Reply to comment

Venturing beyond the Lévy flight foraging hypothesis: Reply to comments on "Liberating Lévy walk research from the shackles of optimal foraging"

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I would like to thank all commentators for their insightful and thought-provoking commentaries. Here I discuss some of the important issues raised by Bartumeus [1], Boyer [2], Cheng [3], da Luz et al. [4], Focardi [5], Humphries [6], MacIntosh [7], Miramontes [8] and Sims [9]. I have grouped together similar commentaries and begin with those that most strongly oppose my hypothesis.

Humphries [6] appears to have misinterpreted the title of my Review [10]. He asserts that I am advocating un-shackling Lévy walk research from 'optimal foraging theory' (a theory concerned with optimizing the exploitation of food-rich patches once found). I am, in fact, arguing that Lévy walk research should not remain wedded to the 'Lévy flight foraging hypothesis' and so stymied by theories concerned with the optimal way to find patches. Humphries [6] begins by suggesting that statistical techniques used to detect Lévy movement patterns look only at the statistical distribution of step-lengths and not at the actual pattern, or structure, of the movement pattern which in analyses can be lost entirely. This is true of most studies but not all. The overall structure of honeybee searching flights have, for example, been ascertained using an array of techniques (de-trended fluctuation analyses, Fourier power-spectrum analyses, and structure function analyses) [11,12]. These whole-path analyses reveal that entire flight patterns resemble Lévy walks. Similarly, power spectra analyses indicate that the overall movement patterns of *E. coli* also resemble Lévy walks [13]. Humphries [6] notes that most kinds of Lévy walk *can* outperform Brownian walks when randomly searching and that this provides useful insights when attempting to understand movement pattern data. I hold the same

view but maintain that selection is not working with a blank canvas, as Lévy walks (usually of the variety reported to optimize random searching) can and do arise freely [10]. Once generated they may be *maintained* by selection or as Focardi [5] remarked be like the "spandrels of St Mark" without biological relevance. Humphries [6] goes on to state that it has been shown "unequivocally" that Lévy walks outperform Brownian walks. I think that this is too strongly put because Lévy searching is advantageous only when certain conditions are satisfied (e.g., searching begins close a target, directionality is lost after target encounters, foragers do not adapt to conditions found along the search, energetic costs of turning are minimal, motion does not degrade perception, searching efficiency does not trade-off with safety from predation) [14–16]. When these conditions are relaxed the relative advantages of Lévy searching can be greatly diminished or even disappear completely [14–16]. This may explain why most terrestrial invertebrates, which by virtue of their bumbling haphazard movements are exemplary probabilistic foragers, do not perform Lévy walks [17].

Sims [9] suggests that the Lévy flight foraging hypothesis and my free Lévy flight hypothesis are different faces of the same coin. They are, in fact, radically different hypotheses. The former predicts that Lévy walks will be common amongst probabilistic foragers, a prediction that I find to be incorrect. The later predicts that the occurrence of Lévy flights is accidental and uncommon even amongst probabilistic foragers and not restricted to searching, just as appears to be the case [10]. Sims [9] notes that some behavioural transitions, for example, switching between intensive and extensive modes of searching in *C. elegans*, can be heritable traits modifiable by the environment. This point is made explicitly in my Review [10]. There I suggested that mussels *Mytilus edulis* and the Australian desert ant *Melophorus bagoti* are perhaps the only known examples of selection for Lévy walking. These organisms appear to mimic Lévy walks as multi-modal walks; a process which requires fine tuning. This adaptation has subsequently been observed in mud snails *Hydrobia ulvae* [18]. It was also reported that molecular transport machinery operating within cells perform Lévy walks and that these Lévy walks may be attributed to selection for optimized searching [19]. Nonetheless, these 4 examples seem to be exceptions rather than the rule because most putative mechanisms for Lévy walking, such as the one that may operate in marine predators, do not require fine tuning [10].

Sims [9] notes that there is no empirical evidence for this particular mechanism. The mechanism is speculative but merely requires that the predators turn away from patches of relatively strong turbulence (a seemingly natural response to buffeting). The alternative hypothesis advocated by Sims [9] is that these Lévy movement patterns are the result of selection for advantageous foraging. This is also speculative because there is little empirical evidence that marine predators forage non-destructively and without significant risk of predation, just two of the conditions required to make Lévy searching advantageous [14]. The alternative hypothesis also leaves open the all-important question of the underlying generative mechanism which, as concluded by Miramontes [8], is the key to understanding and prediction.

Sims [9] returns to the case of wandering albatross which has become a touchstone for Lévy flight research. It has become clear, that despite previous claims to the contrary [20], wandering albatrosses do, after all, execute Lévy flights across the oceans [21]. I agree with Sims [9] that it is unlikely that these Lévy flight patterns are *solely* the result of interactions with odours; a possibility described at some length in my Review [10]. Nonetheless, since the appearance of my Review [10] this theoretical possibility has gained considerable empirical support from an analysis of 210 shearwaters [22]. After foraging in the open ocean, shearwaters, like wandering albatrosses, are able to pinpoint their breeding colonies, often located on small remote islands in apparently featureless seascapes. They can also locate distant preferred feeding locations. The new analysis [22] suggests that this remarkable navigational ability can be attributed to the birds assembling cognitive maps of wind-borne odours; a trait which manifests itself as Lévy flight patterns [22]. Lévy searching, if it exists at all, may therefore be restricted to searching within preferred feeding locations for food-rich patches. This could also be true of the wandering albatross since they are closely related to shearwaters.

Before closing Sims [9] remarks that the general applicability of the Lévy free hypothesis is undermined by observed transitions between Brownian walks when resource targets are abundant and Lévy walks when targets are sparsely distributed. This view is not supported by recent observations [23]. de Jager et al. [23] observed that Lévy walking is frequently arrested when the targets of a search are abundant and that this gives the *impression* Brownian walking.

da Luz et al. [4] suggest that emergent Lévy walks can be tuned by selection if their emergence is contingent on particular behavioural responses to the external environment. As noted above, this appears to be case with mussels, mud snails and Australian desert ants. Nonetheless, most of the putative generative mechanisms identified so far are not plastic. Instead they typically result in the kind of Lévy walks that optimize or near optimize search efficiencies