

# Adaptive encounter-conditional heuristics outperform Lévy flights in search for patchily distributed prey

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## Abstract

A theoretical and applied literature has suggested that foragers should search using Lévy flights, since Lévy flights can maximize the efficiency of search in the absence of information on the location of randomly distributed prey. Foragers, however, often have available to them at least some prior information about the distribution of prey, gained either through evolved mechanisms, experience and memory, or social transmission of information. As such, we might expect heuristics that make use of such information to further improve the efficiency of random search—and be selected for on that basis. In this paper, we derive a formal model of random flight searching behavior in the presence of a very limited set of information about patchiness in the distribution of prey and a few heuristics for improving search efficiency conditional on such information. Using a simulation model, we demonstrate the efficiency gains of these search heuristics, and illustrate the resulting differences in the distributions of step-size and heading they imply, relative to Lévy flights. We conclude by presenting a set of empirically testable, quantitative predictions that contrast our model of heuristic search with the Lévy flight foraging hypothesis.

*Keywords:* foraging theory, search, partial information, animal movement

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## 1. Introduction

A theoretical and applied literature has suggested that foragers<sup>1</sup> should search using

approximations to Lévy flights, since Lévy flights can maximize the efficiency of search in the absence of information on the location of prey—the Lévy flight foraging hypothesis [1, 2, 3]. There has been some empirical success in testing this hypothesis in humans [4] and non-human animals [5, 6]. On the other hand, many empirical studies have either failed to find evidence of such search behavior or found evidence of more nuanced patterns of search in humans (e.g.

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<sup>1</sup>Note that we will continually refer to “foragers” and “prey” for ease, but foragers could be any searcher of something, and prey could be anything being searched for.

[7]) and other animals (e.g. [6, 8]). Additionally, recent theoretical work has shown that two-scale search methods outperform Lévy flights [9]. There is also outstanding debate in the literature as to whether or not the positive and negative tests of the hypothesis have been properly conducted, or if issues with measurement have prevented effective tests of the underlying ideas (see [6], [10], and [11]).

An empirical literature on the movement patterns of marine predators [6] suggests that while Lévy flights are common (even prevalent) across many individuals, other movement patterns frequently occur. Specifically, they show that movement tends to look Lévy in less-productive ecologies, and Brownian in more-productive ones [6] (see also [12]). The authors read this behavior as consistent with the Lévy flight foraging hypothesis, with the addendum that revised theoretical models have suggested that Lévy flights should occur in environments where prey is sparse, but that Brownian motion should occur where prey is abundant [13].

From a theoretical perspective, however, even if Lévy or Brownian movement can maximize the efficiency of search in the absence of information on the location of prey, it is surprising to think that natural selection should favor their use on these grounds. Foragers frequently have at least some prior information about the distribution and characteristics of their prey, either through evolved mechanisms [14, 15], experience [16, 17], or social transmission of information [18, 19, 20, 21]. As such, we might instead expect natural selection to favor search heuristics that exploit such information and further improve the efficiency of random search relative to pure Lévy or Brownian movement [9].

In this paper, we draw on insights from Benhamou and Collet [9], who developed an algorithm that uses two-scale, cue-driven, adaptive modulation of step-size (i.e. the distance traveled in a given time interval) to outperform Lévy flights in random search. We generalize the idea, however, to consider how both step-size and heading direction should respond to environmental cues, and we allow for a continuous rather than two-scale relationship between forager behavior and environmental cues. Our theoretical models have the desirable property of being both generative models of data (for running simulations), as well as being explicitly defined Bayesian statistical models (for estimating parameters from empirical data). We use simulation methods to demonstrate the efficiency gains of our search heuristics, and illustrate the differences in the distributions of step-size and heading they imply relative to Lévy flights. We recover classic findings linking Lévy-like or Brownian-like movement to prey density and clustering, but also extend prior work by deriving explicit models of how step-size and change in heading should deviate from both of these models of random search according to the distribution of prey. We conclude by presenting a set of empirically testable, quantitative predictions that contrast our model of heuristic search with the Lévy flight foraging hypothesis.

### 1.1. Theoretical models of optimal search

Under the Lévy flight foraging hypothesis, it is proposed that since Lévy flights can maximize search efficiency in the absence of information on prey location, natural selection should lead to search strategies that approximate Lévy flights [3]. However, foragers frequently have prior information about prey. For example, they may have

some knowledge, whether conscious or not, of average prey density. They may have some knowledge of the clustering, or spatial correlations in prey items. They may have some knowledge of the geographic range of clusters and the distance between clusters. Additionally, the process of search itself provides information of use to the forager—specifically, if prey items are clustered then encountering a prey item at a given place and time suggests that other prey items are more likely to be found nearby.

To investigate these ideas more formally, let us assume that a forager’s search behavior in two dimensions can be approximated by discrete points in space  $(x_{[t]}, y_{[t]})$  connected by line segments, with a constant temporal separation of  $t \in \{1, \dots, T\}$ . While most empirical data sets of forager movement (GPS tracks, for example) will be of this form, such data are easily transformed to a more theoretically relevant form via Cartesian-to-polar mapping [22]. For the purposes of search, we are interested in modeling the differences between locations in space across each time-step. As such, we can parameterize this model such that  $r_{[t]} \in \mathbb{R}^+$  gives the linear distance between points  $(x_{[t]}, y_{[t]})$  and  $(x_{[t-1]}, y_{[t-1]})$ , and  $\theta_{[t]} \in (0, 2\pi)$  gives the corresponding angle:

$$r_{[t]} = \sqrt{(x_{[t]} - x_{[t-1]})^2 + (y_{[t]} - y_{[t-1]})^2} \quad (1)$$

$$\theta_{[t]} = \arctan^* \left| \frac{(y_{[t]} - y_{[t-1]})}{(x_{[t]} - x_{[t-1]})} \right| \quad (2)$$

where the  $\arctan^*$  function is the standard  $\arctan$  function after adjusting the angle for the quadrant of the point in Cartesian space (see [22]).

Note that while  $r$  can vary between time-steps, let us make the simplifying assumption that energy investment between time-step  $t$  and  $t + 1$  is constant, with the intuition being that greater investment in active search occurs when  $r$  is small and greater investment in rapid locomotion occurs when  $r$  is large. This assumption allows us to simplify treatment of energy expenditure.

### 1.2. Lévy flight foraging hypothesis

The Lévy flight foraging hypothesis asserts that we should expect:

$$r_{[t]} \sim \text{Lévy}(\alpha, \beta, \xi, \zeta)T[0, \infty] \quad (3)$$

$$\theta_{[t]} \sim \text{Uniform}(0, 2\pi) \quad (4)$$

in empirical measurements. The symbol  $T[0, \infty]$  indicates truncated support on  $\mathbb{R}^+$ , and the Lévy (or ‘stable’ [23, 24]) distribution described above reduces to the truncated Cauchy distribution for the stability parameter  $\alpha = 1$  and the truncated Normal distribution for  $\alpha = 2$ , as long as the skewness parameter  $\beta = 0$  [25]. Note that  $\xi \in \mathbb{R}$  and  $\zeta \in \mathbb{R}^+$  give the location and scale parameters. While the step-size distribution of Lévy flights, broadly conceived, may have varying degrees of heavy tails (based on the value of  $\alpha$ ), when researchers refer to Lévy flights they tend to imply a heavy-tailed step-size distribution of some form or another and not necessarily a stable distribution (e.g. truncated Lévy, Weibull, log-normal, Pareto, and truncated Pareto distributions have all been used to model Lévy flights and empirical movement patterns [26]).

### 1.3. Adaptive encounter-conditional heuristics

While the predictions of the Lévy flight foraging hypothesis are both intuitive and

theoretically motivated [3] for the case of an informationless forager, foragers typically have opportunities to acquire prior information about their prey distributions. If we assume that foragers possess a few basic bits of information about their prey and two simple heuristics, then we should expect different distributions of both  $r$  and  $\theta$ .

First, we assume that foragers:

1. Have information about the level of spatial correlation in the distribution of their prey—they know if their prey items tend to come in clumps or patches.
2. Are able to assess if they have encountered prey in each of the last  $S$  time-steps.

Next, we assume that foragers have these heuristics:

1. *If a forager is unlikely to be in a patch, then it should search using larger step-sizes than it would if it were likely to be in a patch.* The intuition here is that if one is not in a patch, then it does not pay to search in great detail nearby; however, if one is presently in a patch (an area of relatively higher local prey density), then small step-sizes will minimize the probability of moving out of the patch.
2. *If a forager is unlikely to be in a patch, then it should be resistant to randomizing its heading (direction of travel).* The intuition here is that if one is presently between patches, then it does not pay backtrack to areas that have already been established as having a low probability of yield; instead, one should efficiently continue on to new territory. Alternatively, if one is in a patch, then

one should randomize heading direction to both minimize the probability of leaving the patch and thoroughly explore it.

### 1.3.1. Modeling prey distribution

We have assumed that foragers have some information about the state of spatial clustering or patchiness of their prey. More specifically, let us assume that prey items (or their biomass, density, utility, or some other measure),  $P$ , are distributed over an arbitrarily large number of points in space according to a Gaussian random field [27], where:

$$P \sim \text{Multivariate Normal Cholesky}(M, \varsigma L_\rho) \quad (5)$$

with  $M$  giving the (constant) mean vector of the distribution,  $\varsigma$  giving the variance, and  $L_\rho$  being defined as the Cholesky decomposition of the correlation matrix,  $\rho$ , where:

$$\rho_{[i,j]} = \exp\left(-\frac{D_{[i,j]}^2}{\ell^2}\right) \quad (6)$$

This expression indicates that the correlation in prey outcomes,  $\rho_{[i,j]}$ , between points in space is a function of the unit-normalized distance between these points,  $D_{[i,j]} \in (0, 1)$ , squared, and a parameter,  $\ell \in \mathbb{R}^+$ , which controls the decay of spatial correlations with inter-site distance.

In the case where  $\ell$  is very small relative to the scale of search, there is little to no patchiness, and encountering a prey item gives very little information about the probability of encountering additional prey items nearby (see Figure 1). However, if  $\ell$  is fairly large relative to the scale of search, this is indicative of spatial correlations in the distribution of prey (which we will call patchiness), and encountering

prey in a given location provides information about the probability of encountering prey in nearby locations. As such, let us assume from now on that  $\ell$  is large enough to provide some level of patchiness to prey items on a scale relevant to the search problem.

[Figure 1 about here.]

### 1.3.2. Modeling forager movement

Our heuristics suggest that when  $\ell$  is large, the optimal change in heading that a forager should make at time,  $t$ , is some increasing function of the probability of being inside of a patch of increased local prey density. For simplicity, let us assume that patches are large relative to a forager's average speed and the length of the time-step. As such, the probability of being in a patch should be an increasing function of the encounters with prey items that have occurred over the last  $S$  time-steps. While there is no general function that we should expect from theory alone, one empirically tractable modeling approach [28] would suggest that the distribution of heading changes can be given by a Beta regression, since these values are interval constrained:

$$\frac{\Delta(\theta_{[t]}, \theta_{[t-1]})}{\pi} \sim \text{Beta}(\mu_{[t]}\nu, (1 - \mu_{[t]})\nu) \quad (7)$$

Note that the  $\Delta(a, b)$  function returns the minimum of:  $|a - b|$  and  $2\pi - |a - b|$ , since a 90 degree right turn is the same as a 270 degree left turn, for example. The mean of the Beta distribution at time  $t$  is then given by  $\mu_{[t]}$ :

$$\mu_{[t]} = \text{logit}^{-1} \left( \psi_0 + \sum_{s=1}^S \psi_{[s]} E_{[t-s]} \right) \quad (8)$$

while the dispersion of the distribution is controlled by  $\nu \in \mathbb{R}^+$ .  $E_{[t]}$  is an indicator

variable (or even a count) of the prey items encountered at time-step  $t$ ,  $\psi \in \mathbb{R}^{S+1}$  is a vector of unknown parameters, and  $\text{logit}^{-1}$  is the inverse logit function.

Likewise, with respect to the optimal step-size a forager should take at time  $t$ , our heuristics suggests that this value should be some decreasing function of the probability of being inside of a patch of increased local prey density. Again there is no general function that we should expect, but one empirically tractable modeling approach would suggest that step-sizes follow a log-normal distribution (another member of the heavy-tailed family), and information theoretic model comparison of step-sizes in Lévy-like movement in humans [26] have shown that the log-normal distribution outperformed other common distributions. As such, we let the distribution of step-sizes be:

$$r_{[t]} \sim \text{Log-Normal}(\eta_{[t]}, \omega) \quad (9)$$

where the mean of the log of the step-size at time  $t$  is given by  $\eta_{[t]}$ :

$$\eta_{[t]} = \left( \phi_0 + \sum_{s=1}^S \phi_{[s]} E_{[t-s]} \right) \quad (10)$$

and the dispersion of the distribution of the log of step-size is controlled by  $\omega \in \mathbb{R}^+$ ,  $E_{[t]}$  is the same indicator variable (or count) of the prey items encountered at time-step  $t$ , and  $\phi \in \mathbb{R}^{S+1}$  is a vector of unknown parameters. We note, however, that the approach here is generalizable to other heavy-tailed distributions.

In addition to the above equations describing a statistical model through which empirical data in the form of GPS tracks can be analyzed, they also describe a generative model that can produce simulated movement sequences in the form of (x,y)



points on a plane, with the caveat that to go from a realization of the absolute value of heading change from the Beta distribution to a value in  $(0, 2\pi)$ , we need multiply by a random variable  $\delta \in \{-1, 1\}$ , which takes each value with equal probability and allows for either clockwise or counter-clockwise turns of between 0 and  $\pi$  radians. In the next section, we use such a simulation model to study the two foraging strategies of interest.

## 2. Simulation results

Previous theoretical research [3] has suggested that there are two important cases of foraging, non-destructive and destructive, or—in the language of Charnov et al. [29]—foraging of renewing and non-renewing prey. In the first case, prey items are not noticeably depleted or destroyed upon encounter; in the second, they are. Most empirical cases of random search are probably somewhere between these extremes, where prey items may be removed, but are then replaced after some period of time. For example, ants on the surface of a mound might be harvested, but replaced by other ants leaving the mound. We compare and contrast our model of encounter-conditional search with a model of search that uses Lévy flights under each of these assumptions about resource recovery.

The simulation model implements the equations presented above to determine the path of a forager moving through a simulated environment. The forager can detect prey items within a small radius of his or her location at each time point (in our simulation, the detection radius was set at approximately  $\frac{1}{3}$  of the average step-size in the Lévy flight). The forager then has the option to make use of the encounter informa-

tion to update his or her search parameters ( $\mu_{[t]}$  and  $\nu_{[t]}$ ) in the next time-step.

All foragers begin their paths at the origin and are run for 500 time-steps. Each simulation was run 200 times, with our findings summarizing the entire resultant distribution. We replicated each contrast under varying levels of spatial correlation. We present results under moderate levels of spatial correlation here, and present further results in the Supplementary Materials; varying the level of spatial correlation alters the numeric values presented in the main paper, but not the qualitative findings. To ensure a fair comparison, the parameters of the adaptive model were set such that the step size distribution is identical to the Lévy walk in the absence of encounters. The simulation code, with the specific parameter values used in the analysis is written in R [30] and is available in the Supplementary Materials; it will be maintained at: [www.github.com/ctross](http://www.github.com/ctross).

### 2.1. Non-destructive foraging

In the case of non-destructive foraging, foragers encounter and consume prey, but the prey item is returned to its original position after a single time step of depletion. While there will almost always be at least some decreasing returns to increasing encounters over short time periods with the same prey item in nature, this model serves to ground one extreme of the search problem. In natural settings, this model may correspond to cases where prey items become only temporarily depleted, where prey items may be encountered but are not easily captured (human blow-gun hunters attempting to harvest hard-to-hit birds), or where mating is the purpose of search.

In our simulation, we see very distinct difference in the behavior of our search al-

gorithms. Figure 2 outlines the principle findings. First, we plot a representative path of the random flight taken by each search algorithm: Figure 2a plots a sample Lévy flight and Figure 2b plots a sample flight of the adaptive encounter-conditional search model (henceforth *adaptive search*). The Lévy flight exhibits its classic behavior, and explores the environment with a heavy-tailed mix of step length, but because there is no feed-back between encounters and behavior, the Lévy flight prematurely leaves high density patches rather than remaining to exploit them. The adaptive search model, however, uses a Lévy-like flight to find a patch, but once there reduces its step-size significantly and increases its average change in heading to increase its probability of remaining in a high density region of prey.

Figure 2c demonstrates this contrast: in the case of the Lévy flight, a single set of parameters control the log of step-size across all environments, as is apparent from the tight clustering of points. In contrast, the adaptive model allows the mean step-size to vary based on environmental feed-backs in the foraging process. Figure 2d demonstrates a similar pattern, but with heading change: in the case of the Lévy flight, a single set of parameters control the heading change across all environments. In contrast, the adaptive model generates an overpropensity to change heading relative to the value expected under pure Lévy movement when in patches, and *vice versa* when not. This ensures increased backtracking and fine-scale resolution of search when in high yield patches, and less backtracking when not in patches. Finally, Figures 2e and 2f present the distributions of mean return rate (in encounters per time-step) and standard deviation in return rate across search

strategies, and demonstrate that adaptive search yields significantly higher average returns than Lévy flights in this foraging context.

[Figure 2 about here.]

## 2.2. Destructive foraging

In the case of destructive foraging, foragers encounter prey items and completely and permanently deplete them for the duration of the simulation. This model serves to ground the alternative extreme of the search problem. In natural settings, this model may correspond to cases where prey items are consumed and not replaced over the entire course of the foraging endeavor.

We again see differences, although not as large as in the non-destructive case, in the behavior of our search algorithms. Figure 3 outlines the principle findings. Figure 3a plots a sample Lévy flight and Figure 3b plots a sample flight of the adaptive model. The Lévy flight exhibits its classic behavior, and explores the environment with a heavy-tailed mix of step lengths. Because there is no feed-back between encounters and behavior, the Lévy flight leaves high density patches prematurely (exactly as in Figure 2a), when they still contain resources that would be harvested efficiently under a more locally adaptive search tactic. The adaptive model, however, uses a Lévy-like flight to find a patch, but once there reduces its step-size significantly and increases its average change in heading to maximize its probability of remaining in a high density region. Eventually, this strategy reduces the prey density in the patch, leading to reduced encounters and a return to an inter-patch heuristic governing motion.

Figure 3c demonstrates this contrast: in the case of the Lévy flight, a single set of parameters control the log of step-size across

all environments, as is apparent from the tight clustering of points. In contrast, the adaptive model allows the mean step-size to vary based on environmental feed-backs in the sampling process, but the contrast is less stark than in the non-destructive foraging case, since prey depletion leads to a return of Lévy-like movement. Figure 3d demonstrates a similar pattern, but with heading change. Finally, Figures 3e and 3f present the distributions of mean return rate in encounters per time-step and standard deviation in return rate across search strategies, and demonstrate that adaptive encounter-conditional heuristics yield significantly higher average returns in encounters per time-step than Lévy flights, even in the case of destructive foraging.

[Figure 3 about here.]

### 2.3. Risk sensitive analysis

Simulation of the two search modes (Lévy vs. adaptive) allows us to compare them for both mean and standard deviation of encounter efficiency, and thus to assess the “risk” associated with the two using the Z-score model [31, 32], at least in contexts when outcomes are distributed approximately normally. In such cases, we are able to say something not just about the mean efficiency differences, but the chances that each strategy produces a deadly food shortfall. The Z-score model states that the optimal strategy from a given strategy set is the strategy which maximizes the value:  $\frac{M(X) - R_{\min}}{S(X)}$ . The function  $M(X)$  gives the mean of some measure of yield,  $X$ ,  $S(X)$  gives the standard deviation of  $X$ , and  $R_{\min}$  gives the minimum amount of  $X$  needed to avoid starvation. The strategy which maximizes this value also minimizes the probability of starvation.

Figure 4a demonstrates an application of the Z-score model of risk minimization to our simulation results (despite the fact that the distributions of encounters are not very Gaussian), for varying levels of  $R_{\min} < 0.4$ . We present the difference in  $\frac{M(X) - R_{\min}}{S(X)}$  between the adaptive search and Lévy flight algorithms (where  $X$ , here, is the fraction of time-steps with encounters of prey items, which are assumed to be of uniform caloric yield). For both non-destructive and destructive foraging, we see that the mean values of  $\frac{M(X) - R_{\min}}{S(X)}$  under the adaptive search heuristics exceed the same values under the Lévy flight model over a range of applicable  $R_{\min}$  values, indicating that the adaptive model better minimizes the probability of starvation.

As a robustness check on the lack of normality, we also calculated 1 minus the integral of the kernel density function of encounters from 0 to  $R_{\min}$  numerically, which yields an approximation of the probability of avoiding starvation. We then calculate the difference in survival probabilities. We present these results in Figure 4b. We draw the same qualitative conclusions as from the Z-score model.

[Figure 4 about here.]

### 2.4. Predictions for empirical studies

A merit of the modeling approach presented here, is that it permits some very explicit empirical test that contrast the adaptive model with the Lévy flight foraging hypothesis. Specifically, with respect to the distribution of the difference in heading (Eqs. 7 and 8), the Lévy flight foraging hypothesis predicts that:

1.  $\mu\nu = 1$  and  $(1 - \mu)\nu = 1$ , which is solved when  $\mu = \frac{1}{2}$  and  $\nu = 2$ .



These results follow from the fact that the Lévy flight foraging hypothesis predicts a random uniform heading, and the absolute value of the difference of two independent random uniform variates (after selecting the shortest path around the circle, see Supplementary Information) also follows a uniform distribution.

And, that:

2.  $\psi_{[1]}, \dots, \psi_{[S]} = 0$ , indicating an absence of relationship between encounters and heading changes over all time lags.

In contrast, the adaptive search heuristics outlined in this paper would suggest—at least when patchiness, as defined by an empirically estimable parameter,  $\ell$ , is strong—that the overall distribution of differences in headings should show a higher density near zero and a lower density at higher values when between patches, and vice versa when in patches.

In general, we would predict a tendency that:

3.  $\psi_{[1]}, \dots, \psi_{[S]} > 0$ , indicating a positive relationship between encounters and heading changes over some range of time lags.

With respect to the distribution of the step lengths (Eqs. 9 and 10), the Lévy flight foraging hypothesis predicts that the mean value of step lengths is constant over time, and that the variance of the log of step lengths should be large enough to produce a heavy tail:

4.  $\phi_{[1]}, \dots, \phi_{[S]} = 0$ , indicating an absence of relationship between encounters and step-size changes over all time lags.

5.  $\omega$  is large. In cases where prey are distributed nearly uniformly in space, however, the Lévy flight foraging hypothesis acknowledges that we would expect little benefit from a large  $\omega$  relative to a smaller value.

In contrast, the adaptive search heuristics outlined in this paper would suggest that the overall distribution of step-sizes should be sensitive both to the degree of auto-correlation in prey items and the likelihood that one is in a patch. We would predict a tendency that:

6.  $\phi_{[1]}, \dots, \phi_{[S]} < 0$ , indicating a negative relationship between encounters and step-size changes over some range of time lags. In cases where prey are distributed with low spatial auto-correlation (small  $\ell$ ), we would expect little divergence from the Lévy flight foraging hypothesis predictions. However, in cases with stronger spatial auto-correlation in prey (large  $\ell$ ), we would expect stronger divergence.

7.  $\omega$  is moderate.

Finally, in cross-population or cross-species comparisons of these search parameters as a function of prey distributions, we would predict a positive relationship between the patchiness of prey and the extent to which forager movement patterns diverge from Lévy flights:

8. As the patchiness parameter of the prey distribution over space,  $\ell$ , increases, we predict a co-occurring increase in the values of  $\psi_{[1]}, \dots, \psi_{[S]}$ , as well as an increase in the number of time-steps,  $s$  for which  $\psi_{[s]} > 0$  holds,

indicating a progressively stronger relationship between encounters and heading change as the patchiness of prey increases.

9. As the patchiness parameter of the prey distribution over space,  $\ell$ , increases, we predict a co-occurring decrease in the values of  $\phi_{[1]}, \dots, \phi_{[s]}$ , as well as an increase in the number of time-steps,  $s$ , for which  $\phi_{[s]} < 0$  holds, indicating a progressively stronger relationship between encounters and step-size as the patchiness of prey increases.

### 3. Discussion

#### 3.1. Simulation findings

In sum, the simulation models suggest that adaptive search outperforms Lévy search for maximizing foraging returns. If prey are patchy in distribution, information-based measures (see also [9]) should behave this way—better information generally allows for better predictive inference.

In the case of non-destructive foraging, we see sharply diverging behaviors of our search algorithms, with adaptive search outperforming the Lévy flight. In the case of destructive foraging, the differences are smaller but adaptive search still outperforms Lévy movement. In the limit, as prey density decreases to zero (along with encounters), the Lévy and adaptive search strategies converge to identical behavior, but as prey become more dense within their clusters and encounters provide information to the forager, gains to adaptive search increase.

Our findings here echo previous theoretical [9, 13] and empirical [6] results demonstrating that a forager’s search behavior is

expected to differ across ecologies; for example, it is frequently argued that Lévy flights should occur in environments where prey are sparse, and that Brownian motion should occur where prey is abundant [13], with foragers being expected to shift strategies as the environment shifts. Our model provides a formal, biologically-rooted explanation for these findings, as it explicitly accounts for the feed-backs between environmental conditions and predator movement, through the use of encounters as a metric of local environmental richness. It advances theoretical understanding of random walk search behavior by considering how both heading and step-size changes between time-steps should be related to environmental conditions. Our results suggest that we might expect to see as much structured variation in heading changes conditional on encounters in empirical data as we observe for step-size changes, and our model provides a theoretical framework which may help to explain such variation.

#### 3.2. Adaptive search heuristics and the marginal value theorem

The adaptive heuristics search model appears to approximate and generalize the marginal value theorem (MVT) [33] to continuous environments with spatially auto-correlated yields rather than discrete, hard-to-define patches. This arises from the fact that once in a high-density region of prey, the forager adaptively shifts step-size and heading change to thoroughly search the local environment (intra-patch behavior). However, once the prey in the local environment become depleted, the forager again adaptively shifts step-size and heading change in order to return to a locomotion style that elevates search efficiency be-

tween high density clusters (inter-patch behavior).

Thus, the “giving up time,” a classic metric from the MVT literature [34, 35, 36] used to measure patch leaving, has a simple formulation in our model. It is the maximum value of time-step lags,  $s$ , such that  $\psi_{[s]} > 0$  for heading changes and  $\phi_{[s]} < 0$  for step-size changes, since these parameters directly measure the relationship between an encounter  $s$  lags in the past, and one’s choice of movement at the present time-step. We leave a more formal exploration of the links between the MVT and our model of search to future work.

### 3.3. Conclusions

We provide reasons to suspect that foragers in natural environments with patchy prey distributions should not have been selected to use Lévy flights as their mode of search. Instead, we propose that adaptive encounter-conditional heuristics can improve search efficiency relative to pure Lévy flights. We use a simulation model to investigate the efficiency of each search mode under non-destructive and destructive foraging tasks. We demonstrate that adaptive encounter-conditional heuristics outperform Lévy flights in both contexts, but are especially useful in cases of non-destructive foraging (and/or when patches have high density). We conclude by presenting quantitative predictions that can be tested using empirical data on forager movement in humans and non-human animals.

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4     Frame (a) plots the difference in the mean values of  $\frac{M(X)-R_{\min}}{S(X)}$  between the adaptive search and Lévy flight algorithms (where  $X$  is the fraction of time-steps with encounters with prey items) as a function of  $R_{\min}$ . Frame (b) plots the difference in probability of survival, estimated using 1 minus the integral of the kernel density function of  $X$  over simulations from 0 to  $R_{\min}$ . In both sub-figures, the dark lines present the mean differences, and the shaded regions provide 95% confidence intervals. For both cases, we note that the entire confidence region rests above the value of zero, which implies that the adaptive search heuristics provide lower average probability of starvation relative to Lévy flights over the entire range of considered  $R_{\min}$  values. Note that in the case of destructive foraging,  $R_{\min}$  values greater than about 0.4 lead to almost certain starvation under both Lévy flight and adaptive heuristics models.

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Figure 1: Sample prey distributions in Cartesian space as realizations from a Gaussian random field with negative values truncated to zero and  $\ell = 0.01$  in frame (a) and  $\ell = 0.1$  in frame (b). When  $\ell$  is small, prey take on a relatively uniform distribution across space, but when  $\ell$  is large, prey items tend to co-occur in clumps or patches. As  $\ell$  grows, encounters with prey provide increasingly valuable information about the probability of encountering prey in nearby locations, and foragers can use this information to adaptively modulate their step-size and heading changes.

(a) Prey distribution in terms of kilos of biomass per unit area (pixel) when  $\ell = 0.01$ .  
(b) Prey distribution in terms of kilos of biomass per unit area (pixel) when  $\ell = 0.1$ .

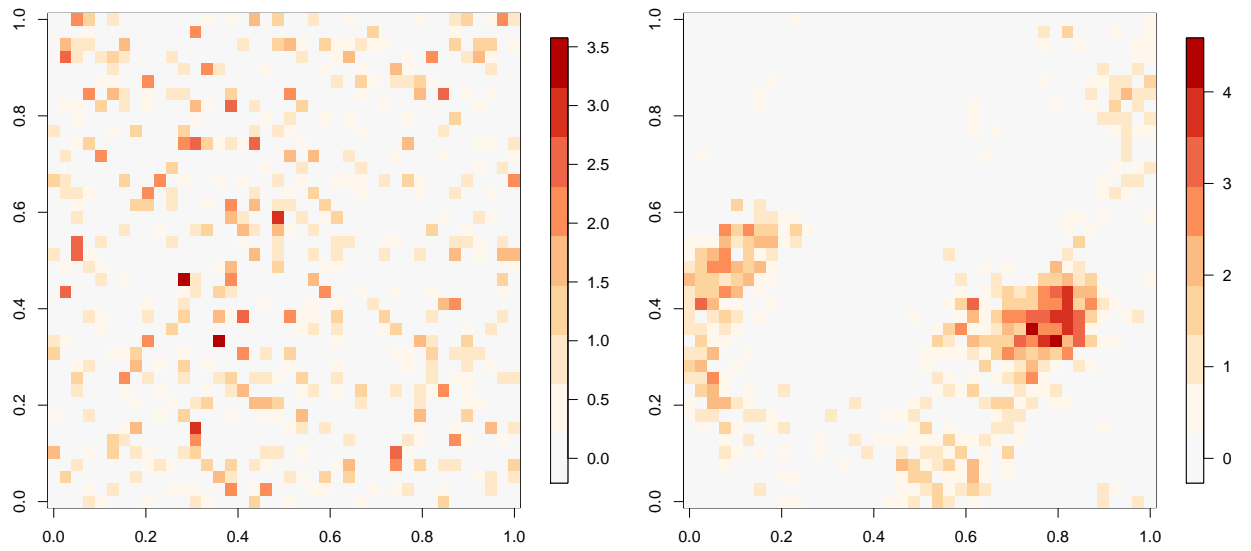
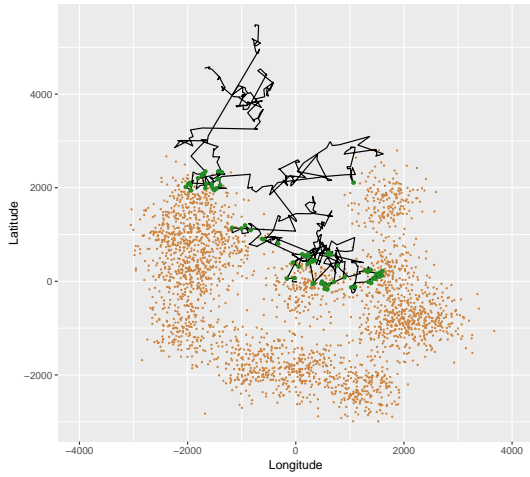
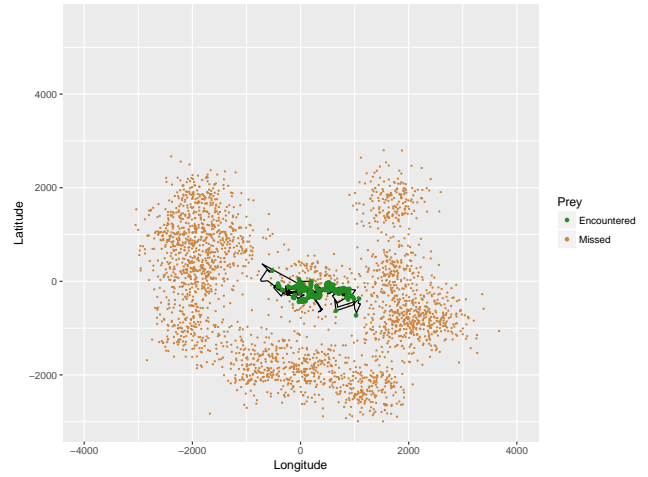


Figure 2: Diagnostics from the non-destructive foraging model over 200 random simulations. Frames 2a and 2b plot example tracks of the search strategies, chosen to demonstrate ‘typical’ behavior; note that the prey distribution was held fixed over simulations. Frame 2c illustrates the distribution of the sample mean and standard deviation of the log of step-size over simulations under each search mode; note that these values are much more variable under adaptive search, since step-size is modulated whenever the forager moves into or out of a high density region of prey, and foragers randomly stumble into patches in some simulations but not others. Frame 2d illustrates the distribution of the sample mean and dispersion of heading change (as a fraction of  $\pi$  radians, or 180 degrees) over simulations under each search mode. Finally, frames 2e and 2f plot the distributions of the mean and standard deviation in encounters (proxies for foraging efficiency) over simulations; a t-test for difference of means in Frame 2e is significant at the 0.001 level, with a mean difference of 0.34 (95PCI: 0.31, 0.37).

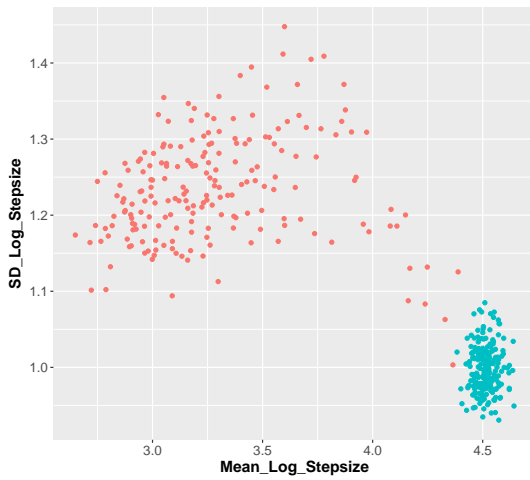
(a) A Lévy flight for 500 steps.



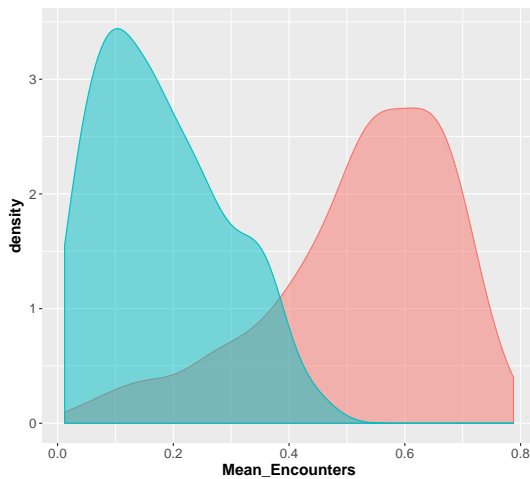
(b) An adaptive search for 500 steps.



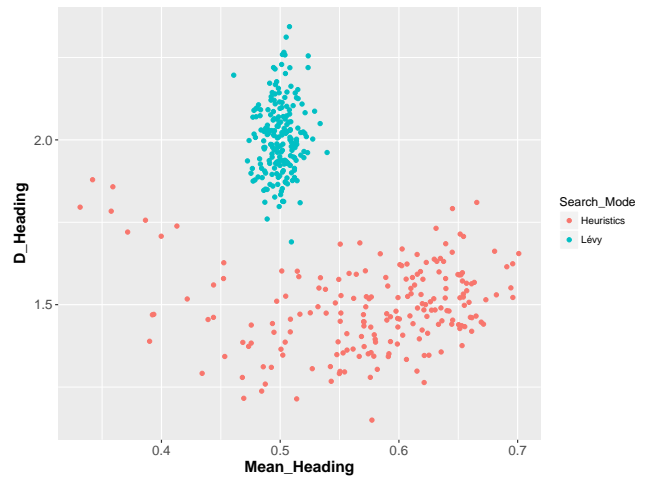
(c) Mean and dispersion of log step-size.



(e) Mean of encounters.



(d) Mean and dispersion of heading change.



(f) Standard deviation of encounters.

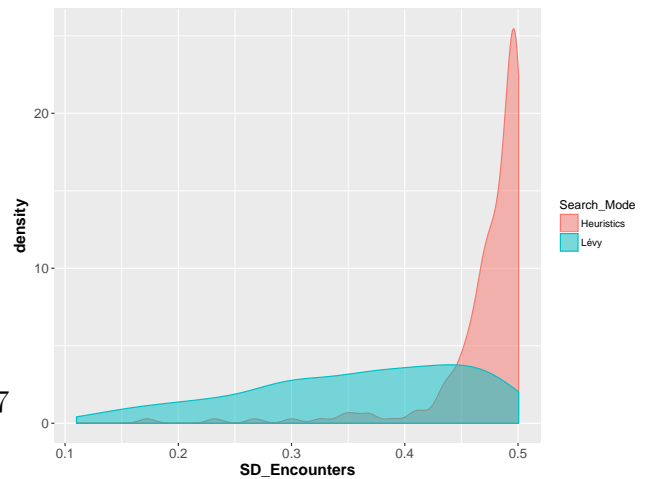
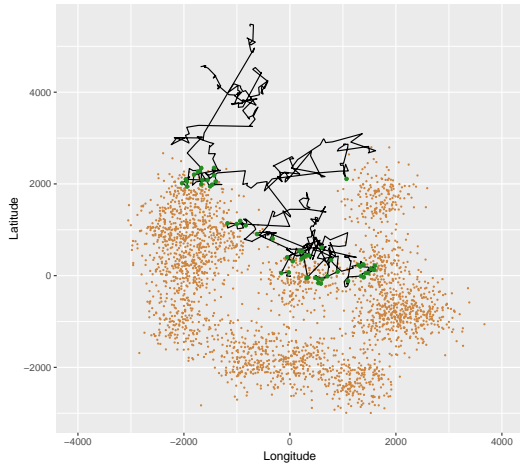
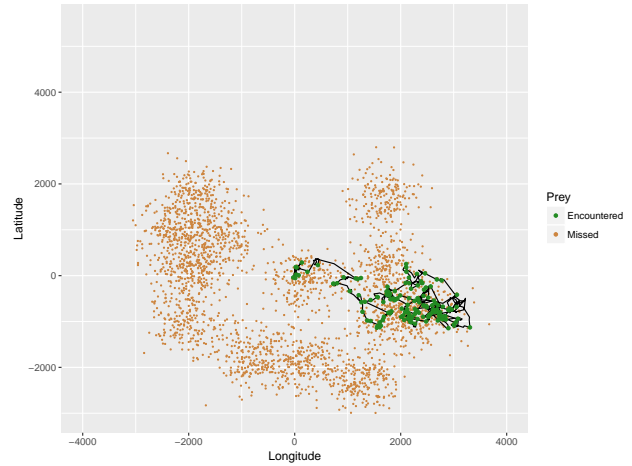


Figure 3: Diagnostics from the destructive foraging model over 200 random simulations. Frames 3a and 3b plot example tracks of the search strategies, chosen to demonstrate ‘typical’ behavior; note that the prey distribution was held fixed over simulations. Frame 3c illustrates the distribution of the sample mean and standard deviation of the log of step-size over simulations under each search mode; note that these values are much more variable under adaptive search, since step-size is modulated whenever the forager moves into or out of a high density region of prey, and foragers randomly stumble into patches in some simulations but not others. Frame 3d illustrates the distribution of the sample mean and dispersion of heading change (as a fraction of  $\pi$  radians, or 180 degrees) over simulations under each search mode. Finally, frames 3e and 3f plot the distributions of the mean and standard deviation in encounters (proxies for foraging efficiency) over simulations; a t-test for difference of means in Frame 3e is significant at the 0.0001 level, with a mean difference of 0.04 (95PCI: 0.02, 0.05).

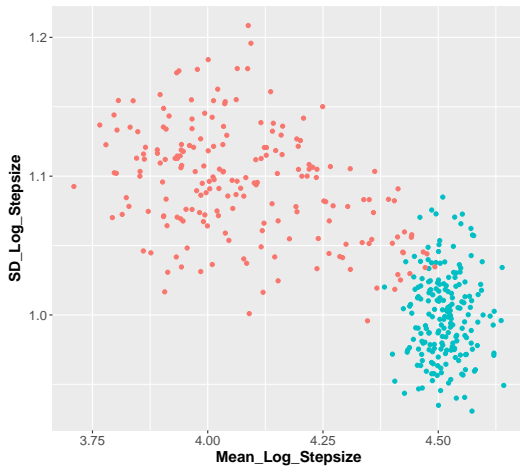
(a) A Lévy flight for 500 steps.



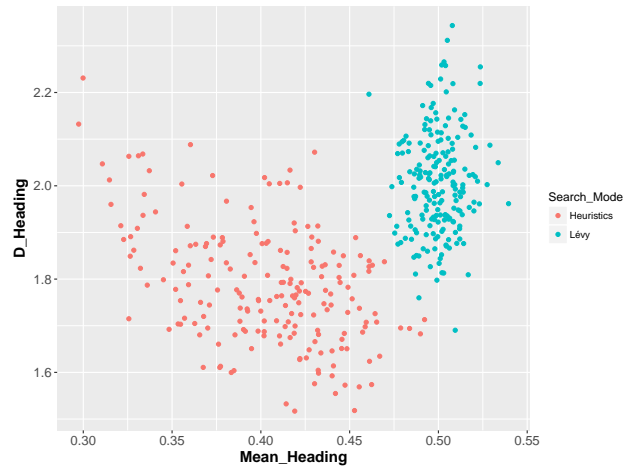
(b) An adaptive search for 500 steps.



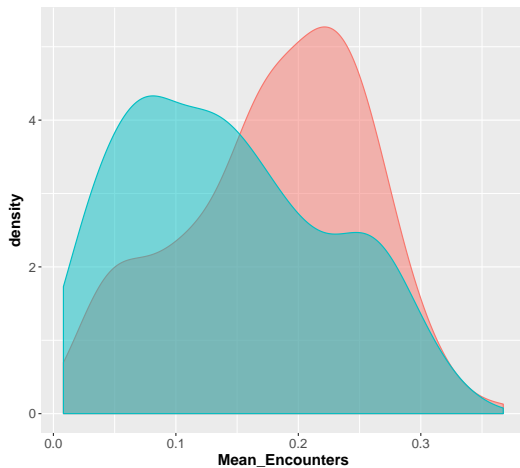
(c) Mean and dispersion of log step-size.



(d) Mean and dispersion of heading change.



(e) Mean of encounters.



(f) Standard deviation of encounters.

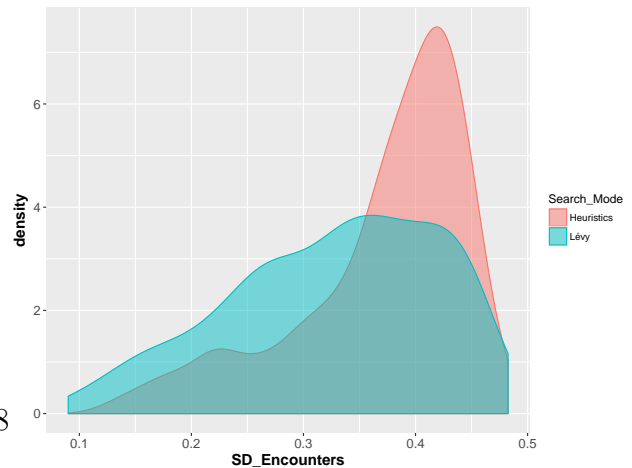
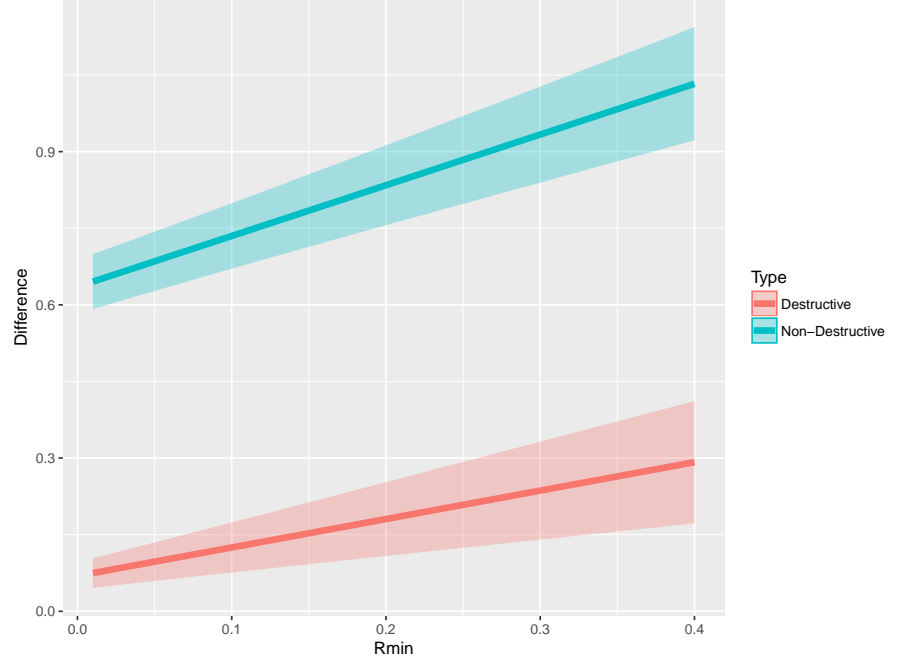




Figure 4: Frame (a) plots the difference in the mean values of  $\frac{M(X)-R_{\min}}{S(X)}$  between the adaptive search and Lévy flight algorithms (where  $X$  is the fraction of time-steps with encounters with prey items) as a function of  $R_{\min}$ . Frame (b) plots the difference in probability of survival, estimated using 1 minus the integral of the kernel density function of  $X$  over simulations from 0 to  $R_{\min}$ . In both sub-figures, the dark lines present the mean differences, and the shaded regions provide 95% confidence intervals. For both cases, we note that the entire confidence region rests above the value of zero, which implies that the adaptive search heuristics provide lower average probability of starvation relative to Lévy flights over the entire range of considered  $R_{\min}$  values. Note that in the case of destructive foraging,  $R_{\min}$  values greater than about 0.4 lead to almost certain starvation under both Lévy flight and adaptive heuristics models.

(a) Difference in risk estimated using Z-score model.



(b) Difference in risk estimated using integral of kernel density function.

