Optimal foraging strategies: Lévy walks balance searching and patch exploitation under a very broad range of conditions

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Highlights

- Lévy walk foragers are optimal under a broader set of conditions than previously thought
- The importance of prey-targeting has been largely overlooked
- Lévy foragers outperform other strategies when prey is sparse and searching is required
- Composite Brownian walk foragers outperform at some high levels of prey abundance, when searching is not required
- Optimal Lévy foragers experience significantly fewer long periods of starvation

Abstract

While evidence for optimal random search patterns, known as Lévy walks, in empirical movement data is mounting for a growing list of taxa spanning motile cells to humans, there is still much debate concerning the theoretical generality of Lévy walk optimisation. Here, using a new and robust simulation environment, we investigate in the most detailed study to date (24 x 10^6 simulations) the foraging and search efficiencies of 2-D Lévy walks with a range of exponents, target resource distributions and several competing models. We find strong and comprehensive support for the predictions of the Lévy flight foraging hypothesis and in particular for the optimality of inverse square distributions of move step-lengths across a much broader range of resource densities and distributions than previously realised. Further support for the evolutionary advantage of Lévy walk movement patterns is provided by an investigation into the 'feast and famine' effect, with Lévy foragers in heterogeneous environments experiencing fewer long 'famines' than other types of searchers. Therefore overall, optimal Lévy foraging results in more predictable resources in unpredictable environments.

1.   Introduction

Empirical evidence for movement patterns known as Lévy walks, which are considered to optimise random searches where targets are sparsely and randomly distributed (Viswanathan et al., 1999), has built steadily over recent years with Lévy walk movement patterns being identified in diverse taxa such as insects (Bazazi et al., 2012; Maye et al., 2007; Reynolds, 2012; Reynolds et al., 2009), jellyfish (Hays et al., 2012), fish, turtles and penguins (Humphries et al., 2010; Sims et al., 2012; Sims et al., 2008), seabirds (Humphries et al., 2013; Humphries et al., 2012) and humans (Raichlen et al., 2014). A theoretical framework, in the form of the Lévy flight foraging (LFF) hypothesis, seeks to explain the prevalence of these movements in terms of optimal search strategies (Viswanathan et al., 2011). A Lévy walk is a specialised random walk with step-lengths drawn from an inverse power-law distribution such that the probability of a given step-length is inversely proportional to its length (i.e. $P(l) \approx l^{\mu}$ where $1 < \mu \leq 3$ and l is the move step-length). These movement patterns are super-diffusive, being characterised by clusters of short move-steps connected by rare long relocations, with the pattern being repeated at all scales (Klafter et al., 1993). Analytical and simulation studies suggest that in prey-sparse, dynamic environments, where new prey patches can be revisited any number of times, are beyond sensory range and where memory may be of limited use (such as in the marine pelagic realm), searches will be optimised if a Lévy walk pattern is employed (Bartumeus et al., 2005; Bartumeus et al., 2002; Sims et al., 2008; Viswanathan et al., 2000; Viswanathan et al., 2001). The LFF hypothesis proposes that because Lévy walks can optimise random searches of individual foragers, organisms should have naturally evolved to exploit movements that are approximated by Lévy walks (Viswanathan et al., 2008; Viswanathan et al., 2011). An important general prediction arising from the LFF hypothesis posits that Lévy movement patterns are optimal when prey is sparsely and randomly distributed, but simpler Brownian (i.e. normal diffusive) movements are sufficiently efficient where prey is abundant.

Empirical tests of the LFF hypothesis have been performed using movement data from electronically tagged marine predators such as sharks, tunas and billfish (Humphries et al., 2010; Sims et al., 2012; Sims et al., 2008). These studies have added support to the LFF hypothesis in that Lévy movements were found to correlate with areas of low prey availability and Brownian (i.e. exponential) movements with areas of higher prey availability. While the aforementioned studies used proxies for prey availability (such as Chlorophyll 'a' concentration for primary productivity) a more recent study by Humphries *et al.* (2012) used albatross prey capture events, recorded by stomach temperature loggers, to estimate actual prey consumption during Lévy and Brownian movements; results confirmed LFF predictions providing further, more robust, support for the hypothesis.

In general, however, thorough and controlled empirical tests of the Lévy flight foraging hypothesis (LFF) are very difficult to perform for a variety of reasons. Field tests require free-ranging animals to be tagged to record their movements which can result in understandably limited information (i.e. often just a time series of swimming depth and water temperature). In addition, there can be no control over prey field densities and little direct evidence concerning what particular activity the animal is actually engaged in at any point in time. Under controlled conditions in the laboratory there are logistical constraints: enclosures or aquaria generally restrict the animal's movements to a large degree and natural searching and foraging behaviour can be affected by required feeding schedules (Wearmouth et al., 2014). Therefore field studies are limited to natural experiments which are inevitably time consuming and expensive (e.g. Kohler and Turner, 2001; Priede, 1984; Sims and Merrett, 1997), while laboratory studies are

limited to smaller organisms (e.g. Bartumeus et al., 2003; Reynolds and Frye, 2007) with necessarily much simpler behaviour. Consequently, as foraging models in more than one dimension are analytically intractable (Hartig et al., 2011), computer simulation studies have been used extensively to test many different aspects of the LFF hypothesis (e.g. Bartumeus et al., 2002; Benhamou, 2007; Reynolds and Bartumeus, 2009; Viswanathan et al., 1999; Viswanathan et al., 2000).

However, there remains a distinct need for a thorough test of the theoretical results because many published studies have come from experiments undertaken by collaborating researchers (see Viswanathan et al., 2011), possibly using the same testing framework and simulation code. While simulations have been undertaken that confirm the results of Viswanathan and co-workers, other researchers, setting out to test the same general ideas, have found conflicting results with different, albeit less comprehensive simulations. Hence some doubts have been expressed about whether a Lévy walk search does indeed confer the advantages proposed in earlier studies. For example, in a recent paper James *et al.* (2011) replicated the simulation performed as part of an empirical study by Sims *et al.* (2008) in which it was demonstrated that, for a 'blind' forager in a sparse prey environment, Lévy movements conferred an advantage over simple, uniform, random movements approximating normal Brownian diffusion. The advantage was found to be greatest when the prey field had a Lévy, rather than a uniform distribution. The results obtained by James *et al*. (2011) appear to be at odds with those found by Sims *et al.*(2008), concluding instead that foraging efficiency (which they define as the proportion of available biomass consumed per unit area searched) eventually converges to a constant value regardless of the movement pattern employed by the forager. The results are summarised in their figure 4 (James et al., 2011), which presents a running mean for each of the four simulation scenarios studied. Further, in many studies, one dimensional (1D) models have been used to explore the Lévy flight foraging (LFF) hypothesis because they are analytically more tractable (Plank and James, 2008). Generally, such investigations show ballistic searches outperform Lévy walks. However, in 1D it is trivial to realise that a ballistic strategy will outperform everything else, as path reversals ('backtracking') in 1D cover exactly the same ground and will only find a target more quickly if the wrong direction was originally selected. However, in 2D or 3D the situation is more complex as backtracking most often will not cover exactly the same area. Therefore, there is some doubt as to whether a 1D model necessarily captures all the subtleties of a full 2D foraging scenario.

There has been, therefore, controversy over the theoretical advantages of Lévy walk search strategies and the Lévy flight foraging hypothesis (Buchanan, 2008), with contradictory papers publishing mathematical analysis and simulation results (e.g. Benhamou, 2007; Oshanin et al., 2009; Plank and James, 2008; Plank and Codling, 2009; Raposo et al., 2003; Reynolds and Bartumeus, 2009; Reynolds and Rhodes, 2009), yet burgeoning empirical evidence of Lévy patterns in recorded animal movements (de Jager et al., 2011; Humphries et al., 2012; Humphries et al., 2010; López-López et al., 2013; Sims et al., 2012; Sims et al., 2008). Consequently, it seems appropriate to present a thorough exploration of Lévy walks as a foraging strategy with the aim of clarifying the conditions under which a Lévy walk provides an advantageous search pattern and gaining a better understanding of when such patterns might be observed in free-ranging animals. Therefore, this study will present results from a robust and straightforward simulation model that allows the efficiency of different foraging patterns, in the form of random walks [e.g. Lévy, exponential (Brownian), ballistic], to be compared under different prey field distributions and foraging scenarios (e.g. destructive, non-destructive). The simulation model is, very much, a null model of foraging/searching; the only difference being

considered between the foragers is the move step-length distribution of the random walk. It is recognised that interaction with the environment, through direct physical encounters and distance senses, such as olfaction and vision, play an important role in the foraging behaviour of the majority of real organisms. However, there are times, especially for pelagic marine predators for example, when new prey patches are beyond sensory range and have a highly dynamic character obviating memory which, therefore, necessitates a random search. Such conditions would also have prevailed in the ancient past, when sensory abilities were more primitive and limited. Under these conditions an optimised, basal, search mode might confer a significant advantage.

Foraging efficiency, in terms of resources obtained for effort expended, is clearly an important biological quantity and is the principal interest of the simulation studies presented here. There is however a further consideration that is of great importance to individual animals, namely the experienced heterogeneity of resource availability. Regardless of the actual abundance of available resources the foraging behaviour of an individual animal has not only to allow the animal to locate sufficient mean resources in a given time, but must do so in a way that avoids long periods without food which increase the likelihood of starvation. Therefore, in the simulation environment used here, resource heterogeneity was studied directly for individual foragers by considering a run of interpolated move steps, performed between each encounter with prey, to represent a single famine period. At the end of each foraging run the famine period duration was recorded. Shorter famine durations indicate higher resource homogeneity, as feeding events must occur more frequently. It was expected that the famine duration would be lower for the most efficient foragers with the optimal foragers therefore having a further advantage in that they would experience a more homogenous prey environment and would, therefore, be less likely to suffer starvation.

Finally, in an attempt to gain a better understanding of how forager movement patterns result in different foraging efficiencies, a path structure analysis was performed on example paths from the simulations in this study. The analysis computes metrics, such as area explored and the extent of over-sampling, that help to characterise the properties of the forager's paths and to build an improved, mechanistic understanding of why, and under what circumstances, some movement patterns are so much more successful than others.

2.   Methods

2.1.   The foraging simulator

For this study a new computer program was developed which more realistically simulates a 2D forager than the study by Sims *et al.* (2008), which was designed specifically to investigate diving behaviour in marine pelagic predators. The simulation comprises a study arena (a 2D grid of cells) into which prey patches can be 'pasted' to generate a prey field into which virtual foragers will be released. The number, distribution and density of prey patches and the overall available biomass can all be specified and can be saved for future reuse, allowing multiple simulations to use exactly the same prey field, thereby controlling for prey field variability in the results.

A single foraging run involves the generation of a random walk through the study arena, in continuous space, with turn angles being drawn from a uniform distribution on the interval $[0,2\pi]$ radians and move steps being drawn from a distribution, such as an exponential or a truncated Pareto (a truncated power-law). Each move step is interpolated (i.e. moved

incrementally) across the prey-field grid with any prey encountered being recorded and, optionally, consumed (i.e. in 'destructive' foraging scenarios). If at any point the boundary is encountered the move is reflected, i.e. the forager is contained within the arena (see Figure 1).

The detection radius of the forager is 1 unit (i.e. the scale of a single grid cell) and is implemented such that the forager is aware only of the biomass status of the cell over which it is located at the end of each interpolated step. If biomass is being consumed (i.e. the destructive scenario) then all biomass in the grid cell is consumed.
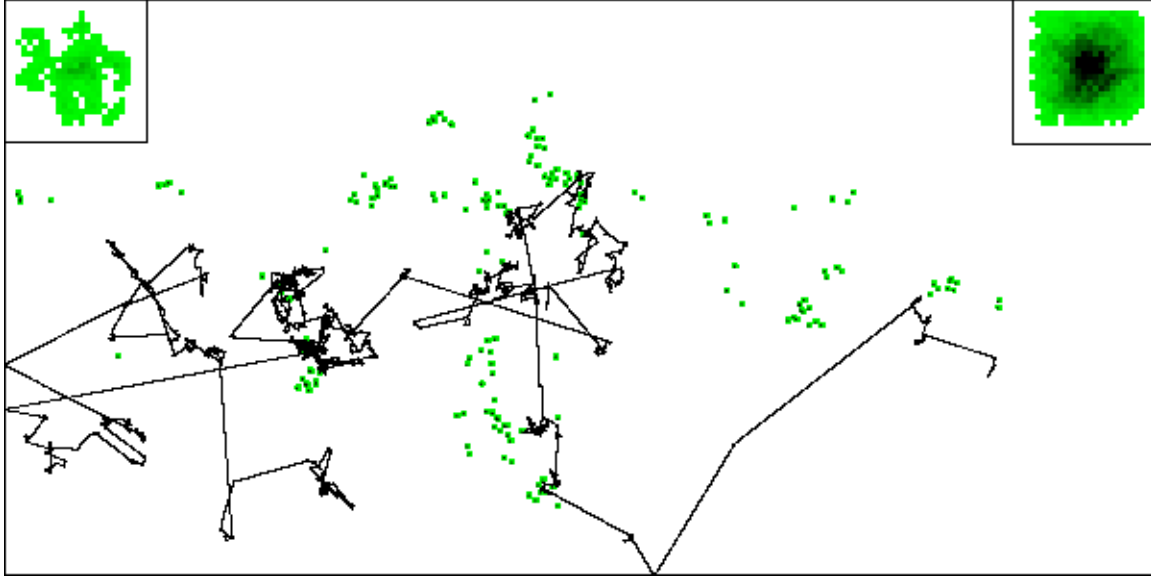

Figure 1: An example foraging run
A truncated Pareto foraging run with x_{min} = 1, μ = 2.0, x_{max} = 2500 and path length = 50,000. The path can be seen to be reflected from the boundary of the arena. Abundant, Lévy distributed prey patches are shown in green. Inset upper left shows a sparse prey patch (biomass = 600), inset upper right shows a dense prey patch (biomass = 6000).

2.1.1   Prey fields

The environment comprised an arena of 5000 x 2500 cells where each cell contained an integer value representing a quantity of prey (biomass), zero being none. Prey was distributed as patches whereby each patch consisted of a small, contiguous group of cells with biomass higher in the central cells and reducing towards the edges, as can be seen in Figure 1. When placing patches, if a patch overlapped an existing patch, the biomass values were added.

The purpose of using patches was to simulate a more realistic environment, particularly when considering marine pelagic predators, where the prey could be shoals of small fish or patches of zooplankton. As an example, the sparse uniform prey field had a total biomass of 6000 units distributed as 10 patches giving a total of 1876 populated cells with each patch enclosed within a 20 x 20 area. This gives a mean biomass density of 0.00048 units per cell and a populated cell proportion of 0.015%. In total, five prey field densities with increasing abundances were used (sparse and Abundant 1-4). Two prey field distributions were considered, uniform and Lévy. In the uniform prey field, prey patches are positioned using uniform random numbers to determine *x* and *y* coordinates. The Lévy prey field was constructed with the first patch being positioned using uniform random numbers for the *x* and *y* coordinates and subsequent patches then located relative to the first patch by calculating a vector (from a truncated Pareto

distribution, with parameters x_{min} = 25, μ = 2.0, x_{max} = 5000) and a uniform turning angle; periodic boundary conditions were observed. The resulting pattern has been referred to as a Lévy 'dust' (Miramontes et al., 2012). Details of all prey field distributions are given in Table 1; the abundant 1, Lévy prey field is illustrated in Figure 1.

Table 1: Details of prey field densities and distributions

Prey field	Total biomass	No of populated cells	Patch biomass	Number of patches	% of populated cells	Average biomass per cell
Sparse	6.00E+03	1876	600	10	0.0150	4.80E-04
Sparse Levy	6.00E+03	1945	600	10	0.0156	4.80E-04
Abundant 1	9.96E+05	61144	6000	166	0.4892	7.97E-02
Abundant 1 Lévy	9.96E+05	59190	6000	166	0.4735	7.97E-02
Abundant 2	3.00E+07	1716802	6000	5000	13.7344	2.40E+00
Abundant 2 Lévy	3.00E+07	1234552	6000	5000	9.8764	2.40E+00
Abundant 3	1.20E+08	5589274	6000	20000	44.7142	9.60E+00
Abundant 3 Lévy	1.20E+08	4144461	6000	20000	33.1557	9.60E+00
Abundant 4	2.40E+08	8666656	6000	40000	69.3325	19.2E+00
Abundant 4 Lévy	2.40E+08	8262186	6000	40000	66.0975	19.2E+00

2.1.2 Foraging strategies

Six different foraging strategies (i.e. move step-length distributions) were investigated as follows: (1) truncated Pareto (TP)X_{min}= 1.0, μ = 1.5, X_{max}= 2500 (TP1.5); (2) as (1) but with μ =2.0, the hypothetically optimal strategy (TP2.0); (3) TP as (1) but with μ = 2.5 (TP2.5); (4) Exponential with X_{min}= 1.0, λ = 0.148 (E); (5) Ballistic (B); (6) Composite Brownian (CB). The exponential foraging strategy was configured to give a mean step-length close to 8, roughly equivalent to the TP2.0. The composite Brownian forager used a 2-exponential distribution with parameters determined by fitting composite exponential distributions to a simulated TP2.0 dataset using R code provided by Jansen *et al*. (2012). Consequently this distribution was finely tuned to the TP2.0 distribution and effectively mimicked it. In some previous simulation studies, composite Brownian random walks have been modelled using an active switch between two exponential distributions, representing either searching or patch exploitation (e.g. Benhamou, 2007). However, the active switch involves sensing and responding to the prey field. We considered this would represent a behavioural response that might provide an advantage to the CB forager over the other, more simply modelled foragers. Consequently the CB forager used here is modelled in the same way as the other foragers, as a straightforward statistical distribution of step-lengths. Composite Brownian (CB, or composite exponential) random walks have been considered by some to be strong alternative models to Lévy walks (Jansen et al., 2012; Reynolds, 2012), however there is conflicting evidence for this (de Jager et al., 2012; Reynolds, 2009; Reynolds, 2013). It was therefore of interest to see how a CB forager would compare to the TP2.0 forager, on which the distribution is based. It should be noted, however, that with sufficient component distributions a CB can be made to fit very closely any Lévy or exponential distribution (Reynolds, 2013), in a manner analogous to fitting a high order polynomial and not dissimilar to the way a complex waveform can be described by composite sine waves determined through a fast Fourier transform. Consequently there is some doubt as to the biological usefulness of these distributions (de Jager et al., 2012).

Note that in all these simulations a truncated Pareto rather than a pure power-law was used for the Lévy foragers. The reasons for this are twofold; firstly pure power-laws are rare in empirical data (Humphries et al., 2010) and therefore using truncated power-law distributions of move step-lengths here makes this work more relevant to empirical field studies; secondly the simulation environment is bounded to dimensions of 5000 x 2500 and pure power-laws would cause excessively long steps that would frequently exceed these boundaries. The accepted range of exponents (μ) for a TP distribution is $1.0 < \mu \leq 3.0$. We could, therefore have used any exponents in this range. However, the values of 1.0 and 3.0 represent the extremes and so values of 1.5, 2.0 and 2.5 were selected to cover a sufficient span of the range without involving behaviours that might be more marginal.

2.1.3   Simulation scenarios

The simulations performed here considered four foraging scenarios: S1: non-destructive foraging, where prey is not consumed and prey patches are therefore 'revisitable'; S2: destructive foraging, where prey patches are depleted; S3: prey-targeting, whereby, on encountering a prey-field cell containing biomass, the current move step is halted (i.e. truncated) and a new move step is selected; S4: both destructive foraging and prey-targeting. The first scenario represents a true null model, where there is no interaction with the prey field, and patches are not depleted.

In the second scenario there is no responsive interaction with the prey field, however prey encountered is consumed and, therefore, prey patches are depleted as the simulation proceeds. This implementation differs from some previous studies, where prey is removed, but becomes available at a later time. The LFF hypothesis would predict that this scenario would favour foragers with patch-leaving characteristics (e.g. ballistic, TP1.5).

The final two scenarios most closely replicate the foraging models presented by Viswanathan *et al*. (1999) by including prey-targeting. It was with this scenario that the optimality of a TP2.0 forager was demonstrated (Viswanathan et al., 1999) and this finding would be expected here. Note however, that as the detection radius of the foragers used here is 1 unit, the forager does not, on locating a target, need to move to the target location, as in the model of Viswanathan, since it is already in that position.

2.1.4   The simulations

In this study 10^5 foraging runs are performed for each simulation. Different step-length distributions result in very different overall path lengths; for example, 5000 steps of a truncated Pareto (TP) distribution with x_{min}= 1, x_{max}= 2500 and μ = 1.5 has a path length $\approx$250,000, compared to a path length $\approx$14,500 with μ = 2.5. Initial investigations, presented below, demonstrated that even with results expressed as biomass consumed per unit distance travelled, the discrepancy in path lengths significantly affects the results and, therefore, the majority of simulations presented here use a maximum path length of 50,000 (approximately equivalent to 5000 steps of a TP with μ = 2.0), rather than a specified number of move steps. In summary, simulations using all combinations of prey field distribution and density were performed with all foragers to test which foraging strategy performed best under each of the foraging scenarios and, consequently, to test the predictions of the LFF hypothesis. In particular, the effects of destructive *vs* non-destructive foraging, prey-targeting and increasing prey abundance were investigated.

2.2. Path structure analysis

To characterise the paths produced by the foragers studied here, a path structure analysis was used with 1000 example paths from each forager. To perform the analysis a 2D grid was laid over each path and for each grid cell a count was made of the number of times the path crossed, or remained within, the cell (i.e. an occupancy value). Many small steps might be performed that do not move the forager outside of the current cell, resulting in a high occupancy (or oversampling) value, while a single long step could traverse several cells, producing an occupancy count of 1 in each cell through which the step traverses. A fast voxel traversal algorithm (Amanatides and Woo, 1987) was used to determine which cells were visited. From these counts it was possible to calculate the following metrics: (i) the total area of the extent of the path, being the area of the path's bounding box; (ii) the % of the bounded area searched, being the % of cells visited at least once; (iii) mean cell occupancy, which is a measure of oversampling. Note that as a path resulting from the ballistic forager is essentially a straight line, the grid occupancy analysis provides no useful information, consequently ballistic paths were not analysed in this way. The grid cell scale, and consequently the overall size of the grid, was determined automatically to produce a grid of, on average, around 60x60 cells; the actual size and shape of the grid was determined by the bounding box of the track. This produced a grid for each path that was appropriately scaled to the size of the track allowing the path structure to dominate the analysis, rather than the path scale.

3. Results

3.1. Sparse prey field investigations

Initial investigations performed using the simplest scenario of non-destructive foraging, the sparse uniform prey field and with foraging runs limited to 5000 move steps, appeared to support the contention by James *et al*. (2011) that all foragers perform equally, with performance converging after about 10^4 runs to a similar value. Closer inspection of the running mean plot (Figure 2a), however, shows that there is considerable variability and that the forager with the greatest variability is that with the shortest overall path length i.e. the TP2.5 forager (Figure 2b), and *vice versa*, i.e. the TP1.5 forager has least variability and appears to have stabilised. An examination of the output from the simulations revealed that the number of successful foraging runs (i.e. runs that found > 0 biomass) was greatest in foragers with longer overall path lengths (such as the TP1.5), suggesting that the increased sampling of the prey field, resulting from the longer path, improved overall foraging success rates (see Table 2). To test this contention, the simulations were re-run using a path length limited to 5×10^4 (slightly longer than the TP2.0 step-limited path length) rather than being limited to 5000 steps. As can be seen in Figure 3, there is now significantly less variability and there is noticeable divergence in the performance of the foragers with differences being significant at $p < 0.001$ (Kruskal-Wallis One Way Analysis of Variance on Ranks). However, variability was still considerable and, again, inspection of the output (given in Table 2) revealed that there were still marked differences in the number of successful foraging runs. A further set of simulations, using a longer path length of 5×10^5, produced much clearer and more stable results (Figure 3, Table 2). From these more reliable results it was clear that the TP2.5 forager was the most efficient, by 4.69% in the uniform and 3.46% in the Lévy prey field. Foraging efficiency in this scenario is related to step-length with those with longer step lengths, and therefore a greater likelihood of leaving a patch,

being the least efficient. Differences were significant at $p < 0.001$ (Kruskal-Wallis One Way Analysis of Variance on Ranks) and all pair-wise differences significant at $p < 0.05$ (Tukey test).

Investigations into convergence with the other scenarios in the sparse prey field, however, produced different results, with the outcomes clearly differentiating and stabilising in both the step-limited simulations (not shown) and those with paths limited to lengths of just 5×10^4 (Figure 4). All remaining simulations therefore used path lengths limited to 5×10^4. All results are given in full in Table 3.

3.2.   Destructive foraging

In scenario 2, the destructive, non-targeted scenario, it is the ballistic and TP1.5 foragers (i.e. those with the greatest patch-leaving propensity) that perform best, as predicted by the LFF hypothesis, with the TP2.5 and exponential foragers performing worst. With destructive foraging there now seems to be an advantage in leaving a patch and exploring further afield; the TP 1.5 forager had more frequent long relocations than the other foragers and consequently spent less time in any given patch. The poor performance of the TP 2.5 and exponential foragers adds weight to this suggestion as these foragers had fewer frequent long relocations and therefore tended to remain in a more localised area, which would then become depleted. Performance of the Lévy foragers is the opposite of the non-destructive scenario. The difference between the TP 2.0 and the exponential forager was 9.66% (Kruskal-Wallis One Way Analysis of Variance on Ranks; $p < 0.001$), and similar to the difference found by Sims *et al.* (2008), which supports the contention that that simulation was consistent with the destructive foraging scenario.

3.3.   The effect of prey-targeting

In the targeted scenarios (S3 and S4), however, the TP 2.0 forager clearly outperformed the others by a substantial margin: 2.28 and 2.14 times greater than the exponential forager in the uniform prey field for the non- and destructive scenarios respectively (see Table 3, Kruskal-Wallis One Way Analysis of Variance on Ranks, $p < 0.001$ in all cases). In the Lévy-distributed prey field the TP2.0 forager outperformed the ballistic forager by 2.59 times and the exponential forager by 2.46 times in scenarios 3 and 4 respectively. Interestingly all the Lévy foragers were found to perform better than all but the CB forager in both the non- and destructive scenarios, with the TP2.5 outperforming the TP1.5 in the non-destructive scenario and the TP1.5 outperforming the TP2.5 in the destructive scenario, as predicted by the LFF.

The success of the TP2.0 forager was in fact much greater than expected, given that the advantage conferred by prey-targeting (in terms of the exploitation of a patch once encountered) was the same regardless of the movement pattern of the forager. Once a patch was encountered, and a step halted, subsequent steps often led immediately to another cell containing biomass, causing a further halt and new step. Because prey lies within only one or two cells of the present location it made no difference what distribution the move step was drawn from and therefore all foragers gained the same advantage once a prey patch was encountered. Once within a patch, therefore, all foragers would tend to proceed by simple Brownian diffusion until they left the patch. A simplified example of such a path is shown in Figure 5. The most likely explanation of the much greater success of the TP2.0 forager, therefore, was that the forager encountered, and was able to exploit, more new prey patches

than the other foragers. Results are summarised in Figure 6a. The CB forager performed as expected, with efficiencies in each scenario that were slightly less than the TP2.0 forager.

In the sparse, Lévy-distributed prey field (Figure 6b), the results from all foragers and scenarios are comparable with the uniform prey field results (Figure 6a), however the Lévy foragers perform even better than in the uniform field, confirming the finding of Sims *et al.* (2008).

3.4.   The effect of increasing prey abundance

A further contention that has been discussed in many studies is that Lévy foraging is only significantly advantageous when prey are scarce (Bartumeus et al., 2005; Bartumeus et al., 2002; James et al., 2011; Reynolds and Bartumeus, 2009; Viswanathan et al., 1999). Therefore, to investigate differences in foraging efficiency caused by prey field abundance, the simulations were repeated using an abundant prey field with 10^6 biomass units distributed as 166 patches with a total of 61,144 populated cells (see Table 1). This gave a mean biomass density of 0.00489 units per cell and a populated cell proportion of 0.489% [as discussed later, a biologically realistic value, based on plankton densities, might be much lower at around 0.26% (Sims, 1999)]. This prey field has the same density as that used by James *et al.* (2011). The expectation for these simulations was that the exponential and uniform strategies would perform as well as the Lévy search (TP) strategies, as suggested by Viswanathan *et al.* (2002). Contrary to expectations, however, the relative performance of the foragers in the abundant prey fields was similar to that of the sparse prey fields, as shown in Figure 6c and d. The principal difference was that the TP2.0 forager now performed even better, particularly in the Lévy prey field, where the efficiency in scenarios 3 and 4 increased to 2.84 and 3.10 times better than the worst forager, which in both abundant prey fields was the ballistic, rather than the exponential.

To investigate the possibility that the prey field being used was simply not abundant enough to provide sufficient difference with the sparse prey field to separate the foraging efficiencies, as expected, three further, increasingly abundant prey fields were tested (see Table 1). The results are given in Figure 6e-j, Table 4 and Table 5. In scenario 1, as abundance increases, the differences in relative performance remain much the same, with the TP2.5 advantage being around 5.8% in both uniform and Lévy prey fields. In scenario 2 the relative efficiencies are, again, virtually unchanged. However, in the targeted scenarios, it is clear that as the abundance increases further the advantage of the TP2.0 forager reduces. However, the Lévy foragers still clearly outperformed the exponential and ballistic foragers. In the Lévy prey fields the TP2.0 performance advantage was less noticeably reduced with increasing prey abundance. Because the Lévy prey field has greater heterogeneity, prey abundance can increase without a concomitant increase in the number of prey encounters, consequently it was likely that the abundance level at which TP2.0 performance would begin to decline would be higher in a Lévy prey field. The results from the abundance investigations from scenario 4 are further summarised in Figure 7 where it is clear that as abundance increases the foraging efficiencies converge, suggesting that at exceptionally high densities the foraging strategy employed makes little difference.

The performance of the CB forager is particularly interesting. In the majority of prey fields and scenarios the performance is slightly below that of the TP2.0 forager. This was as expected, given that the CB forager is essentially tuned to the step-length distribution of the TP2.0. However, in the Abundant 2 uniform and in both Abundant 3 prey fields, in the two targeted scenarios, the CB forager outperforms the TP2.0 forager by as much as 4.8%. Interestingly,

however, this advantage is lost in the most abundant prey fields (Abundant 4), with the TP2.0 forager again being the most efficient, now just outperforming the CB forager by 0.83% and 1.67% in the uniform and Lévy prey fields respectively.

3.5.   *Feast and famine*

Recorded famine period durations were analysed for all foragers in the Abundant 1 uniform and Abundant 1 Lévy-distributed prey fields in scenarios 3 and 4 (non- and destructive foraging with prey-targeting). Abundant prey fields were used to ensure sufficient encounters for reliable statistics. Results are shown in Figure 8 (and Table 6) where it is clear that, as expected, the TP2.0 forager experienced the shortest famine durations in all scenarios and prey fields. Importantly, the TP1.5 and TP2.0 foragers experienced the lowest proportion of long famine periods. In all cases the exponential forager had the longest durations. In general the famine duration results reflect the foraging efficiencies, however, in the Lévy prey field the TP2.5, Exponential and CB foragers experience a much higher proportion of very long famine periods.

3.6.   *Path structure analysis*

 The results of the analysis are summarised in Figure 9 and examples of the analysis output, illustrating the essential structure of example paths produced by each forager, are shown in Figure 10. Firstly, it was confirmed that the grids generated to perform the analysis were of a similar scale (Figure 9a), with the mean grid having 3400 cells. The extent of the path (Figure 9b), i.e. the area of the bounding box of the path, was, as expected, greatest for the TP1.5 forager and least for the exponential forager. The CB forager, also as expected, covered much the same area as the TP2.0, on which it was modelled. Percentage of the bounded area searched (i.e. the % of cells visited at least once, Figure 9c) was highest in the exponential and CB foragers, as expected from the normal diffusive character of these foragers; a Brownian random walk covers a smaller area than a super-diffusive random walk, but is more intensive. Oversampling values (Figure 9d) were as expected for the Lévy foragers, with the TP1.5 having the lowest and the TP2.5 having the highest value, reflecting the area searched (higher areas resulting in lower oversampling). However, unexpectedly, the exponential forager proved to have a much lower oversampling value than the TP2.5 forager, having a value very similar to the TP2.0 forager. The CB forager performed as expected, being similar to the TP2.0.

4.   Conclusions

It is clear from the simulations performed here that foraging efficiencies do not converge on a single outcome regardless of foraging strategy, as suggested by James *et al.*(2011), but are in fact highly divergent. In the more biologically realistic scenarios, that include prey-targeting, and in the less abundant prey fields, which require a search strategy, the TP2.0 forager is most efficient, while in other scenarios and in some extremely abundant prey fields, other foraging strategies can perform slightly better. An important finding of the current study is that the TP2.0 search strategy shows persistent stability in its optimal performance across a much broader set of environmental conditions than previously identified compared to many other types of search strategies. Thus, it appears the TP2.0 Lévy walk strategy determined by Viswanathan et al. (1999) to be optimal when prey are sparse but can be targeted, is in fact not a limiting case. We show that the TP2.0 Lévy strategy is optimal for foraging in natural-like environments varying greatly in resource density, distribution and patch revisitability. As such it is arguably a general

'rule of thumb' for efficient searching in heterogeneous natural environments when an organism can target prey when encountered within its sensory detection range, but has no or only an incomplete knowledge of where resources are located beyond their sensory range.

4.1.   Scenario 1, the null model

The relative efficiencies of the foragers under this scenario were remarkably consistent. In all cases the TP2.5 forager was the most successful by as much as 6.2%, with either the TP1.5 or ballistic the least; in fact success here is closely and inversely related to the mean step-length. It might be that the lower patch-leaving behaviour inherent in the TP2.5 forager ensures that when a patch is encountered it is exploited more completely than with the other foragers; however it is still somewhat surprising that this is sufficient to balance the much lower likelihood of patch location of the other foragers. It is also noteworthy that the TP2.5 forager performs so much better than the exponential forager, given that Lévy movements with higher exponents tend towards a more Brownian-like pattern.

4.2.   The stability of destructive or targeted foraging

One of the most striking results from these investigations is the robust stability of the destructive and targeted foraging scenarios, all of which settle to the final outcome after fewer simulation runs, and with shorter path lengths, than scenario 1. In the destructive non-targeted scenario the ballistic, and most ballistic-like Lévy forager, the TP1.5, were always the most efficient, as predicted by the more rapid patch-leaving behaviour that these foragers will exhibit. The advantage was highly significant and consistent at around 30% better than the worst performer (TP2.5). Destructive foraging is biologically realistic since fish shoals and plankton patches may become functionally depleted eventually (i.e. a forager is unable to feed at net energetic benefit since any remaining individuals would not yield sufficient energy to cover the costs of its collection; Sims, 1999). This result therefore confirms one of the Lévy-flight foraging hypothesis' predictions: that with destructive foraging Lévy foragers with low exponents are most efficient (Bartumeus et al., 2005). It is interesting to note that in this scenario the TP2.5 forager was always the least efficient. Comparing a typical TP2.5 path (which is more Brownian-like than the other Lévy foragers) with an exponential path reveals the TP2.5 to have significantly more long relocations, but, nonetheless, to cover considerably less of the prey field than the exponential forager (as shown in Figure 11). Using ImageJ (Rasband, 1997-2012) to compute a histogram from each image gives a value that represents the proportion of the image covered (i.e. the proportion of black pixels, see Figure 11). The results show that the TP2.5 forager covers 2.0%, while the exponential forager covers 6.0%, confirming that the TP2.5 forager would encounter less biomass and have a lower foraging efficiency.

It is interesting that incorporating destructive foraging reduces stochastic variability sufficiently for the performance of the foragers to settle reasonably quickly (i.e. within 3.5×10^4 simulations). As some studies have performed only 10^4 simulations it seems likely that previously reported results (e.g. James et al., 2011) show foragers that have not reached efficiency stability. As a final comment on the destructive non-targeted scenario it is interesting that in all simulations the TP2.0 forager outperforms the exponential forager by between 9.21% and 11.24%, a figure that is in close agreement with the result found by Sims *et al*. (2008), confirming that the simulations performed in that study were perhaps closer to a destructive foraging scenario because patches could not be revisited.

4.3. The importance of prey-targeting

In the original studies by Viswanathan (1999; 2000) the foraging model included prey-targeting. The results presented here make it very clear, firstly, that with prey-targeting the TP2.0 forager consistently emerges as the most efficient searcher and, secondly, that the relative performance of the other foragers is also strongly conserved. Overall the foraging efficiencies shown by the TP2.0 forager and the relative performances of the other foragers were robust to prey field abundance, prey field distribution, and prey patch revisitability, indicating a Lévy walk with $\mu = 2$ is optimal over a much wider range of environment types than previously demonstrated. It is worth reiterating that the destructive scenario used here differs from that of Viswanathan *et al.* (1999) where solitary prey items were used. In our study, much of a prey patch remained when a single item (grid cell) was destructively consumed, which is perhaps more comparable to natural prey patches. As mentioned in the results it is somewhat surprising that prey-targeting should produce such a stable outcome, given that the advantage gained when a patch is encountered is the same for all foragers (Figure 5).

Prey-targeting adds a further dimension to the simulation in that it represents a feedback response from the prey to the forager in the form of a behavioural switch; on encountering prey the move step is terminated and a new step is started. With a power-law distribution of move-steps subsequent steps are likely to be small, representing a slowing of movement, or increased tortuosity. The virtual foragers in this study cannot alter their move-step distribution in order to respond to prey-fields with changing densities, a behaviour that would be expected in real foragers, with switching to area-restricted search being commonly observed when prey-field densities are greater (Hamer et al., 2009; Pinaud and Weimerskirch, 2005; Sims and Quayle, 1998). It is all the more interesting, therefore, that prey-targeting is so important in differentiating between the different foragers tested here.

4.4. Prey abundance is less important than first thought

In the non-targeted scenarios prey abundance made little difference to the relative foraging efficiencies. In the targeted scenarios, however, as prey field abundance was increased the difference between the foragers reduced as predicted. However the level of abundance required for parity was much higher than expected based on previous studies that concluded Lévy foraging is only more efficient when prey is sparse (Bartumeus et al., 2002; Viswanathan et al., 1999; Viswanathan et al., 2000; Viswanathan et al., 2002). With increasing prey abundance searching becomes less important than patch exploitation. The success of the composite Brownian forager in the Abundant 2 and 3 prey fields most likely, therefore, results from more efficient patch exploitation than the TP2.0 forager, while the success of the TP2.0 forager in the sparser prey fields results from more efficient location of distant patches. It is interesting that the slight advantage gained by the CB forager is lost when the prey field abundance is increased further. This suggests that the CB forager is less resilient to changes in prey field density than the TP2.0 forager. If an organism was to adopt a single strategy, then the TP2.0 would be the most successful over a broader range of environments. In the mathematical analysis by Viswanathan *et al*. (2000) the conclusion regarding prey abundance - i.e. that Brownian movement is sufficiently efficient - is applicable when the abundance is such that the distance to the next prey item is less than or equal to the radius of detection (described in the paper as $\lambda \leq r_v$). The radius of detection used in this simulation is set to 1 unit, the most conservative value, and clearly it is not possible to have prey abundance set to such a density without all cells being populated. It is worth noting that even the level of prey abundance in these simulations

represents a very dense concentration. For example, if the scale of the simulation here represented a 1cm grid and the biomass represented zooplankton, such as copepods (e.g. *Calanus helgolandicus*), with each unit of biomass comprising a single copepod, then the prey density in the most abundant prey field, which had an average density of 19.2 units per cell, would be equivalent to 19,200,000 copepods m^{-3}. Even at this density in the simulation parity between the model foragers was not quite achieved. So how do resource fields in the natural environment compare with the simulated density? One field measurement of zooplankton density, recorded by Sims (1999; based on total zooplankters) was found to be around 2600 m^{-3}. This density was the highest reported in that study and agrees well with other studies that put maximum regional concentrations at around 10^3 individuals m^{-3} (Pendleton et al., 2009), yet is much lower than the density at which a significant difference between the foragers was still found here. While much higher plankton densities have been recorded on scales of < 1m, associated with the sea surface boundary (Gallager et al., 1996) these represent micro-scale aggregations and are not representative of the patch as a whole. At a larger scale such densities could represent fish within a shoal as opposed to the distribution of shoals within the ocean. The important point here is that at the very high levels of prey field density in our simulation, random searches are no longer required and the most efficient movement patterns will be those associated with patch exploitation, rather than patch location. Thus, large, oceanic predators, such as blue sharks (*Prionace glauca*) are likely to experience sparse prey fields and will benefit from optimal Lévy search strategies, whilst terrestrial herbivores, grazing in abundant patches, benefit most from patch exploitation strategies, such as composite Brownian walks (sometimes termed multi-modal walks in the ecology literature).

4.5. *Feast and famine*

Heterogeneity in prey availability requires energetically expensive adaptations to deal with the resulting periods of feast or famine, such as excess digestive capacity (Armstrong and Schindler, 2011) and lipid storage (Arrington et al., 2006). Piscivores in particular have been found to have empty stomachs more often than other feeding guilds (Arrington et al., 2002) and, while difficult to observe in the wild (although stomach loggers are becoming available for sharks: Papastamatiou et al., 2007), a feast and famine feeding pattern has been observed in captive seven-gill sharks (*Notorynchus cepedianus*) (Vandykhuizen and Mollet, 1992). In this context a TP2.0 foraging strategy delivers a double benefit; increasing the number of new prey-patch encounters not only increases the quantity of prey available but minimises the time to the next feeding event. Thus, Lévy foraging results in more predictable resources in unpredictable environments. Importantly, the results show that both the TP1.5 and TP2.0 foragers both experience significantly fewer long famine periods than the other foragers, in all cases, but especially in the Lévy distributed prey fields. In the Lévy prey fields, which are considered more biologically realistic, the TP2.5, Exponential and CB foragers experience significantly more long famine periods, placing them at much greater risk of starvation (Faustino et al., 2007). The high performance of the TP1.5 forager is particularly interesting and suggests that while the TP2.0 is theoretically most efficient, natural selection pressures might result in lower observed exponents. Theoretically, Lévy foragers, with a range of exponents, are therefore less likely to starve than exponential or CB foragers, which clearly confers many physiological benefits. These findings make it increasingly likely that movement patterns approximating a Lévy walk would have been naturally selected since the advantages to net energy gain appear very marked.

4.6. Path structure

The aim of the path structure analysis was to gain a more detailed understanding of how different movement patterns, in the form of different move step-length distributions, may lead to differing foraging efficiencies. Several questions arise from the current study that might be addressed with this analysis: for example, why does the TP2.5 forager perform so consistently well in scenario 1, why does the TP2.0 forager outperform by such a significant margin the other foragers in most of the prey-targeting scenarios, and what leads the CB forager to perform better in the very abundant prey fields, yet lose this advantage in the most abundant prey fields?

With reference to the first question, our study identifies a significant difference between the TP2.5 and exponential foragers. Both foragers search similar areas, however, the oversampling value of the TP2.5 forager greatly exceeds that of the exponential forager. This difference is indicative of a fundamental difference in the underlying movement pattern, whereby the TP2.5 forager performs many more very small move steps, thus keeping it within a small area, until a rare, much longer step is performed which takes it well beyond the previous position. This pattern allows the forager to explore a larger overall area, while at the same time focussing most movements on very small areas. By contrast, the exponential forager diffuses more gradually, covering the area more evenly. For the TP2.5 forager in a non-destructive scenario, an encountered patch is more likely thoroughly exploited by the concentrated tortuous movements, while the rare longer relocations find new patches. The exponential forager, however, locates fewer patches and exploits those that are encountered less thoroughly. The TP2.5 characteristic of thoroughly exploiting an area before moving to the next might be what provides the advantage when prey is consumed non-destructively.

The CB path in Figure 10e shows how this forager combines characteristics of both the Lévy and exponential foragers. The overall structure is similar to that of the exponential, but there are more long steps, therefore the CB is more efficient than the exponential at locating new patches, but at the same time it has intensive patch exploitation characteristics. This explains why the CB forager performs well when prey is very abundant, as it is exploitation, rather than searching that becomes advantageous. However, it is not clear why this advantage should be lost when the prey field abundance is increased further.

Insight into why the TP2.0 forager is the most efficient in the majority of prey fields in the targeted scenarios is not aided by the path structure analysis. All the Lévy foragers perform substantially better than the exponential forager under all the targeted scenarios. All combine larger search areas (resulting from long relocations) with strongly focused patch exploitation, as a result of the large number of very small steps. All that can be confirmed is that, in the majority of cases, the TP2.0 strikes an optimal balance of patch location (exploration) and patch exploitation, with the long relocations being rare enough to allow patches to be exploited, but long enough to allow a large area to be explored and new patches to be encountered. The path structure analysis does, however, indicate clearly the fractal self-similarity of the Lévy foraging paths; the scale invariant nature of the resulting searches is clearly advantageous.

4.7. Summary

Even the most biologically realistic scenario presented here falls far short of the behavioural complexity exhibited by an apex predator such as a shark. No account is taken of refined sensory input, memory effects or the sophisticated hunting and foraging behaviour that is ubiquitous

among higher organisms. The foragers presented here are therefore very much a null model of foraging; all that is being studied is how simple, basal movement patterns affect the efficiency of an uninformed random search. It is likely that even nematodes, such as *Caenorhabditis elegans*, by sensing chemical gradients (Ohkubo et al., 2010), have at least some knowledge of their wider resource environment. Nevertheless, it is clear that differences in these simple patterns produce significant differences not only in foraging efficiency but also in experienced prey field homogeneity, which are robust to differences in prey abundance or distribution. The differences are not small; in the Abundant 1, Lévy-distributed prey field the TP2.0 forager has a foraging efficiency > 2 times that of the exponential forager. Given that all that is required for an organism to produce a Lévy movement pattern is a time-fractal activity pattern (Bartumeus and Levin, 2008), which has been observed in even simple animals such as *Drosophila* (Cole, 1995), it seems unlikely that such behaviour would not have been selected for during evolution since adopting Lévy movements optimises foraging in a wide range of environments. In further support of the proposition that Lévy movement could represent an intrinsic, basal movement pattern, a study by de Jager *et al.* (2014) has found evidence for Lévy movements in young mussels (*Mytilus edulis*) during settlement. When the crawling movements were uninterrupted by the presence of conspecifics the resulting movement pattern was Lévy like; however, when moves were more frequently truncated, an exponential pattern emerged.

When studying complex organisms, such as marine vertebrates, these simple movement patterns are only going to be observed on those occasions when the animal is actively engaged in foraging, when information of the location of prey is absent and when other behaviours, such as prey avoidance, migration or response to environmental cues are not dominating the animal's movement. It is therefore to be expected that empirical evidence for these patterns will be relatively rare. There is at the present time burgeoning empirical support for Lévy movement patterns in a range of taxa, including insects (Reynolds and Frye, 2007; Reynolds et al., 2007), dinoflagellates (Bartumeus et al., 2003), marine molluscs (de Jager et al., 2011; de Jager et al., 2014; Seuront et al., 2007), marine turtles, fish and seabirds (Humphries et al., 2013; Sims et al., 2008) and primates (Ramos-Fernandez et al., 2004) including humans (Brown et al., 2007; Gonzalez et al., 2008; Raichlen et al., 2014; Rhee et al., 2008). Perhaps it is expected that Lévy patterns would not be common in terrestrial animals as stable environmental structures (i.e. landscape features, forest trees etc.) provide very persistent clues as to the location of prey or other resources. Nor are they likely to be common among higher vertebrates such as bears, (*Ursus arctos)*, where the animals rely on good spatio-temporal mental maps of resource availability and rarely perform large-scale random searches (Bojarska and Selva, 2012). Therefore, it seems likely that Lévy search patterns should be most common in dynamic environments such as the open sea because resources are often highly sparse and have complex distributions that are transported by tides and currents over widely different spatio-temporal scales. Submerged predators are, therefore, only likely to have an incomplete knowledge of resource location and the detection of such resources at distance (e.g. vision, olfaction) will be limited by the seawater medium compared to terrestrial or aerial environments. Hence, it is unsurprising that, to date, the most robust tests of the Lévy flight foraging hypothesis have come from the study of pelagic open ocean predators. Future empirical studies on a wider range of organisms will provide a more complete picture of the species that exhibit Lévy movement patterns and when and where they are employed. However, as we demonstrate here, the clear and persistent foraging advantages that Lévy walk search patterns confer on model organisms in a very wide range of model environments provides further strong support for the contention that searching movements approximated by Lévy walks should have naturally evolved.
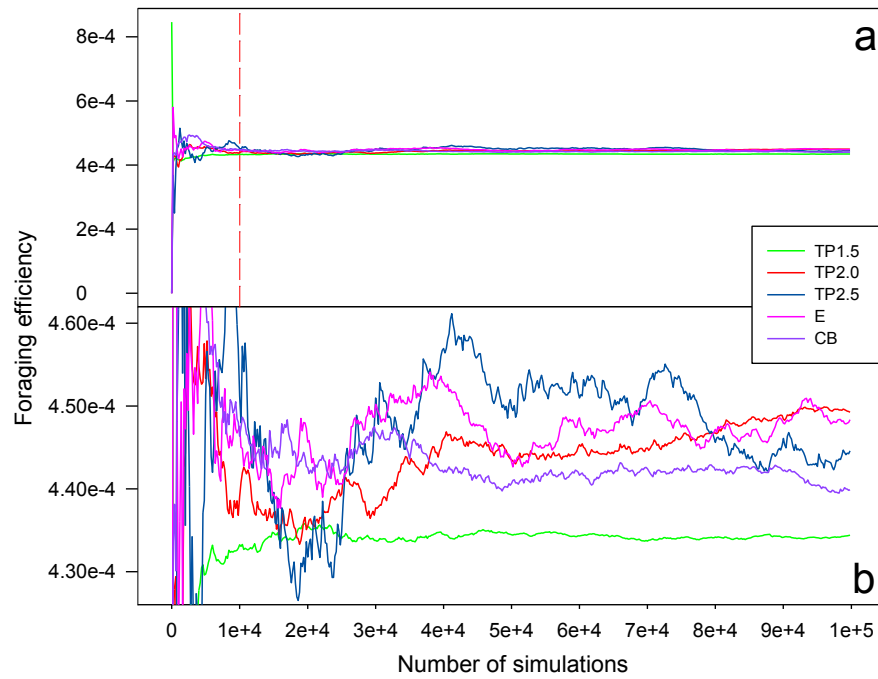
5.   Figures

Figure 2: Convergence of simulation outcomes under scenario 1

   a. Approximate reproduction of the analysis from James *et al.*(2011). The red dashed reference line indicates simulation no. 10^4 which is the limit of the simulations performed by James *et al*. The simulations appear to continue to converge beyond this point. b. At a more appropriate scale, however, there does appear to be some differentiation between the forager's efficiencies, despite the large variances. However, note the low variance of TP1.5, the forager with the longest overall path length, and the very high variance of the TP2.5 forager, with the shortest overall path length. The difference in variance suggests that the overall path length is having an effect of the foraging outcomes, despite efficiency being reported as biomass consumed/path length.
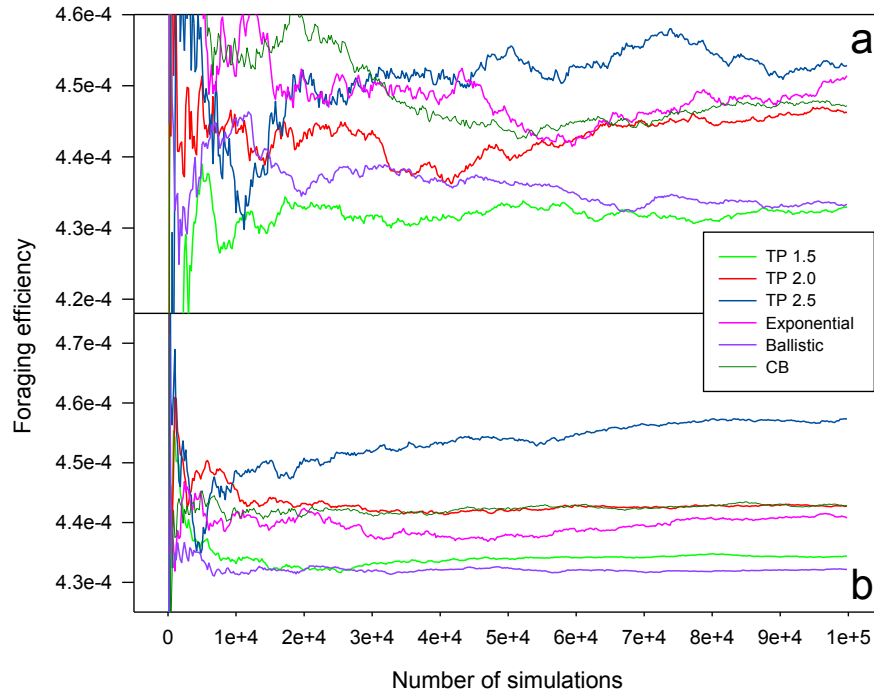
Figure 3: Path limited simulations of scenario 1

(Note that we now include a ballistic forager.) a. With a 50k path, although variance is still high, it seems clear that the relative performance differs between the foragers. This suggests that the differences in overall path length were significantly affecting the results in the step-limited simulations. b. With the path length increased to 500k the results are now stable and clearly differentiated. This scenario favours foragers with shorter mean step-lengths; the TP2.5 forager has a mean step-length of 2.89, the TP2.0, E and CB have mean step-lengths close to 8, while the TP1.5 and Ballistic foragers have the longest mean step-lengths, close to 50. Differences in efficiency are modest (best performer is 5.8% better than the worst) but significant at p< 0.001 (Kruskal-Wallis One Way Analysis of Variance on Ranks).
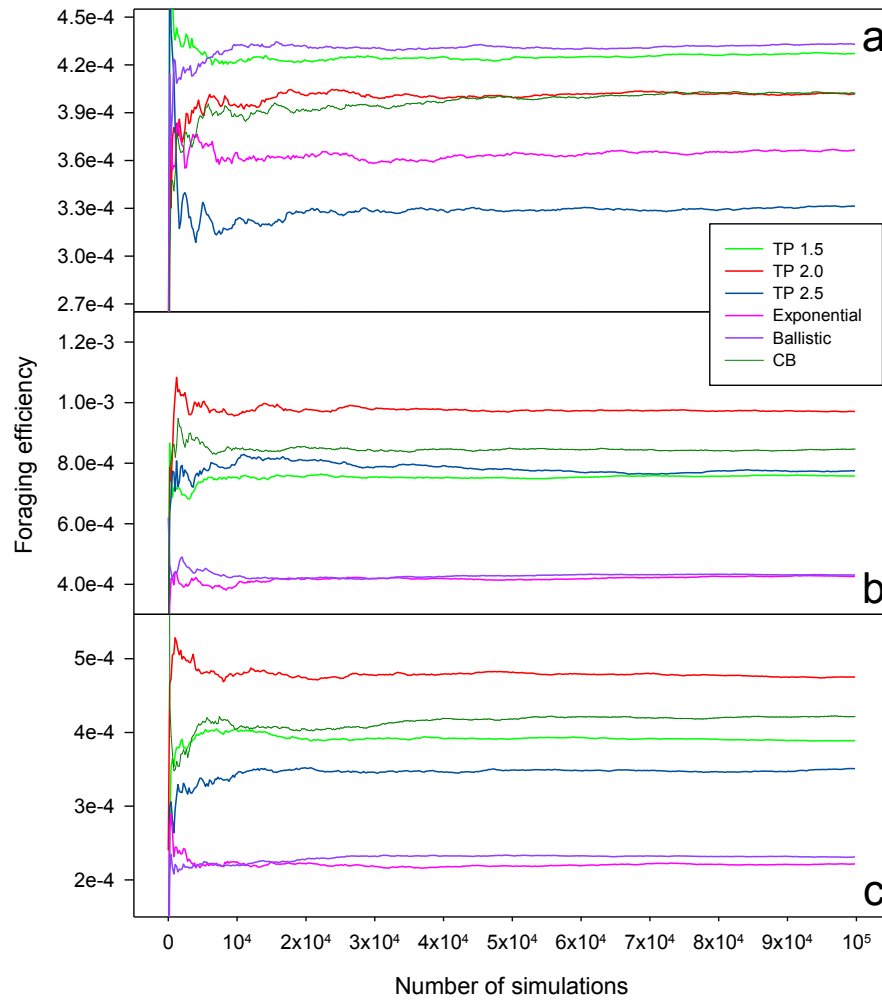
Figure 4: Destructive foraging and prey-targeting

It is interesting to note that with these scenarios the simulation outcomes are stable and clearly differentiated at path lengths of only $5x10^4$. a. Destructive foraging. As predicted the ballistic and TP1.5 foragers perform best (those with the longest step lengths) while the one with the shortest step lengths (TP2.5) performs worst. TP2.0 and CB performs better than exponential. Differences are greater than in scenario 1, with the best performers (ballistic & TP1.5) being 30% better than the worst (TP2.5). b. Prey-targeting. Here the optimality of the TP2.0 forager is clear. Note the greater separation of performance compared to any of the other scenarios. All the Lévy foragers (including the CB) perform considerably better than the exponential or ballistic foragers. c. Destructive foraging with prey-targeting. While the quantity of prey consumed is, as expected, less than in (b), leading to lower efficiencies, the overall results are very similar, with the exception of the TP2.5 forager, which now performs noticeably worse than in b).

Table 2: Percentage of successful foraging runs as a function of overall path length

In the step limited simulations there was considerable difference in the overall path length and

also in the number of successful foraging runs (i.e. runs that found >0 biomass), probably as a result of the more thorough sampling of the prey field with longer path lengths. In simulations with the path limited to $5x10^4$ (roughly equivalent to the TP2.0 step-limited forager) the difference was reduced but was still considered to be affecting the results. With the path limited to 500k the differences are considerably reduced.

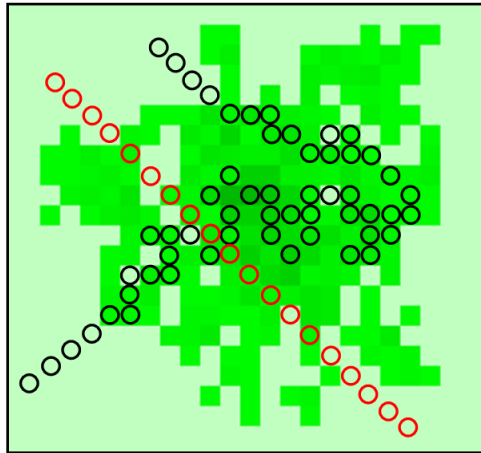| Forager	Step limited	Step-limited Path length	Path limited to $5x10^4$	Path limited to $5x10^5$
TP1.5	97.05%	249938	43.24%	99.93%
TP2.0	31.43%	39006	31.92%	99.18%
TP2.5	6.09%	14541	14.89%	83.82%
E	14.18%	38755	14.39%	77.29%
CB	29.43%	40246	28.93%	98.00%

Figure 5: Prey-targeting allows greater prey-patch exploitation

A forager with prey-targeting (black circles) performs a complex, diffusive random walk throughout the prey patch, halted at every move that encounters prey. Consequently significantly more of the prey patch is exploited than is the case with the simple forager (red circles) that moves blindly through the patch, as a virtual forager would in this simulation, without prey-targeting.
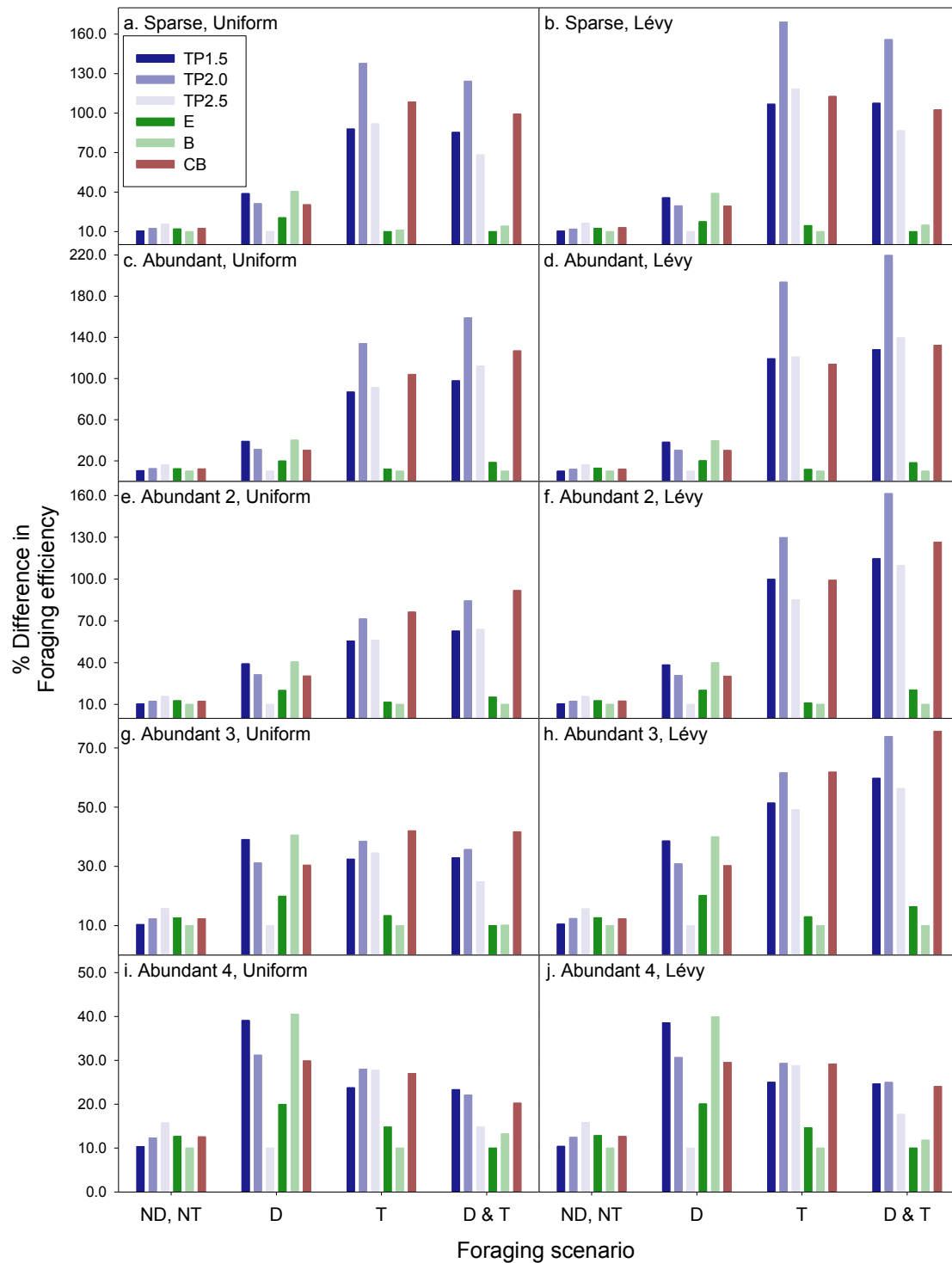
Figure 6: Summary of foraging efficiency results

      Foraging efficiency results, expressed as % differences in prey consumed per unit distance travelled, relative to the worst performing forager in each case. Results shown for the 2 prey field distributions, 5 prey field densities, 4 foraging scenarios (ND non-Destructive; NT non-Targeted; D Destructive; T Targeted) and 6 foragers (TP truncated Pareto, with exponents of 1.5, 2.0 and 2.5; E Exponential; B Ballistic; CB Composite Brownian)(24 x 10^{6} simulations in total). The overall

pattern of relative efficiencies between foragers and scenarios is similar in all prey fields for each scenario. With the non-targeted scenarios the increasing prey abundance makes little difference to the relative efficiencies. With the targeted scenarios, however, the extent of the differences reduces as the prey abundance increases. In general, differences are slightly greater in the Lévy distributed prey fields, likely due to the patchier distribution resulting in locally more sparse prey. The exponential and Ballistic foragers perform very poorly in the targeted scenarios. To allow zero results to be visible in these plots, 10% has been added to all results.
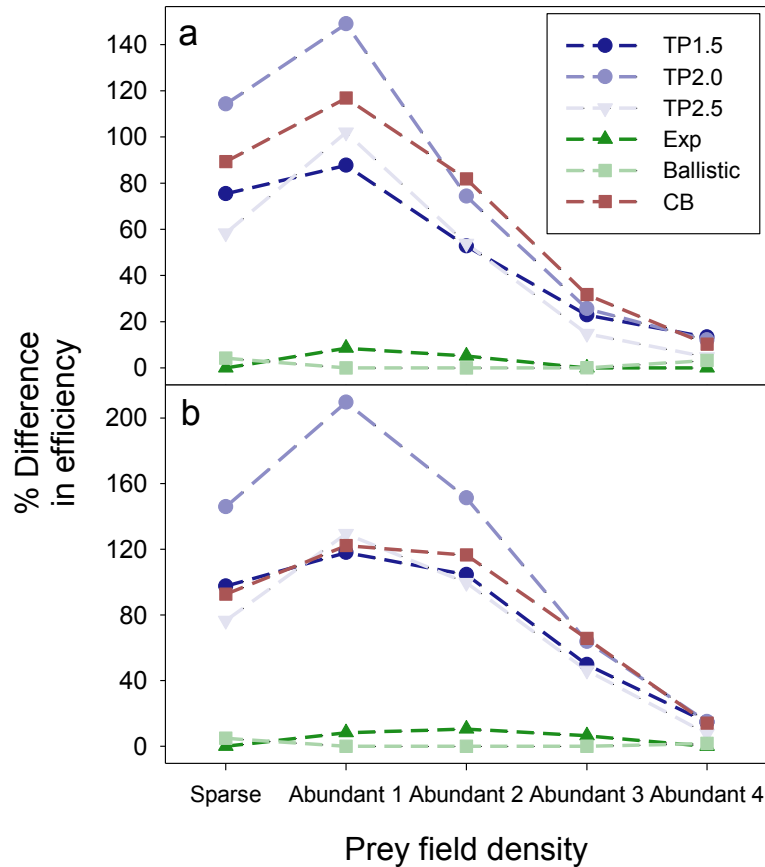

Figure 7: Response of relative efficiency to increasing abundance

The graphs show differences in efficiency (prey consumed per unit distance travelled) relative to the worst performer in the destructive, prey-targeting scenario. a) is a uniform prey field and b) a Lévy prey field; TP is a truncated Pareto forager with, for TP1.5 μ=1.5, for TP2.0 μ=2.0, for TP2.5 μ=2.5; Exp is exponential; CB is a bi-exponential composite Brownian. At all prey abundances the TP2.0 forager is significantly more efficient than all but the CB forager. The exponential and ballistic foragers are consistently the worst performers and have relative efficiencies that are not affected by changing prey field abundance. Interestingly, for the Lévy and CB foragers, efficiency is better in the Abundant 1 prey field, before diminishing as the abundance increases further. This could be due to the sparse prey field being too sparse to generate properly sampled results. Even at the highest abundance it is clear that a Lévy or CB forager will easily outperform an exponential or ballistic forager.

Figure 8: Median famine durations

Median famine durations calculated from the number of interpolated steps between prey encounters (i.e. distance travelled or time elapsed); a & b non-destructive targeted, scenario (S3); c & d destructive, targeted scenario (S4). Uniform and Lévy distributed, Abundant 1 prey fields were used. Note the log scale for famine durations. Horizontal bar shows median, boxes show 25th and 75th percentiles, whiskers show 10th and 90th percentiles; outliers show 5th and 95th percentiles. In all cases the TP2.0 forager experiences the shortest famine periods and, consequently, the most homogenous prey availability. Note that in a & c the exponential 95th percentile is off the scale.

Figure 9: Path structure analysis results

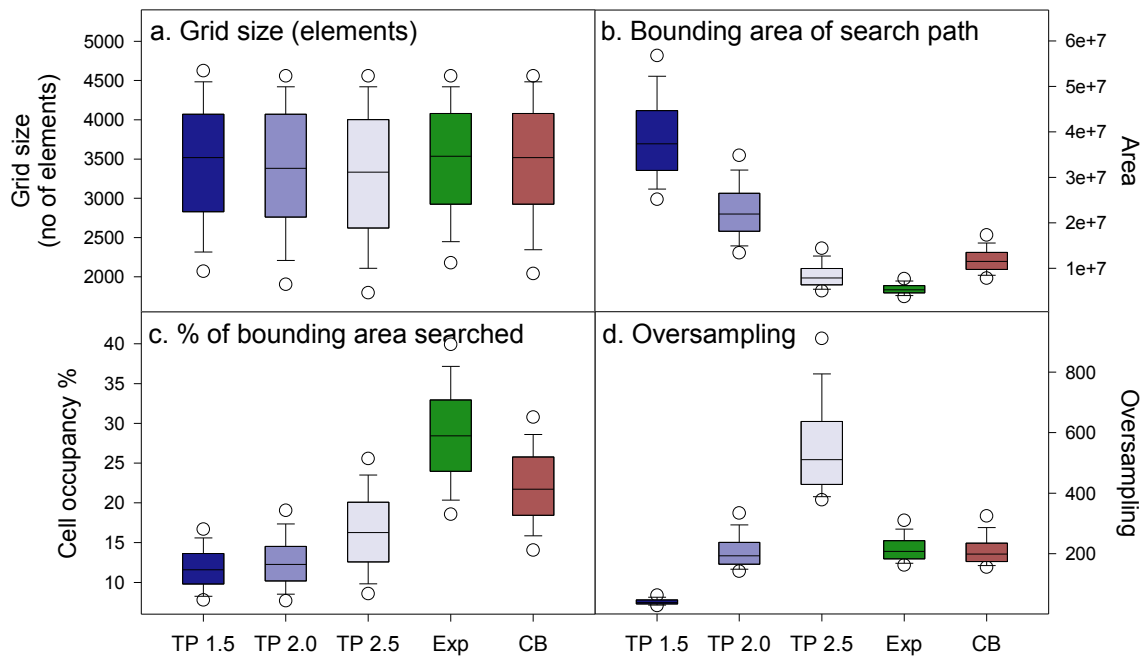a. Confirmation that the grid used for each forager was appropriately scaled and comprised a similar number of grid cells to allow path structure, rather than scale, to dominate the analysis. b. The bounding area is, as expected, higher with super-diffusive foragers such as TP1.5 and is lowest for the exponential. c. Although the area bounded by the exponential path is low (b) the percentage of the area explored is greatest. This result illustrates the diffusive nature of exponential paths. The TP1.5 path, which is the most super-diffusive, explores the lowest percentage of the area bounded by the extent of the path, as expected from the more ballistic characteristics. d. The oversampling value of the Lévy foragers increases with increasing exponents, as a consequence of fewer long steps. Oversampling in the exponential path is low compared to the 'Brownian like' TP2.5 path, further illustrating the essential structural difference between an exponential and a Lévy path and the diffusive character of an exponential path.

Figure 10: Example plots from the path structure analysis

The plots show the results of the path structure analysis for foragers a) TP1.5; b) TP2.0; c) TP2.5; d) Exponential and e) CB. Warmer colours indicate higher oversampling values. The faint grey lines indicate the analysis grid and confirm that the relative grid size is the same in all cases. The structure of the TP foragers can be seen to alter as the exponent is increased, resulting in fewer long steps and increased oversampling. The structure of the exponential path is quite different from the Lévy foragers, having no long relocations and a more extensive use of the space. The CB forager falls part way between the TP and exponential foragers, having more long steps than the exponential, but less intensive space use.

Figure 11: Example foraging paths for TP2.5 and exponential foragers
Four sample paths from each of a TP2.5 (left), and exponential forager (right), arranged so as not to overlap. It is clear, simply from the overall darkness of each image, that the TP2.5 forager searches a smaller proportion of the prey field.

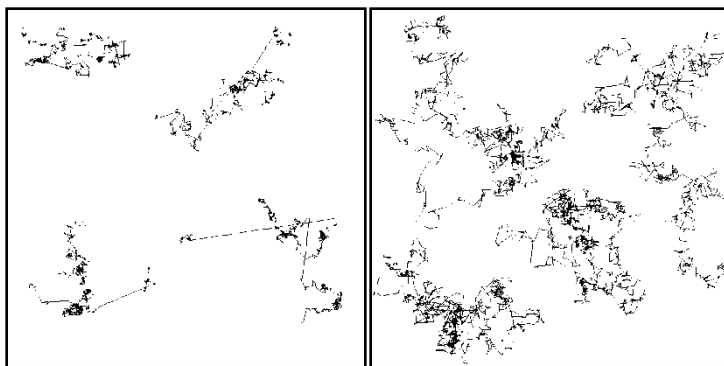# 6. Tables of results

Table 3: Foraging efficiency results for the sparse and abundant 1 prey fields

Scenario	Destructive	Targeted	Forager	Sparse, uniform		Sparse, Lévy		Abundant 1, uniform		Abundant 1, Lévy	
				Efficiency	Diff	Efficiency	Diff	Efficiency	Diff	Efficiency	Diff
1	No	No	TP1.5	4.33E-04	0.00	4.34E-04	0.62	7.21E-02	0.55	7.19E-02	0.00
			TP2.0	4.46E-04	3.02	4.41E-04	2.30	7.35E-02	2.54	7.32E-02	1.89
			TP2.5	4.53E-04	4.69	4.46E-04	3.46	7.61E-02	6.17	7.63E-02	6.20
			E	4.51E-04	4.19	4.45E-04	3.35	7.35E-02	2.45	7.41E-02	3.10
			B	4.33E-04	0.07	4.31E-04	0.00	7.17E-02	0.00	7.19E-02	0.05
			CB2	4.47E-04	3.30	4.50E-04	4.43	7.33E-02	2.27	7.33E-02	2.02
2	Yes	No	TP1.5	4.27E-04	28.86	4.23E-04	25.66	7.08E-02	29.04	7.09E-02	28.23
			TP2.0	4.02E-04	21.21	4.03E-04	19.64	6.65E-02	21.18	6.65E-02	20.28
			TP2.5	3.31E-04	0.00	3.37E-04	0.00	5.49E-02	0.00	5.53E-02	0.00
			E	3.66E-04	10.53	3.62E-04	7.56	6.04E-02	9.95	6.09E-02	10.13
			B	4.33E-04	30.63	4.34E-04	28.94	7.14E-02	30.13	7.17E-02	29.65
			CB2	4.02E-04	21.37	4.02E-04	19.41	6.61E-02	20.35	6.65E-02	20.21
3	No	Yes	TP1.5	7.58E-04	77.95	8.37E-04	96.84	1.25E-01	76.88	1.48E-01	109.23
			TP2.0	9.70E-04	127.80	1.10E-03	159.16	1.58E-01	124.07	2.00E-01	183.63
			TP2.5	7.75E-04	81.92	8.86E-04	108.26	1.28E-01	81.33	1.49E-01	110.85
			E	4.26E-04	0.00	4.45E-04	4.58	7.21E-02	2.00	7.18E-02	1.69
			B	4.30E-04	1.01	4.25E-04	0.00	7.07E-02	0.00	7.06E-02	0.00
			CB2	8.48E-04	99.00	8.62E-04	102.72	1.37E-01	93.98	1.44E-01	103.95
4	Yes	Yes	TP1.5	3.89E-04	75.40	4.35E-04	97.55	4.55E-02	87.75	5.30E-02	118.01
			TP2.0	4.75E-04	114.27	5.42E-04	145.89	6.03E-02	148.98	7.52E-02	209.58
			TP2.5	3.51E-04	58.33	3.89E-04	76.57	4.89E-02	102.08	5.57E-02	129.51
			E	2.22E-04	0.00	2.20E-04	0.00	2.63E-02	8.54	2.63E-02	8.29
			B	2.31E-04	4.22	2.31E-04	4.90	2.42E-02	0.00	2.43E-02	0.00
			CB2	4.21E-04	90.13	4.25E-04	92.57	5.25E-02	116.83	5.40E-02	122.28

Table 4: Foraging efficiency results for the Abundant 2 and 3 prey fields

Scenario	Destructive	Targeted	Forager	Abundant 2, uniform		Abundant 2, Lévy		Abundant 3, uniform		Abundant 3, Lévy	
				Efficiency	Diff	Efficiency	Diff	Efficiency	Diff	Efficiency	Diff
1	No	No	TP1.5	2.17E+00	0.33	2.17E+00	0.42	8.68E+00	0.35	8.68E+00	0.50
			TP2.0	2.21E+00	2.26	2.21E+00	2.29	8.84E+00	2.26	8.85E+00	2.38
			TP2.5	2.29E+00	5.73	2.28E+00	5.71	9.15E+00	5.79	9.13E+00	5.65
			E	2.22E+00	2.57	2.22E+00	2.62	8.87E+00	2.61	8.87E+00	2.66
			B	2.16E+00	0.00	2.16E+00	0.00	8.65E+00	0.00	8.64E+00	0.00
			CB2	2.21E+00	2.30	2.21E+00	2.44	8.85E+00	2.30	8.84E+00	2.29
2	Yes	No	TP1.5	2.13E+00	29.15	2.13E+00	28.40	8.52E+00	29.08	8.53E+00	28.57
			TP2.0	2.00E+00	21.35	2.01E+00	20.89	8.00E+00	21.18	8.02E+00	20.84
			TP2.5	1.65E+00	0.00	1.66E+00	0.00	6.60E+00	0.00	6.64E+00	0.00
			E	1.82E+00	10.04	1.83E+00	10.19	7.26E+00	9.92	7.31E+00	10.19
			B	2.15E+00	30.55	2.16E+00	30.00	8.62E+00	30.55	8.63E+00	30.00
			CB2	1.99E+00	20.49	2.00E+00	20.38	7.95E+00	20.42	7.98E+00	20.21
3	No	Yes	TP1.5	3.12E+00	45.58	4.07E+00	89.81	1.05E+01	22.43	1.21E+01	41.41
			TP2.0	3.46E+00	61.42	4.71E+00	119.77	1.10E+01	28.49	1.30E+01	51.61
			TP2.5	3.13E+00	45.98	3.75E+00	75.15	1.07E+01	24.51	1.19E+01	39.14
			E	2.17E+00	1.54	2.17E+00	1.04	8.84E+00	3.32	8.81E+00	2.97
			B	2.14E+00	0.00	2.14E+00	0.00	8.56E+00	0.00	8.56E+00	0.00
			CB2	3.56E+00	66.34	4.05E+00	89.12	1.13E+01	32.03	1.30E+01	51.81
4	Yes	Yes	TP1.5	1.17E+00	52.73	1.31E+00	104.59	4.00E+00	22.90	4.00E+00	49.75
			TP2.0	1.33E+00	74.34	1.61E+00	151.31	4.09E+00	25.67	4.38E+00	63.85
			TP2.5	1.17E+00	53.85	1.28E+00	99.66	3.73E+00	14.78	3.91E+00	46.29
			E	8.03E-01	5.20	7.06E-01	10.49	3.25E+00	0.00	2.84E+00	6.43
			B	7.63E-01	0.00	6.39E-01	0.00	3.25E+00	0.12	2.67E+00	0.00
			CB2	1.39E+00	81.78	1.38E+00	116.53	4.28E+00	31.71	4.43E+00	65.64

Table 5: Foraging efficiency results for the Abundant 4prey field

Scenario	Destructive	Targeted	Forager	Abundant 4, uniform		Abundant 4, Lévy	
				Efficiency	Diff	Efficiency	Diff
1	No	No	TP1.5	1.74E+01	0.36	1.73E+01	0.42
			TP2.0	1.77E+01	2.29	1.77E+01	2.45
			TP2.5	1.83E+01	5.73	1.83E+01	5.86
			E	1.77E+01	2.65	1.78E+01	2.83
			B	1.73E+01	0.00	1.73E+01	0.00
			CB2	1.77E+01	2.57	1.77E+01	2.66
2	Yes	No	TP1.5	1.70E+01	29.10	1.71E+01	28.56
			TP2.0	1.60E+01	21.20	1.60E+01	20.65
			TP2.5	1.32E+01	0.00	1.33E+01	0.00
			E	1.45E+01	9.98	1.46E+01	10.06
			B	1.72E+01	30.52	1.72E+01	29.92
			CB2	1.58E+01	19.88	1.59E+01	19.52
3	No	Yes	TP1.5	1.94E+01	13.75	1.97E+01	15.00
			TP2.0	2.02E+01	18.00	2.05E+01	19.30
			TP2.5	2.01E+01	17.76	2.04E+01	18.79
			E	1.79E+01	4.80	1.79E+01	4.62
			B	1.71E+01	0.00	1.72E+01	0.00
			CB2	2.00E+01	17.03	2.04E+01	19.17
4	Yes	Yes	TP1.5	7.09E+00	13.32	6.98E+00	14.65
			TP2.0	7.01E+00	12.09	7.00E+00	14.97
			TP2.5	6.55E+00	4.78	6.55E+00	7.68
			E	6.25E+00	0.00	6.08E+00	0.00
			B	6.46E+00	3.24	6.19E+00	1.80
			CB2	6.90E+00	10.25	6.94E+00	14.05

Table 6: Feast and famine results

The table shows the analysis of famine period durations, computed as the number of simulation steps between encounters with prey. Prey fields were the Abundant 1 density, to ensure sufficient encounters.

Scenario	Destructive	Targeted	Forager	Uniform			Lévy		
				Median	25%	75%	Median	25%	75%
3	No	Yes	TP1.5	247.68	169.23	387.02	235.16	140.19	463.54
			TP2.0	200.47	133.33	330.21	198.82	101.24	558.20
			TP2.5	285.27	157.70	690.78	902.84	145.77	47573.00
			E	524.03	268.72	1443.24	23025.00	334.70	46212.00
			B	443.84	287.64	728.58	488.51	288.04	929.41
			CB2	234.90	151.74	407.56	363.88	136.30	3558.90
4	Yes	Yes	TP1.5	441.08	316.75	646.44	428.25	263.74	788.75
			TP2.0	359.49	250.06	561.30	361.42	190.35	941.85
			TP2.5	512.67	302.73	1131.98	1440.67	276.32	47572.00
			E	891.63	490.82	2103.86	23071.00	592.59	46213.00
			B	786.18	543.88	1156.49	862.80	541.26	1464.72
			CB2	414.64	280.62	678.17	652.22	255.65	4642.38

7. Acknowledgements

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