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Ultimate failure of the Lévy Foraging Hypothesis: Two-scale searching strategies outperform scale-free ones even when prey are scarce and cryptic☆

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HIGHLIGHTS

- Scale-free Levy Walks (LW) are controversially claimed optimal searching strategies.
- Spontaneous (cue-free) scanning may be advantageous when prey are difficult to detect.
- Two-scale two-mode random walks outperform LW in any case.
- Evolution should favour strategies that better processes available information.

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ABSTRACT

The “Lévy Foraging Hypothesis” promotes Lévy walk (LW) as the best strategy to forage for patchily but unpredictably located prey. This strategy mixes extensive and intensive searching phases in a mostly cue-free way through strange, scale-free kinetics. It is however less efficient than a cue-driven two-scale Composite Brownian walk (CBW) when the resources encountered are systematically detected. Nevertheless, it could be assumed that the intrinsic capacity of LW to trigger cue-free intensive searching at random locations might be advantageous when resources are not only scarcely encountered but also so cryptic that the probability to detect those encountered during movement is low. Surprisingly, this situation, which should be quite common in natural environments, has almost never been studied. Only a few studies have considered “saltatory” foragers, which are fully “blind” while moving and thus detect prey only during scanning pauses, but none of them compared the efficiency of LW *vs.* CBW in this context or in less extreme contexts where the detection probability during movement is not null but very low. In a study based on computer simulations, we filled the bridge between the concepts of “pure continuous” and “pure saltatory” foraging by considering that the probability to detect resources encountered while moving may range from 0 to 1. We showed that regularly stopping to scan the environment can indeed improve efficiency, but only at very low detection probabilities. Furthermore, the LW is then systematically outperformed by a mixed cue-driven/internally-driven CBW. It is thus more likely that evolution tends to favour strategies that rely on environmental feedbacks rather than on strange kinetics.

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1. Introduction

Since the pioneering papers by Viswanathan et al. (1996, 1999; but see Edwards et al., 2007), the “Lévy Foraging Hypothesis” (LFH) has emerged as a highly controversial paradigm in movement ecology, and resonates across a broader range of disciplines as a possible way to optimize searching processes (Harris et al., 2012; Kello et al., 2010; Todd et al., 2012). According to this hypothesis, a forager having limited sensory skills and looking for patchily distributed prey whose locations are unpredictable should improve its searching efficiency by performing a Lévy walk (LW) with an intermediate μ exponent (i.e. close to 2). A LW is a special type of random walk. Whereas reorientations (performed at the end of each step) are drawn at random over the whole circle as for

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a discrete Brownian motion, step lengths L longer than a given threshold l_{min} are drawn, independently of each other and of their orientations, with a probability $P(L)$ proportional to $L^{-\mu}$, with $1<\mu<3$. Thus, very long steps are sufficiently frequent to obtain an infinite variance (heavy-tailed distribution). As a result, LW is characterised by strange, scale-free kinetics (Shlesinger et al., 1993): it is superdiffusive, and the timing of reorientation events is fractal. With $\mu<1.1$, huge step lengths are drawn quite often, so that the LW then behaves essentially as a straight line movement. With $\mu>3$, the variance becomes finite and the resulting walk can then be considered as a form of Brownian motion rather than a LW. With intermediate μ values, the searching efficiency is maximised and the resulting movement pattern mimics quite well the behaviour of animals alternating extensive (relocation) and intensive (area-concentrated) searching phases (Bartumeus et al., 2005, 2014).

It is however important to recall two key points in this context. (1) Following Viswanathan et al. (1999), only truncated LWs are considered. In such walks, long steps corresponding to relocation phases are truncated by the detection of a prey item. Truncations affect the fundamental properties of LW only marginally (provided they remain scarce; de Jager et al., 2014) and eventually result in a fraction of all intensive searching phases being performed in vicinity of prey patches. This considerably improves LW efficiency. Indeed, without truncations, intensive searching phases occur only at fractal times irrespective of the local resource density, and the dynamics is dominated by the occurrence of very long steps. As a consequence, a non-truncated LW is no more efficient than a simple straight line walk (Benhamou, 2007). (2) A LW with an intermediate μ value has been shown to be the best strategy when compared to a LW with μ close to 1, used to model a strategy involving mainly long relocations, or to a LW with $\mu>3$, used to model a strategy involving only intensive searching (Viswanathan et al., 1999; Bartumeus et al., 2005; James et al., 2011). In other terms, when the only possible strategy is to use a random walk with step lengths L drawn from an inverse power law distribution with exponent μ, it is indeed advantageous (1) to stop the current relocation phase where a prey item has been detected and (2) to rely on an intermediate exponent value. However, this result does not preclude that other random strategies mixing relocation and intensive searching phases can be more efficient for harvesting patchily-distributed prey whose locations are unpredictable.

In particular, it has been shown that, when resources are scarcely encountered but systematically detected when encountered, the best LW is largely outperformed by an elementary cue-driven Composite Brownian walk (CBW; Benhamou, 2007). Such a two-scale two-mode strategy consists simply in moving along a straight line in a random direction until a prey item has been detected, and then to perform a discrete Brownian walk with short step lengths until a given threshold distance has been travelled without detecting any new item. Although the movement patterns generated by CBW and LW processes are visually quite similar (see Fig. 1 in Benhamou, 2007), the larger efficiency of the CBW is not surprising because it eventually rests on a more rational use of information than the LW, which is only partially cue-driven through flight truncation.

This lack of rationality in LW strongly suggests it would be time to abandon the LFH (Pyke, 2015). Indeed, it can be assumed that animals adopting the LW strategy would be unable to survive in a competitive context because of a clear advantage in relying on environmental feedbacks instead of mostly internally-driven programs to forage efficiently. However, the advantage of CBW may really exist only if prey items are highly detectable. One can thus wonder to what extent, in a context where prey are hardly detectable, a forager would take advantage to stop for scanning the environment at places where no prey has been detected, as postulated by the LFH (Bartumeus, 2007; Bazazi et al., 2012, Kölzsch et al., 2015). Intermittent (also called "saltatory", "stop-and-go", or "pause-travel") search is indeed a valuable strategy for a forager that has limited detection capacities during movement (Kramer and McLaughlin, 2001), or equivalently, searches for extremely cryptic resources. In the most extreme case, a forager that is fully "blind" during relocation phases can detect prey only when stopping and scanning the environment at more or less regular times. In this context, performing internally-driven rather than cue-driven environmental scans is mandatory, and the time fractions devoted to relocation and intensive searching can be optimized (see Bénichou et al. (2006a, 2006b) for CBW and Reynolds (2006), for LW). As it inherently mixes internally-driven and cue-driven shifts from relocation to intensive searching, LW may be competitive when the probability to detect encountered prey during relocation phases is low. Although the LW process has been assumed to be an efficient strategy when the forager has limited detection skills, most studies considered this constraint only in terms of prey "encounterability". Besides the few studies mentioned above focusing on the extreme case of foragers assumed to be fully blind while moving, studies that took the probability to detect encountered resources into account are very scarce (e.g. Reynolds and Bartumeus, 2009, but which did not consider strong alternatives to LW).

The previous demonstration (Benhamou, 2007) that LW is outperformed by a simple cue-driven CBW when prey items are scarcely encountered but fully detectable during movement is therefore not sufficient to condemn the LW strategy as an evolutionary cul-de-sac. It is necessary to determine whether, in a context where prey are not only scarcely encountered but also hardly detected when encountered, LW may not outperform a two-scale CBW variant mixing cue-driven and internally-driven scans. In this paper, we used computer simulations to determine the level of prey detectability below which it becomes advantageous to perform intensive searching in the absence of cue, and whether, in this context, relying on the peculiar kinetics of LW does result in better efficiency than using a more classical (diffusive or advective-diffusive; Codling et al., 2008) movement process such as the CBW.

2. Methods

2.1. Simulated environment

The environment was modelled as a square of 500 × 500 arbitrary length units (alu), with wrap-around margins (i.e. periodic boundaries). Two types of environment were considered (Fig. 1): a "rich" one encompassing a total of 10,000 prey items randomly allocated to 250 patches, and a "poor" one, encompassing 250 prey items randomly allocated to 25 patches. The patches had undetectable boundaries. Their centre coordinates were randomly drawn from a uniform distribution ranging over the square-shaped environment and their radii depended on the number of items they contained. Prey items were randomly located within their respective patches, with a mean density set to 0.5 (rich environment) or 0.1 (poor environment). Consequently, the number of patches per unit area, the number of prey items per patch, and the number of items per unit area within patches obeyed Poisson distributions.

Any prey item detected by the forager was harvested and therefore removed from the environment, thus involving a local depletion of the patches. It was replaced to its initial location after the forager had travelled 500 alu, to keep the overall prey distribution constant. Thus, even if moving along a straight line through the wrap-around margins, the forager experienced a renewed environment, which was therefore virtually infinite. It is worth noting that a number of LW studies focused on "non-destructive" foraging in a homogeneous environment, but this approach simply corresponds to a mathematically tractable proxy for "destructive" foraging in a patchy environment (Bartumeus et

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