm{min}} < L < L_{\mathrm{max}}$, may become artificially narrowed. Furthermore, choosing t_{obs} smaller than this truncation-related limit requires a more complex equation relative to equation (1.1), with movement steps expressed more explicitly as a function of time [23].

To what extent equation (1.1) represents a pattern of real animal movement has been surrounded by controversy, as reviewed by Viswanathan *et al.* [13]. This controversy has been enhanced by simulation results showing that a superposition of scale-specific processes—for example, movement consisting of a mixture of two BM components with different scale constants and frequency of occurrence—may generate an LW-like pattern under specific boundary conditions, and hence appear statistically as a scale-free process [24–27]. This power-law look-alike paradox from tuning of scale constants of a composite BM creates serious challenges for statistical verification of a true scale-free process for real data. The challenge adds to the fact that power-law compliance from a purely statistical perspective is notoriously difficult to verify owing to the influence of step-length truncation [19], as expressed by L_{max}. This truncation around L_{max} is a function of the mean path constraint under the Markov process premise, and the maximum movement speed during the chosen time intervals for observation (t_{obs}).

However, simulations presented below illustrate how this 'power law in disguise' paradox from a composite BM may be resolved by shifting the focus from a purely statistical analysis of step lengths to a more process-focused kind of hypothesis testing, derived within the framework of statistical mechanics. Next, the LW simulation design is further extended to illustrate the effect from adding long-term memory mimicking a memory map utilization and homing, which implies a potential for scale-free dynamics both in the spatial and the temporal domain (within practical scale range constraints).

2. SCALING AND MEMORY

An LW-like distribution of step lengths can—as an alternative to invoking a qualitatively new framework relative to classical BM and diffusion—be constructed by fine-tuning a superposition of two BM processes with different scaling constants (a proxy for mean step length) and relative frequencies of occurrence. This composite BM approach—from randomly mixing bouts of scale-specific movement at different scales—is feasibly described as intra-patch movement mixed with less frequent inter-patch movement [24,28]. Plank & Codling [29] extended Benhamou's [24] exemplification of Lévy look-alike processes from composite BM, by exploring a broader range of scale constants and conditions for the scale-specific components under a range of sampling lags on the generated series. They found that a strong directional persistence (correlated random walk) for the coarser-scale process in combination with low frequency of appearance of this component relative to the finer-scaled process led to an LW-like pattern. However, their methodology was criticized by Auger-Méthé *et al.* [30] (but see Plank & Codling [31]). In short, these approaches are stretching the BM paradigm under classical statistical mechanics to embed scale-free patterns by adding more Markov compliant model components under the premise of a superposition of scale-specific space use.

On the other hand, a power law-kind of pattern has also been explored in the form of an explicitly postulated scale-free process, the MRW model, which extends the LW model by adding long-term memory effects [15,32]. Scale-free space use—mimicked by an LW component in simulations—is supplemented by homing in the form of occasional returns to previously visited locations. The result is a self-organized home range (an emergent property of site fidelity) with fractal properties [33]. Contrary to LW, the scaling and memory aspects are implemented under a postulate of parallel processing over a continuum of process rates (see below) rather than assuming Markov compliance at a specific temporal unit scale t for the simulations [14,16]. Thus, power-law compliance is explained as an emergent property from a complex cognitive process, which may be mimicked in statistical mechanical terms by the MRW model design.

In short, three qualitatively different space-use processes—Markov compliant and scale-specific composite BM; Markov compliant and scale-free LW; and memory-enhanced and scale-free MRW—may all explain the statistical pattern in equation (1.1). Hence, this field of research is currently in a state of confusion and controversy. Not only has the traditional approach towards testing for log–log linearity based on equation (1.1) (regression analysis) been questioned and more sophisticated statistical methods advocated (in particular, the Akaike model approach), but even these advanced approaches have been cast in doubt for some parameter range of β [29]. Thus, some alternative protocols for distinguishing between these processes from a statistical mechanical perspective, by studying fractal properties of space use, have been proposed [16,34].

Below, an additional statistical mechanically inspired protocol—as opposed to a more pattern-focusing statistical approach—is illustrated by simulation results. This method is based on analysis of the traditional double-log-transformed distribution of step lengths and testing for power-law compliance using linear regression, by some considered ‘obsolete’ in the light of the Akaike approach [31,35]. However, a supplementary aspect of this linear regression approach is in focus here. Rather than struggling statistically to estimate the degree of (non)linearity and the power-law parameter β, the regression line's y intercept and its dependence on observation lag t_{obs} is applied to reveal a compliance with scale-specific or scale-free space use. While both correlated random walk and LW can show ‘super-diffusion’, i.e. by satisfying that the r.m.s. deviation from a path's starting point expanding more rapidly than proportionally with the square root of time, only a Lévy-like process (i.e. truly scale-free) will maintain this property over a substantial range of observational scales. To visualize and analyse this distinction, a double-log plot where step-length distributions from several observational lags are superimposed is applied to estimate the behaviour of the scatter plot and the regression line (linearity and intercept). Hence, this statistical distinction not only provides a novel approach to test for scale-free space use, but also points towards the deeper qualitative difference between Markovian- and non-Markovian-based statistical mechanics.

3. METHODS

Appendix S1 in the electronic supplementary material provides details on the simulation methods, which are summarized below. A composite BM—an LW ‘look-alike’—was simulated as a superposition of four movement components, representing inter-independent spatial scale levels of space use, $j = 1–4$, with increasing characteristic step length λ_j and decreasing relative frequency of occurrence (relative weights: $0 < w_j < 1$). Successive steps of length L_{BM} were generated from $L_{\mathrm{BM}(j)} = -\lambda_j \ln(\mathrm{RND})$. RND is a random number between 0 and 1. For each of the respective levels j, this algorithm leads to a statistical step-length distribution $F(L) = \partial \mathrm{e}^{-\partial L}$, where $1/\partial$ is the mean movement length [27]. In other words, in a statistical mechanical context, $1/\partial_j = \lambda_j$ represents the mean free path of the moving object at spatial scale j and temporal scale t. A higher frequency of short-range steps at the expense of long ones is reflected in a larger ∂. In contrast, the power-law function that defines LW does not contain the scale specificity defined by $1/\partial$ and λ.

Successive steps L_{BM} were randomly performed in compliance with scale level 1–4, with relative weights w_j (probability of occurrence), with proportionally smaller w_j for larger λ_j (the product $\lambda_j \times w_j = \text{constant}$). Hence, the algorithm followed the superposition principle, where the individual during a unit step interval t is postulated to obey the rule for one specific level only (as expressed by λ_j), in order to obey the Markovian property. For example, when the individual is traversing in an inter-patch mode—by moving more persistently and unidirectionally in comparison to finer-level intra-patch foraging—it follows this coarser level's characteristic perception of its environment. Thus, potential direction-influencing inputs at finer resolutions are filtered away and ignored. In other words, to mechanistically mimic a difference in mean free path between the levels within the BM paradigm the animal is assumed to turn a blind eye to environmental input at finer spatial resolutions than the level j characterizing the current step. If a foraging individual opportunistically interrupts its current high j level step to take advantage of a smaller grained food patch, then the composite BM structure would not be maintained. Hence, a superposition of independent BM components puts strong constraints on the biological–ecological interpretation of the processing algorithm.

An LW process implies that the scale-free part of the distribution of step lengths originates from intrinsic (i.e. cognitive) causes alone, and not from a combination of the cognitive process (flipping between movement 'moods') and environmental forcing, expressed by the product $\lambda_j \times w_j$ and the respective resulting mean free paths under the composite BM design.

In a series of 26 563 steps, on average 20 000 were set to take place at level $j = 1$, 5000 took place at level $j = 2$; 1250 at level $j = 3$; and 313 at level $j = 4$ (in random order during step iteration, with $\lambda_1 = 100$; $\lambda_2 = 400$; $\lambda_3 = 1600$ and $\lambda_4 = 6400$, i.e. forced power law scaling from boundary conditions; $\lambda_j \times w_j = \text{constant}$). One series consisting of $N = T = 26\,563$ steps was simulated, and all N steps were collected for analysis; $t_{\text{obs}} = t = 1$ (unit lag). Three additional series were generated and collected at lag $t_{\text{obs}} = 10$, 100 and 1000, respectively, with a similarly increasing series length factor to compensate for sub-sampling. These series represented T increased by a factor of 10, 100 and 1000, but with a constant N. This approach by analysing the space-use pattern over a range of observational scale, $1 \leq t_{\text{obs}} \leq 1000$, will influence specific parameter estimates. This variation may allow for a simple protocol to distinguish a look-alike scale-free process (composite BM) from a true scale-free process.

Four separate BM series of length $N_{\text{ind1}} = 20\,000$, $N_{\text{ind2}} = 5000$, $N_{\text{ind3}} = 1250$ and $N_{\text{ind4}} = 313$ steps were also run. The respective scaling constants were similar to the four-level composite BMs: $\lambda_{\text{ind1}} = 100$, $\lambda_{\text{ind2}} = 400$, $\lambda_{\text{ind3}} = 1600$ and $\lambda_{\text{ind4}} = 6400$. These separate single-level series were produced to compare space use by a population of independently moving individuals where the LW-like pattern is apparent at the population level only (by pooling the set of movement lengths from several individuals, each showing classical BM in isolation but responding to a direction-influencing interrupts at different scales). The total time period T was defined to be equal for the four individuals despite a difference in N, implying a difference in relative unit time owing to a difference in relative step frequency (electronic supplementary material, appendix S1). All individuals were postulated to move with the same speed, but owing to a postulated longer interval without directional interruption for the coarser-graining individuals, they will on average show a larger net displacement per unit time than their finer-scale responding conspecifics.

LW was simulated as a set of successively independent steps with length $L_{\text{LW}} = \alpha(\text{RND})^{-1/(\beta-1)}$ with $\alpha = 1$ and $\beta = 2$. It was implicitly assumed that during a given step at unit lag t, a sufficient number of (virtual) micro-steps at finer spatio-temporal resolutions had taken place to ensure (i) an absence of inter-step directional persistence even for high-frequency fix sampling at $t_{\text{obs}} = t$ and (ii) a Lévy-stable distribution of step lengths [21]. These two assumptions imply that a simulated path was conjectured to represent coarse graining to the statistical mechanical level of system abstraction even at the simulation's temporal execution scale. Four series were run at $t = t_{\text{obs}} = 1$, and additionally sampled at lag $t_{\text{obs}} = 10$, 100 and 1000, respectively, for a final sample size of 20 000 steps from each series (thus, the fourth series was run for 20 million steps to compensate for larger lag). A maximum step length was set to 40 000 length units at lag $t = 1$, to mimic a simplified step truncation effect.

MRW was simulated and sampled under the same conditions as for LW, but extended with its algorithm expanded with a rule for memory-dependent strategic return steps: on average at every 100th time increment, the individual jumped back to a randomly chosen previous location in the series (electronic supplementary material, appendix S1).

When generating successive steps from a movement process at coarse lags (the assumption behind the present simulations), an LW pattern is expected to be similar to a Lévy flight pattern owing to self-similarity, and thus allowing for equation (1.1) in the text. However, influence of step-length truncation is expected and should be accounted for [12]. By assuming that the simulations' execution scale reflects coarse-grained lags, one also circumvents the chronically difficult issue of defining 'move length' (between successive re-orientations) at the mechanistic level t of the true movement process. What is a re-orientation event? Reynolds & Rhodes [12] and others have proposed various rules of thumb when analysing real data, but these remain subjective. By defining the simulations' execution scale to represent a coarser statistical mechanical level, a given step distance is normally the result from a series of what in mechanistic terms would have been defined as independent, successive moves. Thus, at this coarser scale, successive step directions become randomized and uniformly distributed over $0-2\pi$.

4. RESULTS

Figure 1*a* shows the spatial distribution from an ensemble of fixes collected from four independent BM paths (representing four individuals) with the different scaling constant λ_{ind} and frequency of occurrence, and observed at $t_{\text{obs}} = 100$ (total time span T is equal between the series, $T = 100 \times 20\,000$ unit time increments). Under a small-λ regime, movement consists of many small steps, and under a large-λ regime steps are larger but fewer over the defined time span. Owing to the premise of fewer direction-influencing interrupts per unit time under a large-λ condition, space use becomes more extended.

Figure 1*b* shows a modified single-individual BM process, expressing a four-level superposition of space use where the respective levels have λ_j, and relative frequency of occurrence w_j similar to the inter-individual values in figure 1*a*. For pedagogic reasons (to conceptually illustrate inter-level process independence), figure 1*b* was generated by pooling the $20\,000 + 5000 + 1250 + 313 = 26\,563$ fixes from the four individuals in figure 1*a* and scrambling the step succession. Because each of the original series reflected BM dynamics over a time span of $T = 100 \times 20\,000$ unit time steps, the total time span for the pooled series in figure 1*b* is implicitly assumed to be $T = 100 \times 80\,000 = 8 \times 10^6$ time steps.

Figure 1*c* apparently shows a pattern similar to figure 1*b*: high frequency of small steps intermingled by less frequent longer steps. However, even if some aspects may appear similar in a statistical sense (see §5), then the *process* under the pattern is distinctly different at a fundamental level from a statistical mechanical perspective.

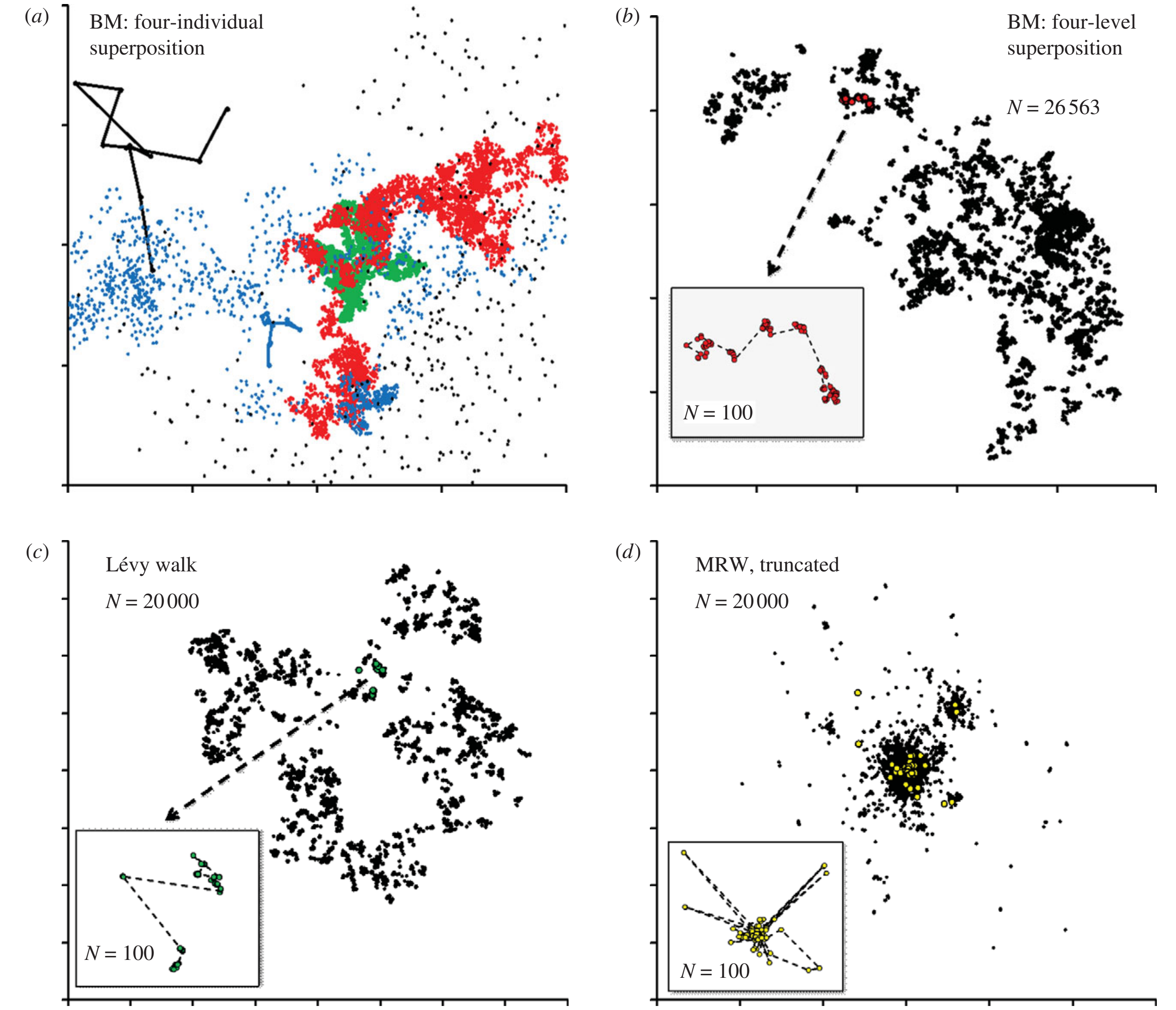

Figure 1. (*a*) Brownian motion compliant movement from four individuals is marked by successive relocations ('fixes' with individual-specific colour) over a total simulation time span $T = 100 \times 20\,000\, t$ time units, and sampled ('observed') every 100th time unit. All individuals move with a constant average speed, but different mean free path for the respective individuals leads to difference in number of steps and diffusion rate (net displacement during T). A 10-step sequence for the two series with the largest mean free path (black and blue) is shown with line segments inter-connecting the successive observed fixes. Owing to the time lag of $100\, t$ for sampling, on average 100 times as many direction-influencing events have taken place between successive fixes for each of the four individuals, relative to sampling 20 000 fixes at unit time interval t. Thus, the straight line segments illustrating step vectors hide some finer-grained jaggedness of the respective paths. (*b*) The fixes from the four individuals in figure 1*a* are pooled and scrambled, to mimic a four-level single-individual BM. A 100-step representative sequence from the series is enlarged, to visualize the random successive mixture of steps from various scale levels. (*c*) $N = 20\,000$ fixes from a Lévy walk, collected at lag $t_{\text{obs}} = 100$ (i.e. total time period $T = 100 \times 20\,000$, which equals the total series length at unit time scale prior to sampling at lag 100). With reference to the iteration procedure specified in Methods, $\beta = 2$ was used. (*d*) $N = 20\,000$ fixes from multi-scaled random walk under condition $\beta = 2$, collected at lag $t_{\text{obs}} = 100$. Owing to return steps taking place at the same time scale (frequency 1 : 100 on average), successive fixes are collected from the transition zone for a spatially auto-correlated and non-auto-correlated series. At a smaller t_{obs}, successive fixes would have tended to appear closer together than more distant fixes in time, as illustrated by the LW in figure 1*c*.

Figure 1*c* shows an LW that represents a kind of space-use process where the true distribution of step lengths is both continuous (i.e. not discretized to a four- or larger component superposition of inter-independent movement levels) and scale-free in a dynamical sense.

Figure 1*d* illustrates fixes from the scale-free and memory-enhanced MRW series, with data sampling at frequency 1 : 100. Owing to return steps happening at the same frequency 1 : 100 on average, the shown sequence of 100 fixes appears less spread out relative to the LW condition in figure 1*c*. Hence, the space use becomes more constrained, with a very fuzzy (statistical-fractal compliant) and multi-modal 'home range' pattern.

Figure 2*a* verifies that a four-component superposition of BM under the chosen boundary conditions generates an LW look-alike distribution of step lengths. After double-log transformation, the slope is approximately linear with a slope close to -2.2 that satisfies $\beta \approx 2.2$ in an LW parametrization (equation (1.1)).

The power-law pattern is very resilient to coarse graining over an observational range $1 \le t_{obs} \le 1000$. The linear regression slopes for the various levels of t_{obs} right-shifted by a factor of *ca* $\log_2(\sqrt{10}) \approx \log_2(3.2) = 1.7$ when t_{obs} is increased by a factor $n = 10$. In other words, when the inter-observation interval is increased n-fold, the animal on average performs a $\sqrt{n}$ times as large net displacement for all bins in the set $\boldsymbol{L}$. Crucially, this 'diffusion rate' regards all four levels in the composite BM, leading to maintenance of the log–log linear relationship in the superposition series. Furthermore, this diffusion rate (as observed at a given scale t_{obs}) is compliant with a BM-compliant process, a 'Fickian diffusion'. In other words, the mean square net step length for all bins of L, $\boldsymbol{L}^2$, expands proportionally with time, despite LW-like (rather than a negative exponential) distribution of step lengths at any given observational scale t_{obs}. Figure 2*a* extends the illustration of this generic and well-known statistical mechanical law of diffusion, by showing that an individual that is moving in accordance to a superposition of independent BM components follows the same law, under a premise of maintenance of the relative magnitudes λ_j and relative frequency of occurrence w_j during T. Thus, the overall impression of a power-law step-length distribution is also maintained.

Figure 2*b* shows how an LW process (truncated at length scale $\log_2(40\,000) = 15.3$ length units at execution scale $t = 1$) also right-shifts its step-length distribution under a coarser observational lag. However, contrary to the composite BM process in figure 2*a*, the diffusion rate for LW reflects the expectation from a true scale-free movement: net displacement changing proportionally with observational scale t_{obs}, i.e. the set of step lengths $\boldsymbol{L}$ is changing (showing parallel-shift in the histogram) proportionally with observational lag. For example, a 10-fold increase in t_{obs} leads to a 10-fold increase in net displacement for a given step length bin. With reference to the $\log_2(L)$ axis in figure 2*b*, $\log_2(10) = 3.3$. This diffusion rate, mean square deviation ($\boldsymbol{L}^2$ in the present context) increasing proportionally with time squared, characterizes LW in general (i.e. super-diffusion). Figure 2*b* also illustrates that the step-length truncation is not visible for $t_{obs} < 1000$, under the given boundary conditions ($\beta = 2$ and $N = 20\,000$). At the level $t_{obs} = 1000$, the truncation becomes apparent as a reduced frequency in bins for steps close to and larger than $\log_2(40\,000) = 15.3$, relative to the expectation from a non-constrained LW. The frequency of step lengths larger than 40 000 is not 0 at $t_{obs} = 1000$, because there is a slight probability for two or more displacements of this magnitude among any given intermediate sequence of 999 steps (executed at scale t) between each sampled location.

Figure 2*c* illustrates a scale-free process under the influence of long-term memory; a truncated LW-like space-use process with a superposition of return events to a previous location at frequency 1 : 100 relative to execution scale $t = 1$. For observational levels $t_{obs} = t = 1$, i.e. $t_{obs} \ll 100$ (to avoid step truncation owing to return steps), this MRW condition reflects a step-length distribution similar to a generic LW. However, a tendency for a 'hockey stick' pattern—an elevated frequency of large steps relative to the expectation from a power law—is increasing in magnitude with t_{obs} approaching 100 t, the defined scale for return steps. As t_{obs} is increased beyond 100 t, the step-length distribution from the return step process—in combination with the step-length truncation—dominates the overall process. The power law aspect of the movement—when expressed through equation (1.1)—then becomes 'hidden' at finer temporal scales, as previously shown by Gautestad & Mysterud [15]. Hence, if an animal space-use process is both scale-free and memory-influenced, then it is crucial to estimate the level of spatial auto-correlation prior to testing for power-law compliance. Unless t_{obs} is chosen substantially smaller than the transition level between spatial auto-correlation and non-auto-correlation ($t_{obs} \approx 100\,t$ in the present simulations, with spatially non-auto-correlated fixes at $t_{obs} \gg 100\,t$), the step-length distribution may (i) either appear hockey stick-like owing to the increasing dominance of the return step component for the large-step classes at these levels of observation or (ii) appear BM-like (closer fit to a negative exponential, as seen at levels $t_{obs} = 100$ and $t_{obs} = 1000$ in figure 2*c*), owing to influence from step-length truncation of both intrinsic ('mood' to return) and extrinsic origin.

Hence, figure 2*c* shows a double-interference with the power-law pattern—a combination of the influence from return events (a superposition of a return step distribution, which leads to a hockey stick pattern when $t_{obs} \to 100\,t$) and an influence from a truncation of steps beyond a given size (physical limit to movement speed at scale t, and/or environmental constraint such as territorial borders). In combination, these independent factors may lead to either a steeper or shallower slope of the step-length distribution for the largest bins relative to unconstrained LW, or they may even more or less cancel each other out at the chosen t_{obs}.

Figure 2*d* illustrates how a MRW without influence from step truncation may make the extreme part of the step-length distribution more 'noisy' in the extreme part of the tail. This jaggedness of $F(L)$ for large L is mainly owing to chance effects from the early phase of a given simulation series. Return steps lead to a self-reinforcing use of some locations at the expense of others (i.e. a positive feedback), and the emergence of a multi-modal distribution function of density of fixes [33]. Initial chance effects with respect to relative distance between the 'winning' clusters from the early-phase self-organization of space use will influence the distribution of return step lengths: of the dominant clusters happen to appear relatively far apart, return steps of length similar to this inter-mode distance will tend to be over-represented (A. O. Gautestad 2012, unpublished results). As shown in figure 2*d*, these inter-mode distances will vary stochastically from one simulation sequence to the next owing to early 'pattern locking' from the positive feedback process, and the peaks in the step-length distribution will vary accordingly.

5. DISCUSSION

The present results lead to four main take-home messages. First, put closer attention to the process behind the statistics. A purely statistical approach, for example,

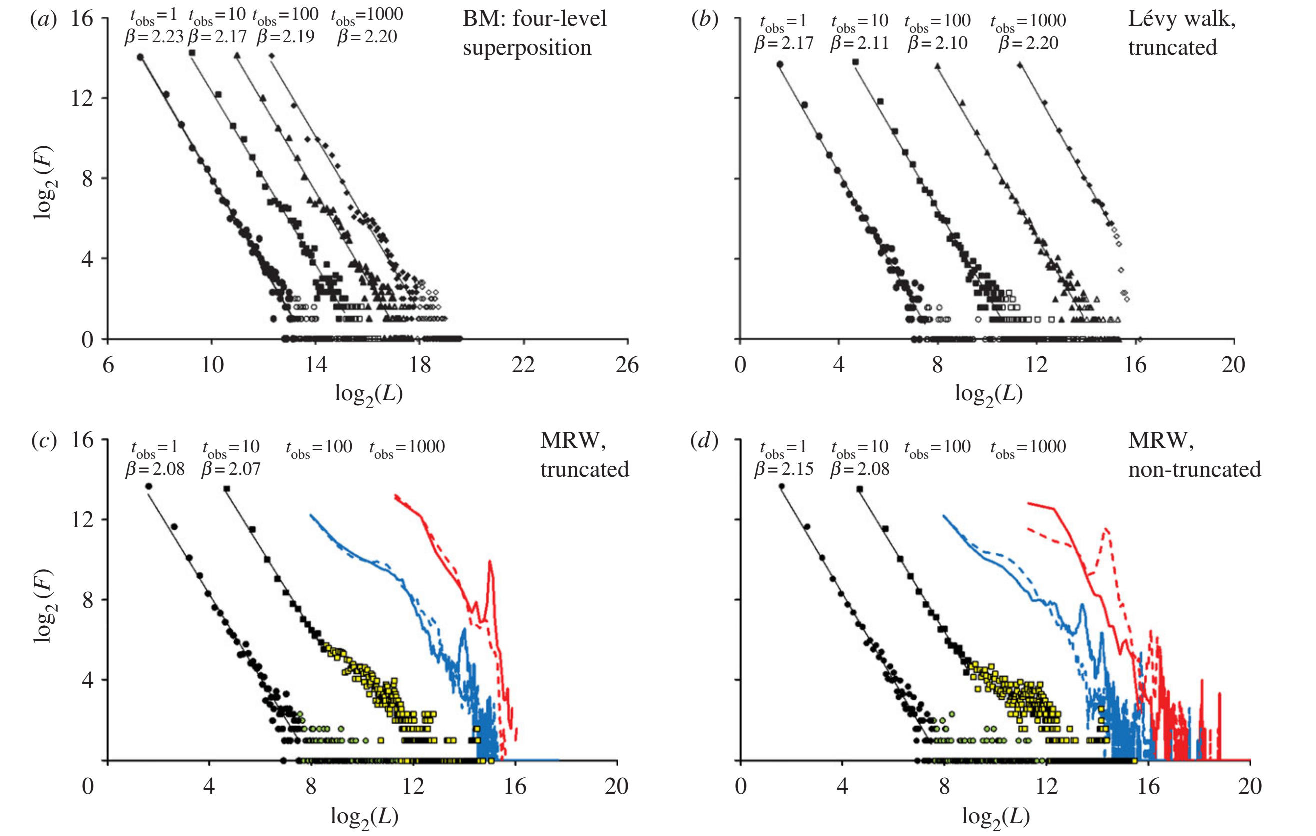

Figure 2. (*a*) Double-log histogram showing the distribution of binned step lengths from a four-level BM process, observed at different temporal resolutions (lags). (*b*) A truncated Lévy walk shows the expected linear slope in a log–log transformation of the step-length distribution, but the scale-free pattern beaks down for step-length bins larger than the truncation scale. (*c*) The step-length pattern from a truncated multi-scaled random walk (truncated LW-like, but extended with memory influence and return steps) shape-shifts from power-law compliance (t_{obs}= 1), through a 'hockey stick' pattern (t_{obs}= 10) to a truncated power-law pattern (larger t_{obs}). (*d*) A multi-scaled random walk without step-length truncation shows a relatively noisy step-length frequency over the extreme step-length bins. Two independent distributions, dashed and solid lines, are included for the two observational scales $t_{obs} = 100$ (blue-coloured) and $t_{obs} = 1000$ (red-coloured), to illustrate how the frequency peaks over the noisy range vary stochastically between series when t_{obs} is similar to—or larger—than the temporal scale for return steps (in these iterations, a return event at frequency 1 : 100 on average). The reason for the noisiness at these coarse levels of observations is explained in §4.

by defining a scale-free process as a Lévy flight is a random walk for which each movement step is independently drawn from a probability distribution that has a heavy power law tail and then use this property as the sole criterion for testing [19], may contribute to an elevated level of confusion and controversy in this field. This definition is an excellent description of the expected pattern from the ideal model, but misses the dynamic aspect of the real-life process. For example, the physical aspect describes the degree of deviation from an ideal power-law pattern in the form of truncation of the tail of the step distribution, and underscores the importance of distinguishing a Lévy flight from an LW. Only the latter has relevance for animal movement [12]. A Lévy flight differs from an LW by showing immediate displacement regardless of distance between successive fixes, whereas an LW describes a movement process with physical realism in the context of observing animal paths at fixed intervals [13,30]. For example, if an individual has a maximum movement rate of 5 km h^{-1}, a scale-free kind of movement *sensu* equation (1.1) will have a step distance of 5 km as the upper limit for successive fixes. This time-dependent aspect of step-length truncation, L_{max}, will thus influence the double-log linearity for bin sizes approaching this limit, and supplement the truncation effects from memory (if the power law distribution arise from MRW) and environmental border effects (e.g. a fish in a lake). Thus, if equation (1.1) and double-log linearity is used as a criterion for testing for power-law compliance, then the test will produce a false negative if the magnitude of t_{obs} is large enough to impose truncation effects on the observed pattern. Further, as illustrated by Benhamou [24] for a two-component model and figure 2 for a four-component model, composite BM may produce an LW in disguise pattern under specific combinations of scale constants. In this case, a false positive may be found from a purely statistical approach. Thus, for a true LW process, equation (1.1) should always be expected to show strong dependence on t_{obs} with respect to the power-law compliant range from L_{min} to L_{max} [26]. A purely statistical approach to the power law aspect does not explain the influence of observational scale on the observed pattern (e.g. the shape-shifting of a MRW step-length pattern from LW-like, to hockey stick-like and finally towards BM-like by increasing t_{obs}).

Second, the notoriously difficult statistical verification (or falsification) of a true scale-free space-use process—as reviewed in the section *Scaling and memory* above—may be simplified by estimating the constancy or variability of the diffusion rate over the set of step-length classes $\boldsymbol{L}$, as a function of observational scale, t_{obs}. The difference expressed between figure 2*a* and figure 2*b*–*d* underscores the potential from this approach. The statistical signal from the parallel shift as a function of t_{obs} is supplementing the compliance with true double-log linearity, and may even survive temporal coarse-graining better than linearity compliance. Thus, analysing space-use data (for example in the form of GPS fixes) at several lags t_{obs} to observe the process over a temporal scale range may provide a clearer distinction between composite BMs (including correlated random walk variants) and LW through multi-scale estimates of diffusion rates. This approach also provides a test to distinguish between LW and MRW by looking for hockey stick and truncation in the transition zone between spatially auto-correlated and non-auto-correlated steps.

Third, by analysing the data with different t_{obs} relative to system-specific boundary conditions, two observers may reach very different conclusions with respect to step-length compliance with a negative exponential or a power law. Both may in fact be right! In particular, if the animal in question has used its habitat under the influence of long-term memory, then the observed pattern at temporal level t_{obs} may shape-shift from power law, through a hockey stick pattern, to a truncated power-law pattern (figure 1*c*), and ultimately to a negative exponential (BM compliance) if t_{obs} is chosen large enough. Hence, this paradox may to some (testable) extent be rooted in a relative difference in observational scale between the respective studies.

Fourth, the advice to study both the spatial scaling (distribution of step lengths) and the temporal scaling (a parallel shift of the double-log regression line as a function of t_{obs}) is rooted in an explicit consideration of statistical mechanical properties of movement. Statistical mechanics—which regards the dual nature of process and statistics from a meso- and macro-scale perspective—is key to a deeper understanding of (and solution to) the paradox of two observers finding qualitatively different patterns in the example in the foregoing paragraph. The statistical mechanical approach implies paying closer attention to classes of meso- and macro-scale laws that emerge from mechanistic micro-scale interactions but where these interactions are analysed from the perspective of a coarser observational scale $t_{\text{obs}} \gg t$. Contrast this with a mechanistic approach, which dominates individual-based modelling [36] and puts the focus on behavioural mechanisms (algorithmic rule-execution close to level t) and looks for statistical patterns that can be compared with similar analyses of data from real individuals. As an example of the coarser-perspective statistical mechanical perspective and what it offers as a supplement to the mechanistic analysis, consider a drunken walker—the random walk archetype. In the long run (or walk), walking with a variable step length and randomly chosen direction for successive steps will be found to bring the person a distance from the starting point which (from statistical mechanical expectation) increases proportionally with the square root of time T from start to the point of location. When averaging over many series of walks, a 100 times larger T will bring the walker 10 times further away. Then contrast this with a very sober walker, who carefully determines direction and goal for successive steps, based on available information at the given point in time. This information is then churned through an extensive set of 'if-then' kind of movement rules, and out comes the step decision. The next step is then taken independently of previous step decisions. The various rules under the algorithm may be purely deterministic, purely stochastic (such as the drunken walker scenario) or a combination. The well-established fact from statistical mechanics is that—again in the long run—the sober and the drunken walker produce the same expectation of r.m.s. distance after time T. Hence, a walk with a simple rule of random steps follows the same statistical mechanical law as a walk with very detailed and more or less deterministic movement algorithm! What they have in common is the Markovian, memory-less processing of successively independent movement-influencing events. Emerging from the hidden world of zillions of micro-scale step (in)decisions at mechanistic level t come the meso- and macro-scale observables at level $t_{\text{obs}} \gg t$, such as the exponential or power-law function of step-length distribution (telling us about main classes of movement), the over-all movement rate (mean square deviation as a function of T, offering important biological and ecological information) and a method to distinguish between a scale-free process such as LW or MRW and a look-alike scale-free process (composite scale-specific walk).

A statistical mechanical approach, representing a bridge between mechanistic and statistical analysis, may thus have a lot to offer to the theory of animal locomotion and space use. In some sense, the controversies in this field may be rooted in too large a distance between the 'statistical' and the 'mechanistic' camps of system analysis. It has clearly created a counter-productive distance between these complementary approaches. A more explicit statistical mechanical approach may bridge the two traditions, for example by paying closer attention to a broader range of the qualitative differences between a scale-specific and a scale-free process and the importance of observational scale [14,16].

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