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Comment

Intrinsic Lévy behaviour in organisms – searching for a mechanism Comment on “Liberating Lévy walk research from the shackles of optimal foraging” by A.M. Reynolds

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The seminal papers by Viswanathan and colleagues in the late 1990s [1,2] proposed not only that scale-free, superdiffusive Lévy walks can describe the free-ranging movement patterns observed in animals such as the albatross [1], but that the Lévy walk was optimal for searching for sparsely and randomly distributed resource targets [2]. This distinct advantage, now shown to be present over a much broader set of conditions than originally theorised [3], implied that the Lévy walk is a search strategy that should be found very widely in organisms [4]. In the years since there have been several influential empirical studies showing that Lévy walks can indeed be detected in the movement patterns of a very broad range of taxa, from jellyfish, insects, fish, reptiles, seabirds, humans [5–10], and even in the fossilised trails of extinct invertebrates [11]. The broad optimality and apparent deep evolutionary origin of movement (search) patterns that are well approximated by Lévy walks led to the development of the Lévy flight foraging (LFF) hypothesis [12], which states that “*since Lévy flights and walks can optimize search efficiencies, therefore natural selection should have led to adaptations for Lévy flight foraging*”.

The idea that organism search strategies naturally evolved to exploit optimal Lévy patterns has gathered pace in recent years [5,7,9,11]. To account for observed Lévy-like behaviour – by which I mean behaviour patterns well approximated by a truncated Lévy distribution – it has been hypothesized that (i) scale-free activities may arise from intrinsic processes [9,11,13–16], (ii) that behavioural adaptations to changes in environmental resources may cue the switching between localized Brownian and Lévy random searching [5,7], or (iii) that sensory interactions with

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heterogeneous environments may give rise to Lévy movement patterns (an emergent phenomena) [17,18]. However, the origins of such potential mechanisms remain elusive.

The review by Reynolds [19] is a timely synthesis of this burgeoning topic. The review proposes that the Lévy flight foraging hypothesis may be too narrowly focused on optimal foraging to be ideal for framing questions aimed at exploring how scale-free movements and behaviours may arise. I do not entirely agree with this position. I hold the view that to understand the mechanisms underlying the observed scale-free (Lévy) patterns it will be necessary to consider both intrinsic and extrinsic processes, in addition to behavioural adaptations that are flexible and including cognitive processes such as learning and sociality. In my opinion a new hypothesis would be particularly valuable if it could unify these different aspects. Whilst I appreciate that the LFF hypothesis may not achieve this aim for all behaviour patterns observed, it is evident that the free hypothesis outlined [19] does not succeed entirely in this endeavour either.

The LFF hypothesis essentially considers natural selection as a driver for widely observed Lévy search patterns of organisms. In this idea it is the competition occurring between individuals that favours the survival of those approaching or exhibiting optimal Lévy searches (for resources such as food or mates) [3]. Reynolds [19] proposes a new synthesis supporting a new hypothesis – the 'free Lévy flight hypothesis' – which states that "*Lévy flights 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 choice of the word 'innate' is problematic because it is not defined, even though historically it has been the source of much controversy in the behavioural sciences [20]. The normal use of the term 'innate' has been to describe a behaviour which was adapted to its present function by natural selection. A so-called innate (inborn) behaviour can be a complex behaviour, one that is developmentally fixed, but this does not necessarily mean it is independent of environmental influences or genetically fixed. Indeed, there are very few behaviour patterns that run to completion regardless of information from the environment and in the light of feedback from the results of an organism's own actions [20]. Nevertheless, it appears that 'innate behaviours' in the proposed free hypothesis is meant to signify behaviour that develops without example or practice and is fixed. Regardless of that contention, the principal idea of the free Lévy flight hypothesis is that Lévy patterns arise as a consequence of factors unrelated to behaviour (e.g. internal factors linked to physiology) [15] – with the assumption that Lévy characteristics are neutral – or that organisms interact with their heterogeneous environment such that Lévy patterns emerge [17]. It is proposed that if either of these are advantageous then natural selection will favour against the loss of these characteristics. On the face of it, the free Lévy flight hypothesis does not appear, as argued, to be a broader hypothesis than the LFF hypothesis. Rather, I would argue, they are somewhat different faces of the same coin.

The proposed free Lévy flight hypothesis is largely focused on explanations that favour the prevalence of scale-free behaviour as an intrinsic, spontaneous behaviour. However, this explanation is not outwith the LFF hypothesis in my view. In addition to it being possible for scale-free activities to be generated intrinsically [13,15,16], it is also possible that an intrinsic pattern is flexible, is under selection and becomes 'optimal' in the general environment in which a species finds itself. For example, the nematode worm (*Caenorhabditis elegans*) undertakes searching movements for food that show behavioural transition between an environmentally informed 'extrinsic' strategy that is influenced by recent experience and controls area-restricted searching, and a time-dependent 'intrinsic' strategy that reduces spatial oversampling and improves random encounter success [21]. A study using quantitative genetic analysis to examine the mechanisms underlying the behavioural transition decision of *C. elegans* to leave a food patch showed genetic variation and environmental cues converge on common neural circuits to regulate this behaviour [22]. This result suggests that behaviours linked to decisions to make longer movement steps away from depleted food patches (*cf.* long steps in a Lévy walk) are heritable traits modifiable by the environment and not solely owing to a fixed and neutral intrinsic behaviour program or to emergent interactions with food patches. This emphasises the need to consider apparently 'innate' behaviours as flexible, i.e. they are capable of responding rapidly to environmental changes and are modified slowly by changes in the genome [22]. This modern understanding of 'innate', intrinsic behaviours sits well within the LFF hypothesis.

The free Lévy flight hypothesis also attempts to incorporate Lévy walks as an emergent property of environmental interaction. However, the arguments are not particularly convincing. For example, it is claimed that emergent Lévy walks are present in marine predators. With reference to previous observations of vertical Lévy movements in diving marine predators [5,7] Reynolds uses his own analytical and simulation study of ocean turbulence to conclude that the numerical results were consistent with marine predators (mainly large fish species) changing their direction of travel