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Corresponding Author: Dr. Nicolas Humphries,

Corresponding Author's Institution: The Marine Biological Association

First Author: Nicolas Humphries

Order of Authors: Nicolas Humphries

Why Lévy Foraging does not need to be ‘unshackled’ from Optimal Foraging Theory

Comment on “Liberating Lévy walk research from the shackles of optimal foraging” by A.M. Reynolds

Nicolas E. Humphries

The Marine Biological Association, Citadel Hill, Plymouth, PL1 2PB

Keywords

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The comprehensive review of Lévy patterns observed in the moves and pauses of a vast array of organisms by Reynolds [1] makes clear a need to attempt to unify phenomena to understand how organism movement may have evolved. However, I would contend that the research on Lévy ‘movement patterns’ we detect in time series of animal movements has to a large extent been misunderstood. The statistical techniques, such as Maximum Likelihood Estimation, used to detect these patterns look only at the statistical distribution of move step-lengths and not at the actual pattern, or structure, of the movement path. The path structure is lost altogether when move step-lengths are sorted prior to analysis. Likewise, the simulated movement paths, with step-lengths drawn from a truncated power law distribution in order to test characteristics of the path, such as foraging efficiency, in no way match the actual paths, or trajectories, of real animals. These statistical distributions are, therefore, null models of searching or foraging activity. What has proved surprising about these step-length distributions is the extent to which they improve the efficiency of random searches over simple Brownian motion. It has been shown unequivocally that a power law distribution of move step lengths is more efficient, in terms of prey items located per unit distance travelled, than any other distribution of move step-lengths so far tested (up to 3 times better than Brownian), and over a range of prey field densities spanning more than 4 orders of magnitude [2].

It is this marked advantage in foraging efficiency, coupled with the apparent ubiquity of these move step-length distributions in empirical data [3-11], that have led to ideas about how natural selection would have favoured power law distributions over simple exponential distributions of step-lengths when animals need to perform random searches. It should be noted that these ‘Lévy’ movements do not need to have an exponent of $\mu = 2.000$ to be more efficient; a range of exponent values, from 1.5 to 2.5 have been shown to easily outperform simple Brownian motion [2]. Therefore, animal movements do not need to be carefully tuned to a specific parameterisation; almost any exponent in the Lévy range ($1 < \mu \leq 3$) will be significantly better than Brownian, making the selection and evolution of these distributions all the more likely. Further, even movement patterns with underlying mechanisms that are not power laws, such as hyper-exponentials (composite Brownian) but which approximate Lévy patterns, can provide significant improvements in foraging efficiency [2].

It is possible that some of the misunderstandings about the ‘Lévy Flight Foraging hypothesis’ have come about through the use of what can now be seen as inappropriate terminology. The statistical distributions of move step-lengths used to identify ‘Lévy foraging’ are not a ‘model of animal movement’. Actual animal movements are complex, with animals responding to a multitude of external factors (environmental cues, conspecifics, predators, prey) and internal drivers (memory, physiological state). A simple statistical distribution of move-step lengths is insufficient to reconstruct a realistic movement path, or to predict how an animal might move throughout a land

(or sea) scape. A Lévy distribution of move step-lengths has been shown to be advantageous when random searching is required – when foraging without the need for searching, the advantage diminishes [2]. Therefore, the presence of a Lévy distribution can be seen as a signature of possible random searching; an activity which might at times be rare or non-existent, or might be present only as very brief bouts in a movement path dominated by other behaviours. Consequently terms such as ‘Random Walk Modelling’ (e.g. [12]), which have been used more to describe the distribution fitting process, should not be misconstrued as meaning modelling as in reconstructing ‘modelled’ movement trajectories. Even the term ‘Lévy Foraging’ might now be considered misleading, as it is only during the search phase that a Lévy distribution of step-lengths is beneficial; less controversy might have arisen if the term ‘Lévy Searching’ had been used, but this is a new field, with new discoveries, and terminology tends to develop as more is learned.

Lévy Searching, therefore, is about improving the efficiency of random searches; i.e. true searches performed where the animal has, at that point in time, no useful clues, or memory, to help locate the next target, whether it be prey, refuge or mates, or simply the next clue, such as an odour trail [13, 14]. Optimal Foraging Theory (OFT) and Marginal Value Theorem (MVT) [15, 16] are concerned more with optimising the exploitation of resources (patches) once located; i.e. how long to stay in a patch before moving on to find another. Lévy searching is about finding those patches. Therefore, it can be seen that Lévy foraging/searching is not in competition with, or shackled to, OFT but is in fact entirely complementary, sitting alongside that body of work, but filling in the gap between patches.

The real utility of the Lévy research field is not, therefore, to accurately model animal movement paths, but as an exploratory tool to aid the behavioural analysis of animal movement datasets. By revealing bouts of searching behaviour in complex time series of movement data, this relatively straightforward statistical analysis can potentially offer a window on the activities of animals that are difficult to observe directly. This is perhaps one reason why the analysis has proved so useful in the study of pelagic marine predators [4, 5, 17].

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References

1. Reynolds, A.M., *Liberating Lévy walk research from the shackles of optimal foraging*. Physics of Life Reviews, 2015(This issue).
2. Humphries, N.E. and D.W. Sims, *Optimal foraging strategies: Lévy walks balance searching and patch exploitation under a very broad range of conditions*. Journal of Theoretical Biology, 2014. **358**(0): p. 179-193.
3. Hays, G.C., et al., *High activity and Lévy searches: jellyfish can search the water column like fish*. Proceedings of the Royal Society B: Biological Sciences, 2012. **279**(1728): p. 465-473.
4. Humphries, N.E., et al., *Environmental context explains Lévy and Brownian movement patterns of marine predators*. Nature, 2010. **465**(7301): p. 1066-1069.

5. Sims, D.W., et al., *Scaling laws of marine predator search behaviour*. Nature, 2008. **451**(7182): p. 1098-1102.
6. Viswanathan, G.M., et al., *Lévy flight search patterns of wandering albatrosses*. Nature, 1996. **381**(6581): p. 413-415.
7. Reynolds, A.M., et al., *Displaced honey bees perform optimal scale-free search flights*. Ecology, 2007. **88**(8): p. 1955-1961.
8. de Jager, M., et al., *How superdiffusion gets arrested: Ecological encounters explain shift from Lévy to Brownian movement*. Proceedings of the Royal Society B: Biological Sciences, 2014. **281**(1774).
9. de Jager, M., et al., *Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity*. Science, 2011. **332**(6037): p. 1551-1553.
10. van de Koppel, J., et al., *Experimental Evidence for Spatial Self-Organization and Its Emergent Effects in Mussel Bed Ecosystems*. Science, 2008. **322**(5902): p. 739-742.
11. Sims, D.W., et al., *Hierarchical random walks in trace fossils and the origin of optimal search behavior*. Proceedings of the National Academy of Sciences, 2014.
12. Humphries, N.E., H. Weimerskirch, and D.W. Sims, *A new approach for objective identification of turns and steps in organism movement data relevant to random walk modelling*. Methods in Ecology and Evolution, 2013. **4**(10): p. 930–938.
13. Reynolds, A.M., et al., *Honeybees use a Lévy flight search strategy and odour-mediated anemotaxis to relocate food sources*. Behavioral Ecology and Sociobiology, 2009. **64**(1): p. 115-123.
14. Reynolds, A.M. and M.A. Frye, *Free-Flight Odor Tracking in Drosophila Is Consistent with an Optimal Intermittent Scale-Free Search*. PLoS ONE, 2007. **2**(4): p. e354.
15. Pyke, G.H., *Optimal foraging theory - a critical-review*. Annual Review of Ecology and Systematics, 1984. **15**: p. 523-575.
16. Pyke, G.H., H.R. Pulliam, and E.L. Charnov, *Optimal foraging - selective review of theory and tests*. Quarterly Review of Biology, 1977. **52**(2): p. 137-154.
17. Sims, D.W., et al., *Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics*. Journal of Animal Ecology, 2012. **81**(2): p. 432-442.