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Review

Liberating Lévy walk research from the shackles of optimal foraging

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Abstract

There is now compelling evidence that many organisms have movement patterns that can be described as Lévy walks, or Lévy flights. Lévy movement patterns have been identified in cells, microorganisms, molluscs, insects, reptiles, fish, birds and even human hunter-gatherers. Most research into Lévy walks as models of organism movement patterns has been shaped by the 'Lévy flight foraging hypothesis'. This states that, since Lévy walks can optimize search efficiencies, natural selection should lead to adaptations that select ***for*** Lévy walk foraging. However, a growing body of research on generative mechanisms suggests that Lévy walks can arise freely as by-products of otherwise innocuous behaviours; consequently their advantageous properties are purely coincidental. This suggests that the Lévy flight foraging hypothesis should be amended, or even replaced, by a simpler and more general hypothesis. This new hypothesis would state that 'Lévy walks emerge spontaneously and naturally from innate behaviours and innocuous responses to the environment but, if advantageous, then there could be selection ***against*** losing them'. The new hypothesis has the virtue of making fewer assumptions and being broader than the original hypothesis; it also encompasses the many examples of suboptimal Lévy patterns that challenge the prevailing paradigm. This does not detract from the Lévy flight foraging hypothesis, in fact, it adds to the theory by providing a stronger and more compelling case for the occurrence of Lévy walks. It dispenses with concerns about the theoretical arguments in support of the Lévy flight foraging hypothesis and so may lead to a wider acceptance of Lévy walks as models of movement pattern data. Furthermore, organisms can approximate Lévy walks by adapting intrinsic behaviour in simple ways; this occurs when Lévy movement patterns are advantageous, but come with an associated cost. These new developments represent a major change in perspective and provide the broadest picture yet of Lévy movement patterns. However, the process of understanding and identifying Lévy movement patterns still has a long way to go, and further reinterpretations and shifts in understanding will occur. In conclusion, Lévy walk research remains exciting precisely because so much remains to be understood, and because, even relatively small studies, are interesting discoveries in their own right.

Keywords: Lévy walks; Lévy flights; Power-laws; Foraging; Movement patterns; Optimal searching

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Then up he got with a light heart,
free from all his troubles,
and walked on till he reached his mother's house,
and told her how very easy the road to good luck was.
[Hans in Luck, Grimm Brothers]

Hypothesis non fingo
[Isaac Newton]

1. Introduction

Lévy walks (also known as Lévy flights in the biological literature) are named after the French mathematician Paul Lévy and arose in a purely mathematical context in the first half of the last century [1]. Shlesinger and Klafter [2] were amongst the first to propose that they could be observed in animal movement patterns. Lévy walks are random walks comprised of clusters of multiple short steps with longer steps between them (Fig. 1). This pattern is repeated across all scales with resulting clusters creating fractal patterns that have no characteristic scale. Because there is no characteristic scale, the overall length of Lévy walks is dominated by the longest step taken and, while the step-length variance grows over time, it nonetheless remains finite even when unbounded by biological and ecological considerations. When bounded, the minimum and maximum truncations introduce characteristic scales that make the movement patterns scale-finite. However, unlike other finite-scale movement patterns, variability around the characteristic scales is huge and self-similar. Due to multiple iterations, Lévy walks take the object/organism much further from its starting position than a Brownian walk of the same length. The hallmark of Lévy walks is the distribution of step lengths, l, with a heavy power-law tail as described by the formula: $p(l) \sim l^{-\mu}$ where μ is the power-law (Lévy) exponent and where '$\sim$' means 'distributed as'. The power-law exponent is constrained by the condition, $1 < \mu \leq 3$, which ensures that the distribution can be normalized with probabilities that sum to unity, and is characterised by a divergent variance.

Shlesinger and Klafter [2] are generally credited with having been the first to recognise that the 'super-diffusive' and fractal properties of Lévy walks can be advantageous during searching because they reduce 'oversampling', i.e. the needless revisiting of previously traversed terrain, and as a consequence may be under positive selection pressure. This was a revolutionary idea at the time because Lévy walks stood outside of the correlated random walk (CRW) paradigm, which was, and remains, the dominant conceptual framework for modelling non-oriented organism movement patterns ([3] and references therein). Underlying the formulation of CRWs is the assumption that movement pattern data have characteristic scales. Shlesinger and Klafter [2] suggested that this seemingly plausible and intuitive assumption was not necessarily true. This realisation gained traction following the seminal paper of Viswanathan et al. [4] whose report on the flight patterns of the wandering albatross, *Diomedea exulans*, was the first test of the fledgling 'Lévy flight foraging hypothesis' using animals in their natural environments. Viswanathan et al. [4] hypothesised that the flight patterns of wandering albatrosses had evolved to be scale-invariant to better exploit sparsely distributed food resources. Later, Viswanathan et al. [5] demonstrated mathematically, and with the aid of numerical simulations, that foragers with Lévy walk movement patterns do, indeed, outperform foragers with other kinds of movement patterns. This paper led to an explosion of interest in Lévy walks as models of movement pattern data, and shaped much of

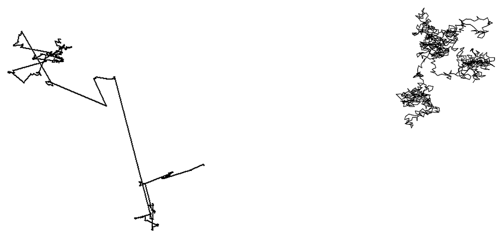

Fig. 1. Example of a Lévy walk (left) and a Brownian walk (right).