



Optimising the success of random destructive searches: Lévy walks can outperform ballistic motions

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ABSTRACT

We re-evaluate the long standing and widely held belief that ballistic movements (i.e. straight-lines movements) outperform Lévy walks when searching for targets that once located are not revisited. The belief stems from the results of analyses of one-dimensional searches, analyses which have not accounted for the fact that target numbers can be continually depleted during the search process. This is a crucial oversight because continual depletion promotes the searching efficiencies of some Lévy walks above that of ballistic motion. The continual depletion effect is not so important for two- and three-dimensional searches. Nevertheless, we show that Lévy walks and ballistic movements can be equally or almost equally effective when searching within two- and three-dimensional environments for randomly and sparsely distributed targets or when searching for targets that are occasionally concealed. We also show that Lévy walks are advantageous when searching for targets that can occasionally evade capture. These situations represent common predator–prey interactions in which predators are involved in ‘imperfect destructive’ searches. Our model suggests that accounting for coevolutionary arms races at the predator–prey detection/reaction scales can explain to some extent Lévy walk searching patterns of predators at larger scales. This result provides new insights into the Lévy walk movement patterns of some destructive foragers.

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1. Introduction

The movement patterns of some foragers (e.g. microzooplankton (Bartumeus et al., 2003) jackals (Atkinson et al., 2002), and diverse range of marine predators including sharks, bony fishes, sea turtles and penguins (Sims et al., 2008)) can be represented by Lévy walks whose straight-line move lengths are distributed according to an inverse-square power-law. Such movement patterns constitute an optimal Lévy walk random searching strategy for the location of randomly and sparsely distributed targets that once visited are not depleted or rejected but instead remain targets for future searches (Viswanathan et al., 1999). As predators, some of the aforementioned organisms may, however, be involved in ‘destructive’ rather than ‘non-destructive’ searches and will not revisit previously visited targets. It is widely believed that ballistic movements (i.e. single straight-line movements without any change in direction) outperform Lévy walks when searching destructively because they minimise the mean distance travelled before encountering a target and so minimise the mean energy expenditure (Viswanathan et al., 1999; Raposo et al., 2003;

Bénichou et al., 2005; James et al., 2008). This calls into question optimal Lévy walk movement patterns as a searching strategy adopted by predators.

In the present work we resolve this long-standing and important question by reconciling destructive searching with the prevalence of Lévy walk movement patterns in predators. We do this in three steps. First, by showing that Lévy walks outperform ballistic motions when the original one-dimensional analysis of Viswanathan et al. (1999) is extended to take account of the fact that target numbers can be continually depleted when searching is destructive. Second, by showing that in two- and three-dimensional environments, changes in direction will rarely result in areas being revisited. As a consequence Lévy walks and ballistic motions can be almost equally effective when searching destructively for targets that are randomly and sparsely distributed or for targets that are occasionally concealed. Finally, by showing that if targets can occasionally evade capture, once detected, then Lévy walk searches outperform ballistic searches. These situations represent common predator–prey interactions in which predators are involved in ‘imperfect destructive’ searches, due to detection and capture errors. These errors can arise prior to an encounter (e.g., prey occasional refuge or crypsis) or upon detection (e.g., predator-induced immobility or escape reactions).

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2. Methods

Viswanathan et al. (1999) considered an idealised one-dimensional model in which a searcher (a predator) moves on a straight line towards the nearest target (a prey item) if the target lies within the 'direct perceptual range', R , otherwise it chooses a direction either forwards or backwards at random and a distance, ℓ , drawn from a power-law distribution $p(\ell) = (\mu - 1)R^{\mu-1}|\ell|^{-\mu}$ when $\ell > R$ otherwise $p(\ell) = 0$, where $1 < \mu < 3$. For $\mu > 3$ sums of length, i.e. total displacements, converge to a Gaussian distribution by virtue of the Central Limit Theorem so that motions are effectively Brownian at sufficiently large scales. Lévy indices $\mu \leq 1$ do not correspond to normalisable distributions with probabilities that sum to unity. Lévy walks with $\mu \rightarrow 1$ correspond to randomly orientated straight-line movements (Viswanathan et al., 1999). The searcher then moves incrementally towards the new location whilst constantly seeking for targets within a radius, R . If no target is detected, it stops after traversing the distance ℓ and chooses a new direction and a new distance, otherwise it proceeds to the target and an encounter with the target arises. Subsequent searches for additional targets follow the same rules and begin with the searcher randomly choosing a direction to move in rather than choosing to move in the direction it was heading prior to the encounter.

Viswanathan et al. (1999) examined two encounter scenarios, commonly referred to as the 'non-destructive' and 'destructive' scenarios. In the non-destructive scenario, targets once visited are not depleted but instead remain targets for future stages. Each new non-destructive search therefore begins in the vicinity of a previously visited target. In the destructive scenario, targets are not revisited because they have been either depleted or rejected. Viswanathan et al. (1999) did not explicitly consider the effects of the continual depletion of target numbers but instead assumed that each new destructive search tends to begin equidistance from adjacent surviving targets. A long-term decrease in target numbers due to predation would arise in the absence of target recolonisation and recruitment through dispersal or regeneration. We show later that when there is a continual depletion starting a new search midway between surviving targets eventually becomes impossible.

We extended the Lévy walk search model of Viswanathan et al. (1999) to: (i) explore the effects of a continuous depletion on target numbers and (ii) to account for the possibility that prey are occasionally concealed (pre-encounter) and/or evade capture (post-encounter). The first is implemented by starting each new search at the location of the last target to be detected but without replacing the target randomly in the search arena. The second is implemented by assuming that the prey are not necessarily detected or captured once detected but instead are detected and captured with probabilities p_d and p_c , respectively. Only when a target is detected is the search interrupted whereupon the searcher moves directly towards the target. If the target is captured then a new search for the remaining targets begins in the vicinity of the capture. If the target can and does evade capture then a new search for the escapee and all other remaining targets begins in the vicinity of the escape.

We also performed one-, two-, and three-dimensional simulations of destructive searching. In these simulations, each new search begins at the location at which a target was last destroyed. The scaling of the simulations is based on the mean distance between targets: $\lambda \sim L^d / NR^{d-1}$ where d is the dimensionality, L is the side length of the search arena, N the number of targets, and R the perceptual range (see Ref. Bartumeus et al., 2008). We present simulation data for the case of low (i.e. $\lambda = 100$) and high (i.e. $\lambda = 1000$) target densities, i.e. for when the mean distance between targets is very much longer

than the direct perceptual range of the predator and when it is more comparable with it. In all cases, targets are randomly and uniformly distributed.

3. Results

3.1. Lévy walks outperform ballistic motions when searching destructively in one-dimension but not in two- and three-dimensions

In their analysis of one-dimensional, destructive searching Viswanathan et al. (1999) assumed that each new search begins mid-way between adjacent non-visited targets. This is a crucial assumption because it leads inevitably to the optimality of straight-line ballistic movements. The assumption neglects a key aspect of destructive searching, namely that as a search progresses the global target density can continuously decrease. Consider, for example, a predator that begins a search mid-way along a chain of prey items, here denoted by ...0000000000... This first search will be truncated once a prey item has been detected and so the next search will begin mid-way between adjacent non-visited targets. The situation can be represented by ...00000LO0000... where L is the location of the depleted prey and the location at which the second search begins. This is exactly the 'destructive' situation envisaged by Viswanathan et al. (1999). But as the search progresses, prey are being continually depleted so that some later time a single region devoid of targets forms ...OXXXXXXLO... where L is the location the last detected prey item and the starting location of the next search and where X are depleted prey items. It is evident that the next search does not begin mid-way between surviving targets. Instead it begins in the vicinity of one surviving target (at the right) and distant from some other previously surviving targets (on the left). In this case, the starting condition of the destructive search resonates with the one found in 'non-destructive' scenarios, and it is well known that in those cases, Lévy walks outperform ballistic motions (Viswanathan et al., 1999). The ineffectiveness of ballistic motions is readily understood. In our example, rightwards movements will take the searcher from the edge of the growing void to the nearby target. Leftwards movements on the other hand, that are randomly chosen 50% of the time, extend right across the void and take the searcher to the more distant target. Ballistic motions are therefore only optimal in the initial stage of a destructive search. As the target void extends, ballistic motions start to be penalised and then the optimal strategy will eventually stabilise at $\mu = 2$ because the situation would be directly analogous to Viswanathan et al. (1999) analysis of 'non-destructive' searching for sparsely distributed targets. Unidirectional motions through one-, two- and three-dimensional search arenas have been recognised as the most efficient (James et al., 2008). However, for the go-straight rule to be optimal some specific conditions are necessary: it is required that predators (i) do not lose their sense of direction after encountering and then subduing a prey, and (ii) have perfect prey-detection capabilities so that there is no benefit in re-examining previously visited locations. Fig. 1a and b shows the optimal Lévy index μ for one-dimensional destructive searches with continual target depletion (a) and with target replacement (b). Here and throughout the searching efficiency is the number of targets found with respect to the distance travelled. The most efficient searches minimise the mean distance travelled before encountering a target and so minimise the mean energy expenditure.

The 'continual depletion effect' is not significant for searches in two- and three-dimensions where space is continuous and where predator movement directions are not restricted (Fig. 1c–f). In such scenarios the search efficiencies with continual

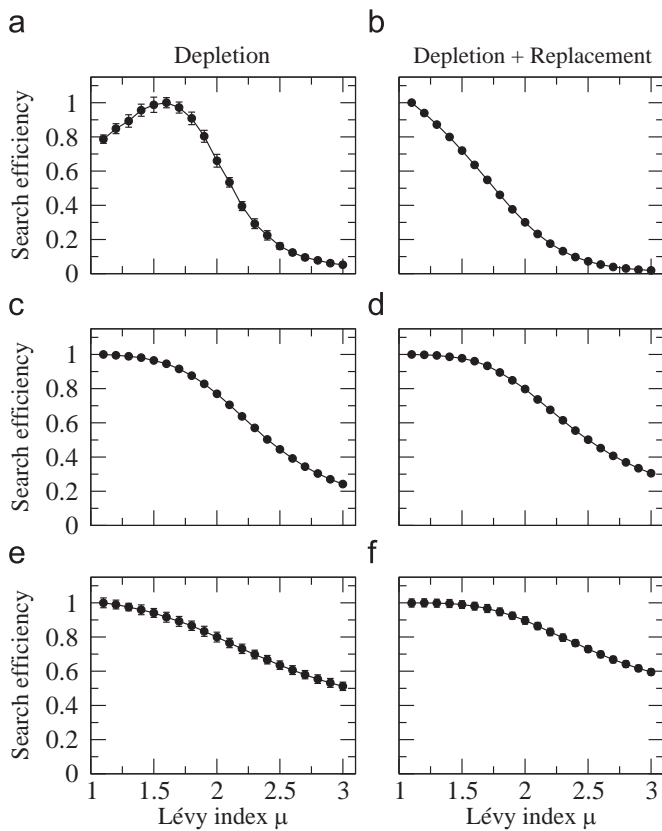


Fig. 1. The relative searching efficiency, n/n_{\max} , of Lévy walkers with target depletion (a, c, e), and target depletion plus replacement (b, d, f). Here n is the mean number of targets located by a Lévy walker with Lévy index μ and n_{\max} is the number of targets located by the most efficient Lévy walker. The search efficiency (percentages in Y-axis) is, thus, relative to the maximum number of encounters. Targets are randomly and uniformly distributed within one- (a, b), two- (c, d) and three- (e, f) dimensional environments. Error bars show standard deviations. In one-dimension, the continual depletion effect modifies the optimal search from ballistic to some optimal Lévy index. In two- and three-dimensions, the search efficiency curves do not depend sensitively on the continual depletion effect and show saturation at the range $1 < \mu < 2$. In all simulations, the average distance between targets is $\lambda = 1000$ space units, the perceptual range $R = 2$ space units, and the distance travelled is $D = 10^7$ space units, except for the three-dimensional case, where due to computational limitations $D = 10^4$ space units. In two- and three-dimensions, the lower the target density the flatter is the plateau at $1 < \mu < 2$ (results not shown).

target depletion (Fig. 1c and e) and with target depletion and replacement (Fig. 1d and f), show a saturating curve for Lévy walks with μ less than some critical value μ_c . Note, however, that because of computational limitations the travelled distances in three-dimensional systems are shorter so that the saturation effect may look less evident (Fig. 1e and f). In any case, the saturation effect is more extensive in two- than it is in three-dimensions and is stronger when target replacement is incorporated than otherwise (see Fig. 1c–f).

Further results based on numerical simulations in two-dimensional systems (not shown) indicate that if the space is discrete (i.e., a lattice) or if the searching involves very restricted movement directions (e.g. N, S, W, E), as in the case of *Drosophila* fruit flies that make 90° turns (Reynolds and Frye, 2007), then the continual depletion effect can be relevant. In these situations, large continuous regions can become depleted of targets. Once this becomes established, most new searches will begin on the periphery of the depleted region where the target density remains high and so where targets are most likely to be detected. As a result most new searches will tend to begin close to some

surviving targets but distant from other surviving targets located on the other side of the void. This is analogous to the non-destructive scenario where Lévy walks outperform ballistic motions (Viswanathan et al., 1999).

Our results illustrate that when studying random search strategies, even if the target dynamic conditions (depletion or depletion plus replacement) are well-specified, the results from analyses of one-dimensional searches do not necessarily carry over into higher dimensions. Much care is also needed when comparing the results obtained in discrete (restricted directions) and continuous (non-restricted directions) space.

3.2. Lévy walks and ballistic motions can be equally or almost equally effective when searching destructively in two- and three-dimensional environments

In the absence of the ‘continual depletion effect’, straight-line movements outperform Lévy walks when searching destructively in one-dimensional environments (Fig. 1a and b) because Lévy walks cause a searcher to needlessly revisit locations that have been searched previously. This does not apply when searching in continuous two- and three-dimensional environments because random and continuous changes in direction will rarely result in locations being revisited. It is therefore not surprising to find simulation data showing that Lévy walks and ballistic motions can be equally or almost equally effective when searching destructively in two- and three-dimensional environments, independently of the target dynamics (i.e. depletion or depletion plus replacement) (see Fig. 1c, d or e, f). Searching efficiencies for Lévy walks with $\mu \leq \mu_c$ plateau and are nearly maximal. This is, in fact, not a new finding. It is, for example, apparent in the simulation data reported on by Bartumeus et al. (2005, 2008), which shows that the lower the target density the more evident is the plateau. The significance of the findings has, however, gone unnoticed. The effectiveness of $\mu \leq \mu_c$ Lévy walk searches can be understood within the context of a simple but approximate analysis. The analysis will show that the overall length of any one of these searches and so the territory covered, is dominated by the length of the longest move in the search pattern.

The analysis centres on the determination of the mean path length $\langle L \rangle$ of a Lévy walk $P(\ell) = \ell^{-\mu}$ containing N moves. When $\mu > 2$, $\langle L \rangle = N \langle \ell \rangle$ where $\langle \ell \rangle = \int_R^\infty \ell P(\ell) d\ell = \int_R^\infty \ell^{-\mu+1} d\ell$ is the mean length of a straight-line movement and where R is the length of the shortest move. For $\mu \leq 2$ the determination of $\langle L \rangle$ is less straightforward because the mean move length, as defined above, is a divergent property. The integral defining the mean length of a move should be cut-off at the length, ℓ_m , of the longest move within the Lévy walk. When the number of moves is sufficiently large, this length can be estimated from $N \int_{\ell_m}^\infty \ell^{-\mu} d\ell \approx 1$, which just expresses that fact that a move with length longer than ℓ_m occurs at most once in the walk. It follows that $\ell_m \approx N^{1/(\mu-1)}$ and so the mean move length $\langle \ell \rangle \approx \int_{\ell_0}^{\ell_m} \ell^{-\mu+1} d\ell \approx \ell_m^{-\mu+2} = N^{-1+1/(\mu-1)}$. The length of the longest move in a $\mu \leq 2$ Lévy walk with N moves therefore makes the dominant contribution to the overall length of the walk because $\langle L \rangle = N \langle \ell \rangle \approx N(N^{-1+1/(\mu-1)}) = N^{1/(\mu-1)} = \ell_m$. This is indicative of scale-free behaviour; the whole walk resembles one single move. The territory covered by Lévy walk searches with $\mu \leq 2$ and containing many moves will therefore be dominated by the single longest straight movement, i.e. $\langle L \rangle \approx \ell_m$. This fact together with the relatively low probability of returning to previously visited territory when moving in two- and three-dimensions explains why the searching efficiencies of two- and three-dimensional Lévy walks with $\mu \leq \mu_c$ are comparable to that of ballistic motions.

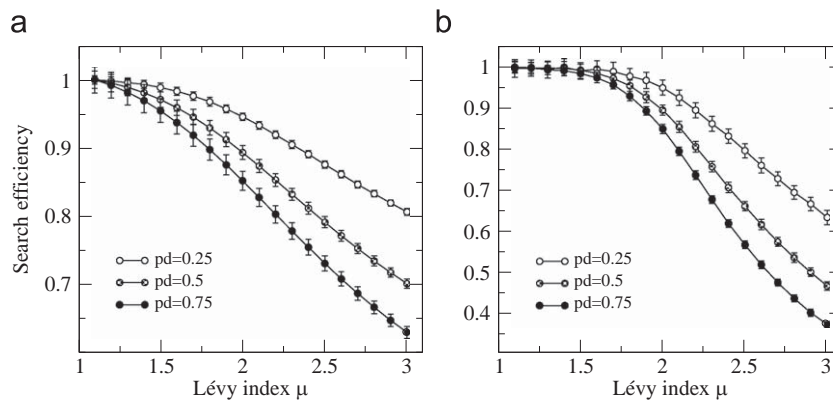


Fig. 2. Detection errors effects on the search efficiency. The relative searching efficiency of Lévy walkers in arenas with low (a, $\lambda = 100$) and high (b, $\lambda = 1000$) target densities. In all simulations, the distance travelled is $D = 10^7$ space units and the perception range is $R = 1$ space units. Error bars show standard deviations. Targets are uniformly distributed within two-dimensional environments and randomly replaced after an encounter. Searching efficiencies plateau at the range $1 < \mu < 2$. When the target detection probability is low or equivalently when targets are in dilute concentration the plateau is more evident.

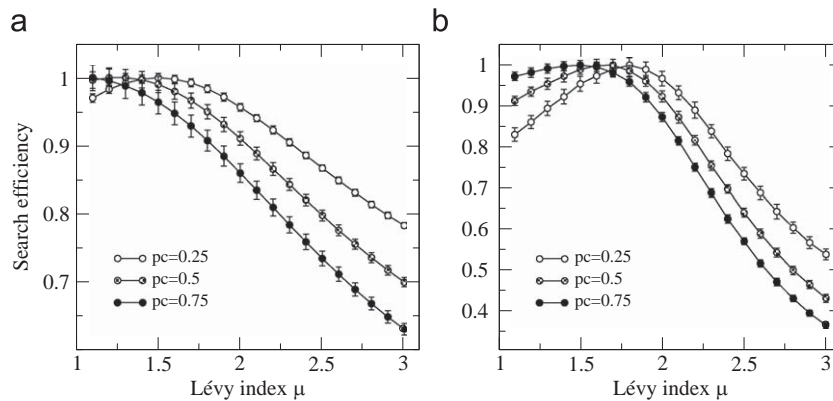


Fig. 3. Capture errors effects on the search efficiency. The relative searching efficiency of Lévy walkers in arenas with low (a, $\lambda = 100$) and high (b, $\lambda = 1000$) target densities. In all simulations, the distance travelled is $D = 10^7$ space units and the perception range is $R = 1$ space units. Error bars show standard deviations. Targets are uniformly distributed within two-dimensional environments and randomly replaced after an encounter. Searching efficiencies peak showing optimal Lévy indices within the range $1 < \mu < 2$. The larger the capture error the larger the optimal Lévy index.

3.3. Detection and capture errors select for Lévy walks instead of ballistic motions in any dimension

A search pattern is only interrupted when a searcher detects a target. The failure to detect the presence of target when it is within perceptual range (i.e. detection error) can, therefore, only promote an ‘attenuation effect’ on actual target densities. The attenuation effect does, however, have consequences for the optimisation of random searches. Fig. 2 shows that two-dimensional Lévy walk searches with $\mu \leq 2$ are near optimal when targets are occasionally concealed so that target density is effectively attenuated. As noted in the last subsection, the lower the target density (i.e. the larger the detection error) the flatter is the searching efficiency curve in the range $1 < \mu \leq 2$. Even at high target densities where ballistic motions would outperform Lévy walks if target-detection capabilities were perfect, imperfect target-perception capabilities can make equally efficient any strategy with $\mu \leq 2$. Optimal one-dimensional searches on the other hand are not dynamically robust unless the continual depletion effect operates. Instead there is a ‘crossover’ from ballistic motions (i.e. Lévy walks with $\mu \rightarrow 1$) being optimal when targets never recover to $\mu = 2$ Lévy walks being optimal when targets immediately recover (Raposo et al., 2003).

When detected prey can readily evade capture or when predators make capture errors, most of the new searches would

begin in the vicinity of the escape event and so close to a previously visited prey. The larger the capture errors, the more prevalent would be this reset condition during the whole search process. In such cases, $\mu = 2$ Lévy walks are optimal (Fig. 3). More generally, the combination of ‘attenuation effects’ (due to detection errors) and the possibility of ‘rewards for revisiting previous areas’ (due to capture errors) make Lévy walk strategies better than ballistic motion (Fig. 4a). For almost half of the combinations, the optimal Lévy indices are within the narrower range $1.8 \leq \mu \leq 2.2$ (Fig. 4b) and consistent with observations (Bartumeus et al., 2003; Atkinson et al., 2002; Sims et al., 2008). The presence of isolated local minima and maxima arose because it was computational prohibitive to resolve differences between optimal and near-optimal searches when searching efficiencies were not strongly peaked functions of μ . The simulation data shown in Fig. 4 were obtained under the assumption that detection and capture errors occur sequentially but are otherwise independent of one another. This is reasonable because detection and capture are distinctly different animal behaviours that can and have been evaluated separately in the field and in the laboratory, see e.g. Taylor (1984). The probability of detection can be computed as the number of times a behavioural reaction occurs due to the presence of nearby individuals. Typically, the probability of attack and avoidance reactions at given distances are computed for predators and prey,

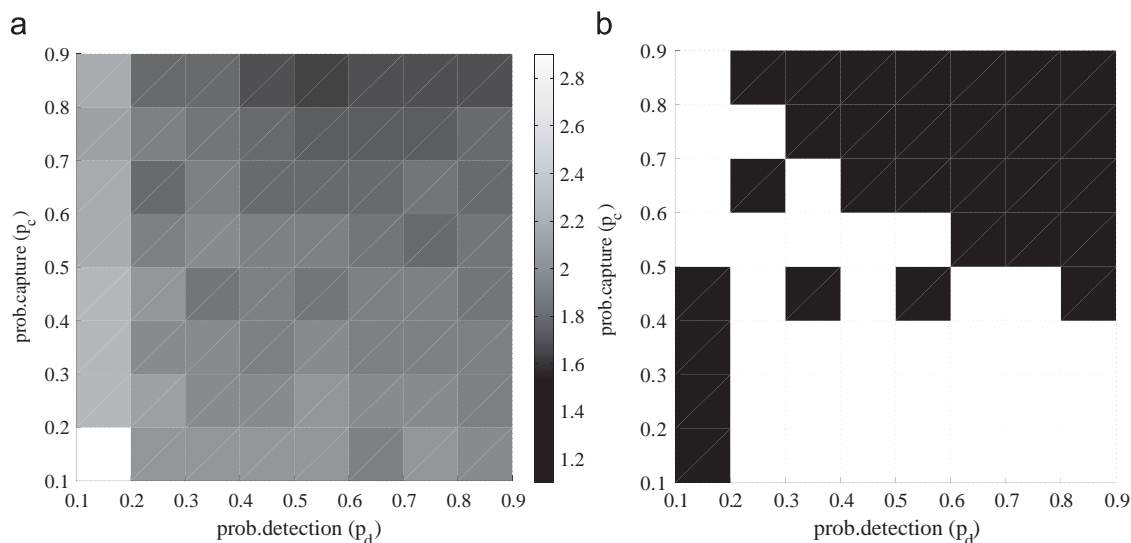


Fig. 4. Imperfect destructive searches where detection and capture errors are combined. Simulation data is shown for $\lambda = 500$ space units, a distance travelled of $D = 10^7$ space units and a perception range $R = 1$ space units. For each detection and capture probability combination, the Lévy index with the larger search efficiency is obtained from 20 independent simulations involving Lévy indices in the range $1.1 \leq \mu \leq 3$ separated a step size of 0.1. (a) Optimal Lévy indices $1 < \mu \leq 3$ obtained for different probabilities of detection p_d , and capture p_c . (b) Dichotomisation of the data. White areas: combinations of p_d and p_c with optimal Lévy indices in the range $1.8 \leq \mu \leq 2.2$. Black areas: combinations of p_d and p_c with optimal Lévy indices in the ranges $\mu < 1.8$; $\mu > 2.2$.

respectively. The probability of capture can be measured by counting how many times an individual escapes during an attack.

4. Discussion

It is intuitively obvious that the likelihood of encountering randomly distributed targets within a search arena is determined by the search pattern and by ‘boundary conditions’, such as the dimensionality of the search arena, the underlying target distribution, and the spatiotemporal scales under consideration (Bartumeus et al., 2005, 2008). Less well known are the impacts that specific *encounter dynamics* can have on searching efficiencies by continuously resetting the initial conditions of the search between two consecutive encounters. Here we considered the impacts of: (i) destructive searching resulting in a continual depletion target numbers; (ii) destructive searching with overall target number being maintained through randomly located replacement; (iii) the failure to detect the presence of some targets; and (iv) the failure to capture some targets once detected. All these scenarios are studied under the key assumption that the searchers fail to re-establish the direction of motion that they had prior to its encounter with a target. The assumption pertains to situations in which an encounter with a target gives rise to a sequence of strong behavioural changes (e.g. attack, capture, handling and digestion) that result in a loss of directional-memory. Exceptions include cases where movements are informed by spatial maps and environmental gradients; scenarios that depart from the random search situations considered herein.

In the present work, we have shown that the *encounter dynamics* determine the ‘initial conditions’ for the next search that begins after each encounter, and can therefore be of crucial importance when attempting to establish mathematically optimal random searches. The important issue is not the target distribution but the ‘initial’ conditions of each new search after the encounter. Target distributions and initial conditions are, nevertheless, closely related. The more heterogeneous the target distribution, the more probable is it that after an encounter a search starts with a nearby target, instead of midway between

adjacent surviving targets. Following this rationale, patchy distributions should favour Lévy walks over ballistic motions in non-informed destructive searches where previous orientation is broken after encounters, see e.g. Bartumeus and Levin (2008).

Attempts to interpret animal movement patterns within the context of optimal random searching must take account of both the ‘boundary’ conditions and the ‘initial’ conditions. Importantly, there is not a universal solution to search problems. As shown here, search problems are sensitive to ‘initial’ and ‘boundary’ conditions. Nevertheless, given some specific set of conditions, one can always define an optimal strategy. Distinguishing optimality rationales based on mathematical models from real adaptive strategies it is also important. In the latter case, the assumption is that the behavioural rules that the model represents should be encoded into biological mechanisms at some level (genetic, physiological, or behavioural), which in turn, should be transmitted generation after generation. Lévy walks can only be considered as adaptive strategies (Bartumeus, 2007) if the behavioural rules and the specific ‘boundary’ and ‘initial’ conditions that led to advantageous or optimal Lévy walks are common and important enough for a species survival.

Viswanathan et al. (1999) showed that ballistic (straight-line motion) corresponding to $\mu \rightarrow 1$ are optimal when searching is one-dimensional and ‘destructive’, so that targets once visited are not revisited because they have either been deleted or rejected. The latter result has led to the long-standing and widely held belief that ballistic motions outperform Lévy walk when searching destructively (Viswanathan et al., 1999; Raposo et al., 2003; Bénichou et al., 2005). This calls into question the relationship between the $\mu \approx 2$ Lévy walk movement patterns of some predators (Bartumeus et al., 2003; Atkinson et al., 2002; Sims et al., 2008) and optimal searching theory. We showed that the belief is misguided and that even in one-dimensional environments Lévy walks outperform ballistic searches when continual depletion of prey numbers is taken into account; a process that was not accounted for in the recent analysis of James et al. (2008) who reported on the apparent optimality of ballistic searches. Terrestrial ecotones such as riparian forests, dune systems or rocky shores with strong depth-environmental gradients, force

'edge'-foraging (one-dimensional) (Bartumeus et al., 2008; Ovaskainen et al., 2008). Lévy walks with $\mu \leq 2$ and ballistic movements can be equally effective when searching within two- and three-dimensional environments for randomly and sparsely distributed targets and/or predators have imperfect perception capabilities. Lévy walks with $\mu = 2$, do however, have an advantage over their $\mu < 2$ counterparts. They are optimal when searching non-destructively (Viswanathan et al., 1999), i.e. they are optimal irrespective of whether targets can recover from predation and in this sense are dynamically robust with respect to the target recovery time, and might represent an evolutionarily stable strategy in changing or dynamic environments (Smith and Price, 1973). Additionally, Lévy walks outperform ballistic movements when prey can occasionally evade capture once detected. The coevolution of predators and their prey can lead to situations in which neither improves its fitness because both populations co-adapt to each other (Dawkins and Krebs, 1979; Vermeij, 1987). In these evolutionary arms race, improvements in the ability of a predator to detect and capture prey (e.g., heightened sensitivity to chemical, mechanical or visual signals, stronger attack reactions) are matched by compensating improvements in the ability of prey to evade detection and capture (e.g., crypsis, feigning death, strong jumps, sudden increase of size, confounding signals). These 'Red Queen' type of dynamics (Van Valen, 1973) preclude the possibility of a perfect searching/capture process. In these scenarios, a Lévy walk could also represent an evolutionarily stable strategy of search (Smith and Price, 1973).

By taking explicit account of imperfections in prey detection and prey capture we also give a relevant clue to resolve a long-standing problem with the interpretation of animal movement patterns in terms of optimal random scale-free searching strategies. We showed that Lévy walk searching patterns of imperfect prey-consuming predators optimise the trade-off between revisiting locations after detection/capture failures and relocating to new locations. Our predictions are compatible with the Lévy walk movement patterns of microzooplankton (*Oxyrrhis marina*) (Bartumeus et al., 2003). It is widely accepted that the swimming patterns of planktonic organisms cannot be fully understood without considering predator detection capabilities (Kiorboe and Visser, 1999; Gilbert and Buskey, 2005), or predator attack and prey escape dynamics (Kerfoot et al., 1980; Stemberger and Gilbert, 1987; MacKenzie et al., 1994; Caparroy et al., 2000; Bundy and Vanderploeg, 2002). Model predictions are also consistent with the movement patterns of a diverse range of destructive predators that includes a species of African jackal (Atkinson et al., 2002) and some marine predators (Sims et al., 2008). However before interpreting these movement patterns as optimal scale-free search strategies it is necessary to know the amount of information available to these searchers and to fully understand the encounter dynamics that is taking place, in order to approximate the real search process to one of the idealised search processes studied here: non-destructive, imperfect-destructive, destructive with continuous depletion or destructive with replacement.

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