



A general model of forager search: Adaptive encounter-conditional heuristics outperform Lévy flights in the search for patchily distributed prey

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ABSTRACT

A theoretical and applied literature has suggested that foragers 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 information about the distribution of prey, gained either through evolved mechanisms, experience and memory, or social transmission of information. As such, we might expect selection for heuristics that make use of such information to further improve the efficiency of random search. Here we present a general model of random search behavior that includes as special cases: area-restricted search, correlated random walks, Brownian search, and Lévy flights. This generative model allows foragers to adjust search parameters based on encounter-conditional and other heuristics. 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 angle change they imply, relative to Lévy flights. We conclude by presenting a statistical model that can be fit to empirical data and a set of testable, quantitative predictions that contrast our model of adaptive search with the Lévy flight foraging hypothesis.

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1. Introduction

A theoretical and applied literature has suggested that foragers¹ 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 (Humphries and Sims, 2014; Viswanathan et al., 2008; 1999). There has been some empirical success in testing this hypothesis in humans (e.g., Raichlen et al., 2014; Reynolds et al., 2018) and non-human animals (e.g., Humphries et al., 2010; Sims et al., 2008). Other empirical studies either have failed to find evidence of such search behavior or found evidence of more nuanced patterns of

search in humans (Miramontes et al., 2012) and other animals (e.g., Auger-Méthé et al., 2016; Humphries et al., 2010; Pearce-Duvel et al., 2011). Recent theoretical work has also shown that two-scale search methods outperform Lévy flights (Benhamou and Collet, 2015). More generally, there is debate 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 (Edwards et al., 2007; Humphries et al., 2010; Plank and Codling, 2009).

An empirical literature on the movement patterns of marine predators (Humphries et al., 2010) suggests that while Lévy flights are common or even prevalent across many individuals, other movement patterns frequently occur. Specifically, movement tends to look Lévy in less productive environments and Brownian in more productive ones (Humphries et al., 2010; Sims et al., 2012). Humphries et al. (2010) read this behavior as consistent with the Lévy flight foraging hypothesis, with the addendum that revised theoretical models suggest that Lévy flights should occur in envi-

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

ronments where prey is sparse, but that Brownian motion should occur where prey is abundant (Bartumeus et al., 2002).

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 unlikely that natural selection should favor their use on these grounds. Foragers frequently have at least some information about the distribution and characteristics of their prey, either through evolved mechanisms (Eaton, 1970; Riffell et al., 2008), experience (Gumbert, 2000; Jackson and Wilcox, 1993), or social transmission of information (Barrett et al., 2017; Hewlett et al., 2011; Kitowski, 2009; Leadbeater and Chittka, 2007). As such, we might instead expect natural selection to favor search heuristics that exploit this information to further improve the efficiency of random search relative to either Lévy or Brownian movement (Benhamou and Collet, 2015).

In this paper, we extend insights from Benhamou and Collet (2015), who developed an algorithm that uses two-scale, cue-driven, adaptive modulation of step-size (the distance traveled in a given time interval) to outperform Lévy flights in random search. We generalize the idea to consider how environmental cues might affect both step-size and heading direction, and we allow for a continuous rather than two-scale relationship between environmental cues and forager behavior. Our extension also builds on existing literatures concerning area-restricted search (e.g., Kareiva and Odell, 1987; Weimerskirch et al., 2007) and correlated random walks (Auger-Méthé et al., 2015), which—like Lévy flights—are special cases of our more general theoretical model. By developing a joint model of changes in step-size and heading direction in light of encounters, our approach unifies a large range of foraging models and illustrates: (1) how apparent Lévy movement can sometimes be produced by the interaction of a prey distribution and a predator employing a simple set of adaptive encounter-conditional movement heuristics (Benhamou, 2007; Boyer et al., 2006; Reynolds, 2015), and (2) why foragers appear to rely on Lévy movement in prey sparse environments and more tortuous area-restricted search or Brownian movement in prey dense environments (Humphries et al., 2010; Sims et al., 2012).

Our approach has the desirable property of being both a generative model of data for running forward simulations and a Bayesian model 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 angle change 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 demonstrating how step-size and change in heading might optimally deviate from both of these models of random search as a function of the distribution of prey. We conclude by presenting a set of empirically testable, quantitative predictions that contrast our model of adaptive search with the Lévy flight foraging hypothesis.

1.1. Theoretical models of optimal search

The Lévy flight foraging hypothesis proposes 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 (Humphries and Sims, 2014; Wosniack et al., 2017). However, foragers frequently have 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 among 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. We argue here that updating one's movement parameters conditional on such encounter information can lead to more effective search.

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, $(x_{[t]}, y_{[t]})$, with a constant temporal separation of $t \in \{1, \dots, T\}$. 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 (Stover and Weisstein, 2014). 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 so that $r_{[t]} \in \mathbb{R}^+$ gives the linear distance between points $(x_{[t]}, y_{[t]})$ and $(x_{[t-1]}, y_{[t-1]})$, and $\theta_{[t]} \in (-\pi, \pi)$ 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 (Stover and Weisstein, 2014).

Note that while r can vary between time-steps, we currently make the simplifying assumption that energy investment between time-step t and $t + 1$ is constant.

1.2. Lévy flight foraging hypothesis

The Lévy flight foraging hypothesis asserts that we should expect:

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

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

in empirical measurements. The symbol $T[0, \infty]$ indicates support on \mathbb{R}^+ , since distances are non-negative. The Lévy or 'stable' (Mandelbrot, 1960) 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 $\beta = 0$ (Borak et al., 2005). Note that $\xi \in \mathbb{R}$ and $\zeta \in \mathbb{R}^+$ give the location and scale parameters. The step-size distribution of Lévy flights, broadly conceived, may have varying degrees of heavy tails based on the value of α . When researchers refer to Lévy flights they tend to imply only a heavy-tailed step-size distribution of some form or another, and not necessarily a stable distribution. For example, truncated Lévy, Weibull, log-normal, Pareto, and truncated Pareto distributions have all been used to model empirical movement patterns as Lévy flights (e.g., Rhee et al., 2011).

1.3. Adaptive encounter-conditional heuristics

While the predictions of the Lévy flight foraging hypothesis are both intuitive and theoretically motivated (Humphries and Sims, 2014) in the case of an informationless forager, foragers typically have opportunities to acquire information about their prey distributions. If we assume that foragers possess a few basic bits of information about their prey and two simple movement heuristics, then we should expect encounter-contingent distributions of both r and θ .

First, we assume that foragers:

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

Next, following models of correlated random walks and area-restricted search (e.g., Benedix Jr, 1993; Hamer et al., 2009; Hill et al., 2000; Hills et al., 2013; Kareiva and Odell, 1987; Weimerskirch et al., 2007), we assume that foragers have two heuristics:

1. If the forager has not recently encountered a prey item, then it infers that it is unlikely to be in a localized area of elevated prey density (i.e., a patch), and should thus reduce turning angles in order to adopt a more linear direction of travel. This minimizes the probability of backtracking into areas already established as having a low probability of yield. Alternatively, if the forager has recently encountered a prey item, then it infers that it is more likely to be in an area of relatively high local prey density, and should minimize the probability of leaving the patch by increasing heading-angle changes (Fauchald, 1999; Weimerskirch et al., 2007).
2. If the forager has not recently encountered a prey item, then it infers that it is likely to be between patches of elevated prey density, and should take larger step-sizes (i.e., move at a higher velocity). Outside of a patch, it does not pay to search in great detail. However, once in a rewarding patch, as evidenced by a recent encounter with prey, it is best to reduce step-size to minimize the probability of leaving the patch or spooking prey with rapid movement (Kareiva and Odell, 1987; Weimerskirch et al., 2007; Winterhalder, 1983).

1.3.1. Modeling prey distributions

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 measured by their number, biomass, density, utility, or some other descriptor, P , are distributed over an arbitrarily large number of points in space according to a Gaussian random field (Abrahamsen, 1997), where:

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

with M representing the mean vector of the distribution, ς representing a diagonal matrix of parameters to scale variance, and ρ representing the correlation matrix where:

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

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.

If ℓ 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 Fig. 1). If ℓ is fairly large relative to the scale of search, this is indicative of spatial aggregation 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 ℓ is large enough to provide some level of patchiness to prey items on a scale relevant to the search problem.

1.3.2. Modeling forager movement

Assume that a forager searches for T total time-steps. From the heuristics outlined above, the optimal change in heading that a forager should make at time $t \in \{1, \dots, T\}$ is some increasing function

of the probability of being inside of a patch—i.e., a localized area of increased prey density. Let us assume that these patches are large relative to a forager’s average speed and the length of the time-step. Then, 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, where S is normally a small fraction of T . While there is no general function that we should expect from theory alone, one flexible and empirically tractable modeling approach (Ferrari and Cribari-Neto, 2004) would suggest that the distribution of heading changes can be given by a Beta regression, since these values are interval constrained:

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

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

$$\mu_{[t]} = \text{logit}^{-1}\left(\psi_{[0]} + \sum_{s=1}^S \psi_{[s]} E_{[t-s]}\right) \tag{8}$$

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 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—a member of the heavy-tailed family. Information theoretic model comparison of step-sizes in Lévy-like movement in humans (Rhee et al., 2011) have shown that the log-normal distribution outperformed other commonly used distributions. As such, we let the distribution of step-sizes be:

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

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

$$\eta_{[t]} = \left(\phi_{[0]} + \sum_{s=1}^S \phi_{[s]} E_{[t-s]}\right) \tag{10}$$

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.

The model is then completed by placing priors on the unknown parameters; see Supplementary Appendix and model code. Eqs. (7)–(10) describe a Bayesian 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 $(-\pi, \pi)$, we need multiply by a random variable $z \in \{-\pi, \pi\}$, which takes each value with equal probability and allows for either clockwise or counter-clockwise turns of between 0 and π radians. In the next section, we use such a simulation model—also provided in the Supplementary Materials—to study the foraging strategies of interest.

2. Simulation results

Previous research (Humphries and Sims, 2014) has suggested that there are two important cases of foraging, non-destructive and



Fig. 1. Sample prey distributions in Cartesian space. The distributions are derived from samples taken 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 ℓ is small, prey take on a relatively uniform distribution across space, but when ℓ is large, prey items tend to co-occur in clumps or patches. As ℓ grows, encounters with prey provide increasingly valuable information about the probability of encountering prey nearby, and foragers can use this information to adaptively modulate their step-size and heading change.

destructive, or—in the language of Charnov et al. (1976)—foraging for renewing and non-renewing prey. In the first case, prey items are not noticeably depleted by harvesting, with effective density remaining constant; in the second case, 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 interior. 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 its environment—see Supplementary Appendix and model code for details on the specific parameter values used. The forager can detect prey items within a small radius of his or her location at each time point; we set this parameter at approximately $\frac{1}{4}$ of the average step-size of the search algorithms. Note here that the forager only evaluates if prey have been encountered at each discrete time-point; prey are not encounterable *en route* between locations. This assumption simplifies the simulation, and ensures that the detection area at each time-step is constant, rather than step-size dependent. The adaptive forager makes use of encounter information to update its search parameters ($\mu_{[t]}$ and $\eta_{[t]}$) in the next time-step, following Eqs. (7)–(10).

All foragers begin their paths at the origin and are run for 500 time-steps. The simulations were carried out both on a flat plane and on a flat torus in order to avoid possible edge effects—we find similar qualitative results in both cases; see Supplementary Materials. Each simulation was replicated 300 times; our findings summarize the entire resultant distribution. We tested each comparison between search models under varying levels of spatial correlation. Here, we present results under moderate levels of spatial correlation. We present further results in the Supplementary Materials. Varying the level of spatial correlation alters the numerical values presented in the main paper, but not the qualita-

tive findings. To ensure a fair comparison, the parameters of the adaptive search model were set such that the distributional properties of both step-size and heading angle change in the absence of encounters were equal to those of the Lévy model. The simulation code is written in R (R Core Team, 2016); the Bayesian model for empirical analysis is written in Stan via rstan (Stan Development Team, 2016). Both workflows are included in the Supplementary Materials and will be maintained at: <http://www.github.com/ctross/adaptivesearch>.

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, unbeknownst to the predator. While there will almost always be at least some decreasing returns to 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 or where prey items may be encountered but are not easily captured.

Our simulation results show strong differences in the behavior of the search algorithms. Fig. 2 depicts the principle findings. First, we plot a representative path of the random flight taken by each search algorithm: Fig. 2a plots a sample Lévy flight and Fig. 2b plots a sample flight of the adaptive encounter-conditional search model. The Lévy flight exhibits its classic behavior, and explores the environment with a heavy-tailed mix of step lengths. Because there is no feedback between encounters and behavior, the Lévy flight prematurely leaves the high density patches it encounters rather than remaining to exploit them; it also enters phases of apparent area-restricted search in the absence of any indication that the area is dense in prey. 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.



Fig. 2. Diagnostics from the non-destructive foraging model over 300 random simulations. Frames 2a and 2b each plot an example track of the indicated search strategy, chosen to demonstrate typical behavior. The prey distribution is held constant over simulation runs, but forager tracks vary from one simulation to the next. Frame 2c illustrates the distribution of the 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 encounters prey, and foragers randomly stumble into patches of prey in some simulations but not others. Frame 2d illustrates the distribution of the mean and (inverse) dispersion of heading change (as a fraction of π radians, or 180°) over simulations under each search mode. Finally, frames 2e and 2f plot the distributions of the mean and standard deviation of encounter rate (proxies for foraging efficiency) over simulations; a t -test for difference of means between the adaptive and Lévy models in frame 2e is significant at the 0.001 level, with a mean difference of 0.79 (95PCI: 0.75, 0.84).

Fig. 2c demonstrates that in the case of the Lévy flight, a single set of parameters controls the log of step-size across all foraging trips, as is apparent from the tight clustering of blue points on the plot. In contrast, the adaptive model allows the step-size distribution on any trip to vary based on encounter-contingent responses to environmental conditions like prey density, as indicated by the more disperse set of red points on the same plot.

Fig. 2d demonstrates that the parameter for heading change shows a similar pattern; in the case of the Lévy flight, a single set of parameters controls heading change across all trips. In contrast, the adaptive model generates an over-propensity to change heading relative to the value expected under pure Lévy movement when in patches. This ensures increased backtracking and fine-scale resolution of search when in high yield patches, and less backtracking when not in patches.

Finally, Fig. 2e and f present the mean return rates of each strategy in encounters per time-step, as well as the associated coefficients of variation. These figures demonstrate that adaptive search yields higher and less variable returns than Lévy flights in this non-destructive foraging context.

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 in the behavior of the search algorithms, although they are not as pronounced as in the non-destructive case. Fig. 3 outlines the principle findings. Fig. 3a plots a sample Lévy flight and Fig. 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 feedback between encounters and behavior, the Lévy flight leaves high density patches prematurely (as in Fig. 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 enhance its probability of remaining in a high density region. This strategy eventually reduces the prey density in the patch, leading to reduced encounters and a return to an inter-patch heuristic governing motion, in a pattern like that predicted by the marginal value theorem (Charnov, 1976).

Fig. 3c demonstrates that in the case of the Lévy flight, a single set of parameters controls the log of step-size across all trips, as is apparent from the tight clustering of points. In contrast, the adaptive model allows the step-size distribution on each trip to vary based on environmental feedbacks in the search process. Nevertheless, the contrast is less stark than in the non-destructive foraging case, since prey depletion leads to a return of Lévy-like, inter-patch movement. Fig. 3d demonstrates a similar pattern, but with heading change.

Finally, Fig. 3e and Fig. 3f present the distributions of mean return rate and standard deviation in return rate across search strategies. These figures demonstrate that adaptive encounter-conditional heuristics yield higher and less variable returns than Lévy flights, even in the case of destructive foraging.

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. Thus, we can assess the risk—i.e., the odds of a

serious food shortfall—associated with the two using the Z-score model (Stephens, 1981; Stephens and Charnov, 1982), at least in contexts where outcomes are distributed approximately normally. The Z-score model states that the optimal choice from a given strategy set is the option which maximizes the value: $\frac{M(X)-R_{\min}}{S(X)}$, where 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 option which maximizes this value also minimizes the probability of starvation.

Fig. 4a demonstrates an application of the Z-score model for varying levels of $R_{\min} < 0.5$. We present the difference in the probability of survival implied by $\frac{M(X)-R_{\min}}{S(X)}$ between the adaptive search and Lévy flight algorithms. Here, X is a vector of the number of prey items encountered at each time-step—these items are assumed to be of uniform caloric yield. For both non-destructive and destructive foraging the mean values of $\frac{M(X)-R_{\min}}{S(X)}$ under the adaptive search model exceed the same values under the Lévy flight model over the entire 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. This procedure yields a finer approximation of the probability of avoiding starvation. We then calculate the difference in survival probabilities. We present these results in Fig. 4b. We draw the same qualitative conclusions as from the Z-score model.

2.4. Innate versus epiphenomenal Lévy patterns

It has been argued that linked predator-prey dynamics can produce gross predator movement patterns similar in structure to Lévy movement depending on the distribution of resources in the environment (Boyer et al., 2006; Reynolds, 2015) and that correlated random walks can lead to Lévy-like movement patterns (Benhamou, 2007). As such, observations of apparent Lévy search are not necessarily indicative of innate adaptations to search with Lévy movement. For example, a forager employing the adaptive heuristics described in the present analysis may have ω in Eq. (9) small enough to produce an approximately Gaussian step-size distribution in an environment devoid of prey, and yet move under an apparently heavy-tailed step-size distribution in the presence of patchily distributed prey. This would be the case if temporal variance in $\eta_{[t]}$ is large, due the non-zero values of $\phi_{[s]}$ coupled with variance in encounters (Fig. 5).

Kölzsch et al. (2015) have used experimental methods to suggest that mud snails have innate adaptations to search with Lévy movement, since they forage in such a manner even under experimental conditions where food items have been removed from the environment. However, our model shows that foragers with innate adaptations to search using encounter-conditional heuristics, will also search using an apparent Lévy flight in an environment devoid of prey, if ω in Eq. (9) is large enough to produce a heavy tail. This results from the fact that: (1) under the Lévy flight foraging hypothesis, the $\phi_{[s]}$ parameters, which control the effects of lagged encounters on step-size are equal to zero, and (2) search in environments devoid of prey ensures that $E_{[t-s]}$ will be zero. As such, in an empty environment, identical values of $\eta_{[t]}$ will be produced by the Lévy and adaptive search models with the same $\phi_{[0]}$ and ω parameters (Fig. 6).

These observations imply that it will be difficult to test whether animals of a given type have specific adaptations for search using Lévy flights or encounter-conditional heuristics using only distribution-level analysis, since both mechanisms can lead to similar distributions of step-size in both prey-possessing and prey-

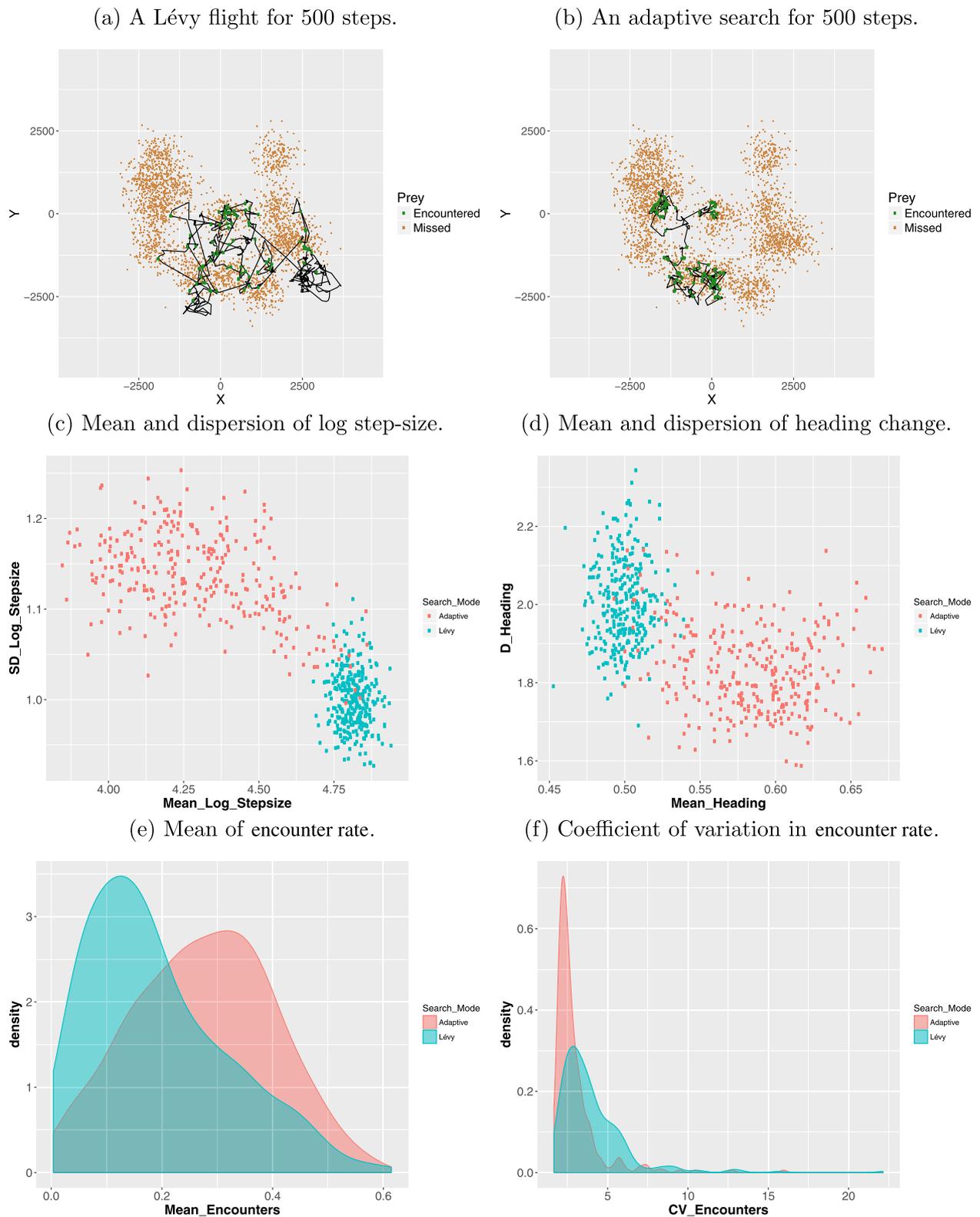
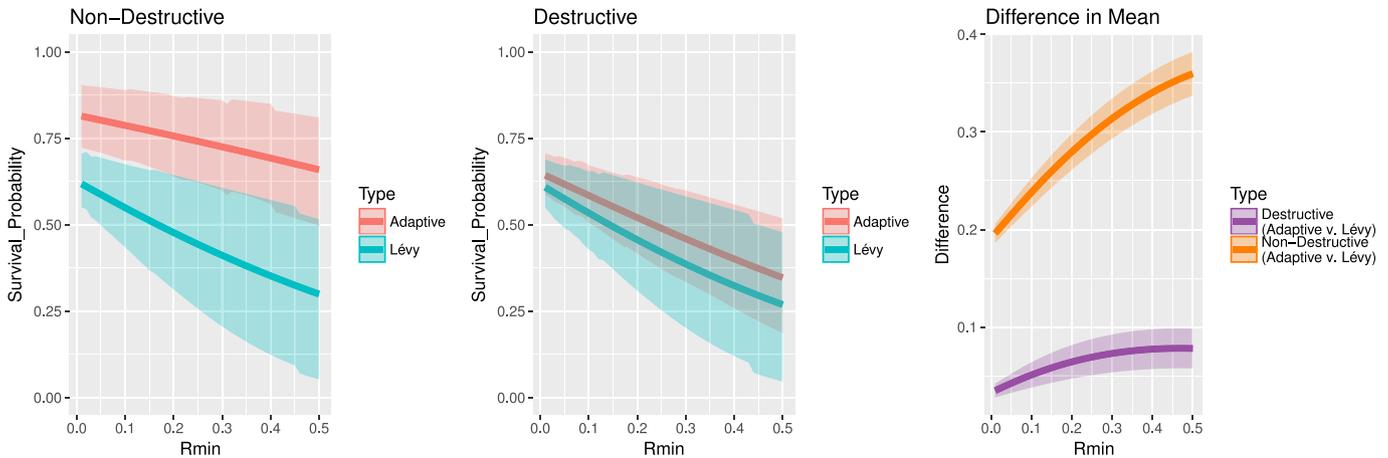


Fig. 3. Diagnostics from the destructive foraging model over 300 random simulations. Frames 3a and 3b each plot an example track of the indicated search strategy, chosen to demonstrate typical behavior. The prey distribution is held constant over simulation runs, but forager tracks vary from one simulation to the next. Frame 3c illustrates the distribution of the 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 mean and (inverse) dispersion of heading change (as a fraction of π radians, or 180°) over simulations under each search mode. Finally, frames 3e and 3f plot the distributions of the mean and standard deviation of encounter rate (proxies for foraging efficiency) over simulations; a t -test for difference of means in frame 3e is significant at the 0.001 level, with a mean difference of 0.08 (95PCI: 0.06, 0.10).

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



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

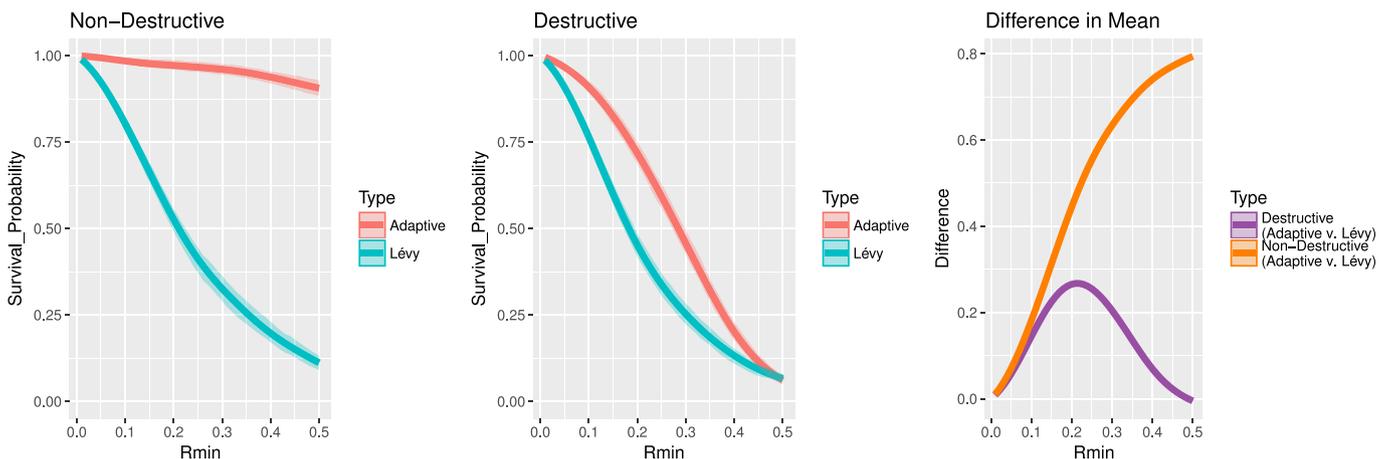


Fig. 4. Risk-sensitive comparison of adaptive versus Lévy search modes. Frame (a) plots the probability of survival with 90% confidence intervals under the Z-score model as a function of R_{\min} in both non-destructive and destructive foraging situations (the first two sub-frames). The final sub-frame plots the mean difference in survival probability between algorithms for each foraging context. Frame (b) plots the same measures, but uses 1 minus the integral of the kernel density function of X from 0 to R_{\min} to define the probability of survival. For both cases, the majority of the confidence region for the difference in survival probability rests above the value of zero, which implies that the adaptive search model provides lower average probability of starvation relative to Lévy flights. Note that, in the case of destructive foraging in frame (b), R_{\min} values greater than about 0.5 lead to almost certain starvation under both Lévy flight and adaptive models.

free environments. Encounter-conditional models, like the one presented here, however, provide a promising empirical means of disentangle these explanations, by separating out the extent to which variance in step-size is driven by encounter-dependent factors, controlled by $\phi_{[s]}$, and encounter-independent factors, controlled by ω .

Moreover, because our approach accounts for heading-angle change and step-size jointly, equal-interval GPS data can be appropriately modeled at fine time-scales, without use of data manipulations (like use of turning angle thresholds to define ‘steps’). Empirically, animal movement measured over small, consistently spaced time intervals are unlikely to be heavy-tailed; there are normally strong limits on maximum foraging velocity. The fact that much animal movement appears to show Lévy-like patterns may reflect a tendency to move with highly correlated direction across time steps (Benhamou, 2007), rather than a tendency to move with a heavy-tailed velocity distribution.

While this qualification is well conveyed in discussions of Lévy search, empirical work has nevertheless focused mainly on analyzing the distributional properties of step-size—but see Auger-Méthé et al. (2016) for a more nuanced analysis of both terms. By considering step-size and heading change jointly, our model, like that

of Auger-Méthé et al. (2016), allows for the differential effects of velocity and heading-angle change on overall foraging dynamics to be estimated. Rather than comparing which of two basic models of search better correspond to the distributional forms of predator movement paths, these more general models allow an estimation of how variation in biologically meaningful parameters of movement are associated with variation in ecological circumstance.

2.5. Predictions for empirical studies

A merit of the modeling approach presented here is that it permits some explicit empirical tests contrasting 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. $\mu v = 1$ and $(1 - \mu)v = 1$, which is solved when $\mu = \frac{1}{2}$ and $v = 2$. 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—also follows a uniform distribution.

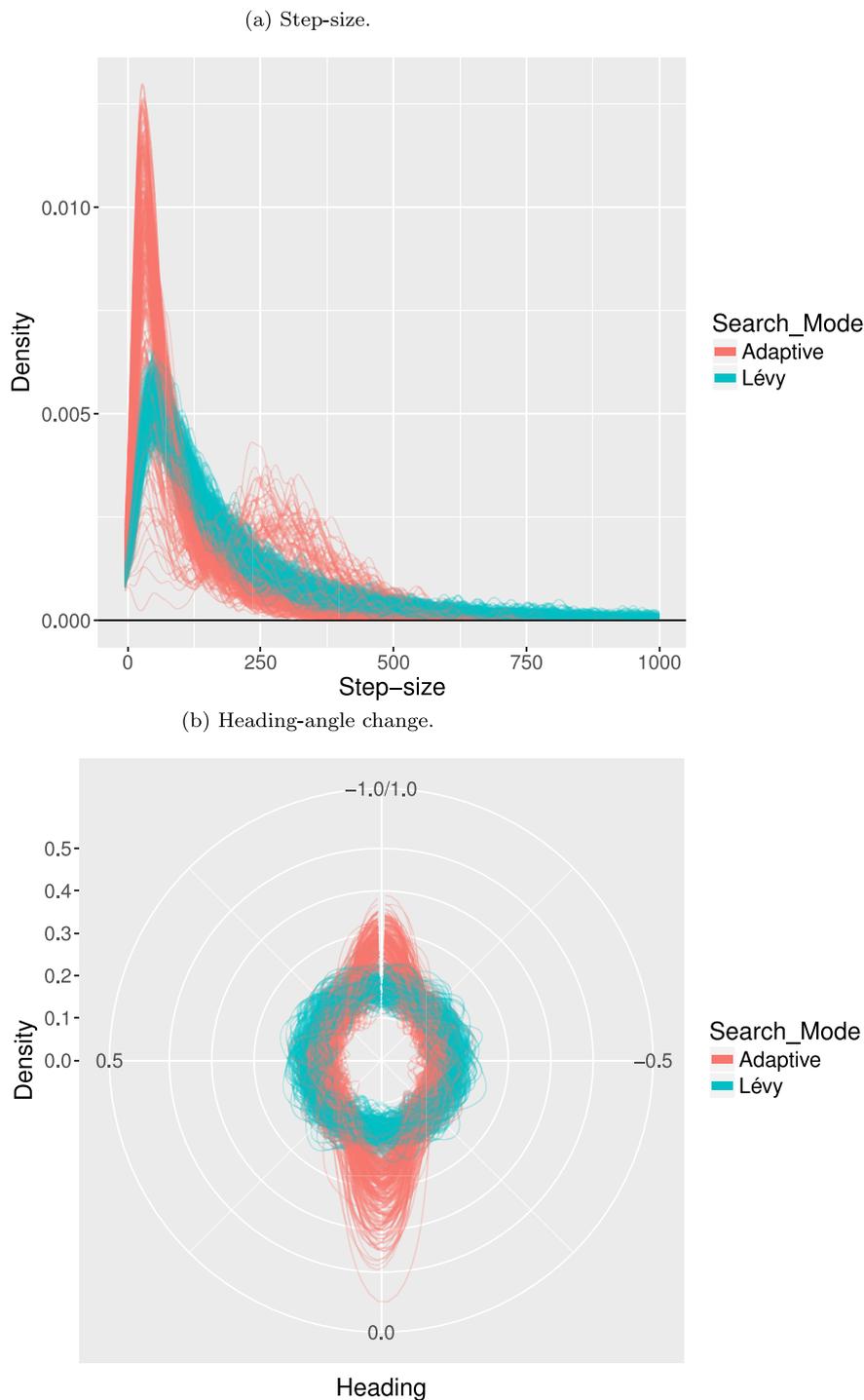


Fig. 5. Simulations ($n = 200$) from an adaptive model and a Lévy model in an environment with prey. The parameters of the adaptive model were set so that: (1) step-size in the absence of encounters is approximately Gaussian, and (2) heading direction is auto-correlated in the absence of encounters, but highly tortuous in the presence of encounters. See Supplementary Appendix for exact parameter values. Frame (a) plots the kernel density distribution of step-size under each simulation. For the majority of simulations, the adaptive and Lévy models produce very similar step-size distributions. In a subset of cases, the adaptive model fails to encounter a patch, and thus spends the majority of its time using a large inter-patch step-size exploring mostly empty space, leading to the secondary density peak between 250 and 500 units. Frame (b) plots the kernel density distribution of heading angle on a circle for each simulation. In this plot, a uniform density forms a circular curve; density peaks correspond to heading angles with increased occurrence. For the adaptive model, we see an elevation of density in the higher-angle, tortuous parameter region (near -1 and 1 radians), and in the low-angle, temporally auto-correlated region (near 0 radians). We see a uniform density on heading change for the Lévy flight.

And, it predicts that:

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

In contrast, in situations of well-defined patchiness—empirically estimable by the parameter, ℓ —the adaptive search heuristics outlined in this paper predict that heading change 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 that:

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

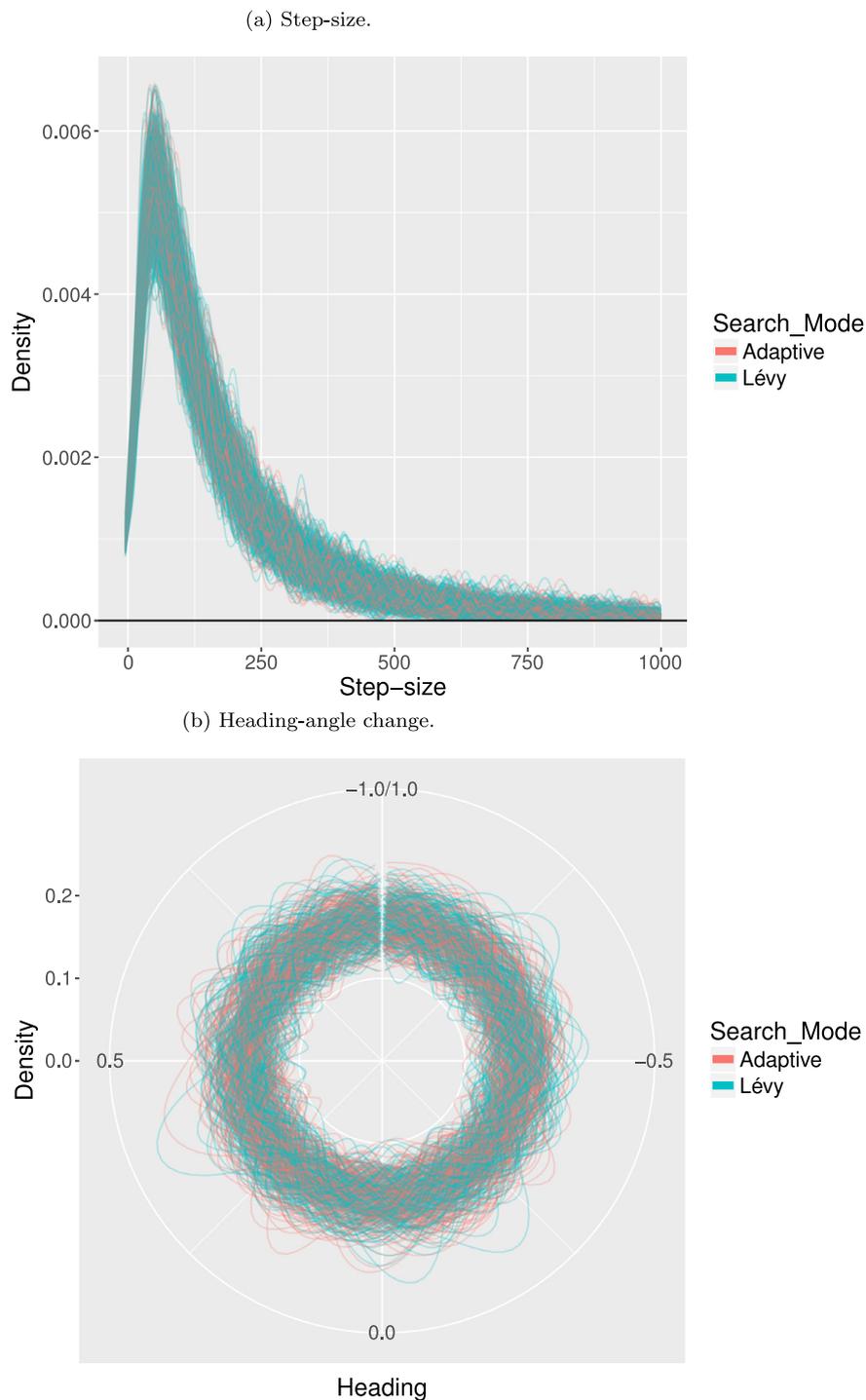


Fig. 6. Simulations from an adaptive model and a Lévy model in an environment with no prey. The parameters of the adaptive model were set to be exactly equal to the Lévy flight parameters in the absence of encounters. See Supplementary Appendix for exact parameter values. Frame (a) plots the kernel density distribution of step-size under each simulation. Frame (b) plots the kernel density distribution of heading angle on a circle for each simulation. In this plot, a uniform density forms a circular curve; density peaks correspond to heading angles with increased occurrence. In both frames, the distributional forms are identical (note that a small jitter was added to help visualize the results).

With respect to the distribution of step-size (Eqs. (9) and (10)), the Lévy flight foraging hypothesis predicts that the mean of the log of step-size is constant over time, and that the variance of the log of step size should be large:

4. $\phi_{[1]}, \dots, \phi_{[S]} = 0$, indicating an absence of relationship between encounters and step-size over all time lags.
5. ω is large enough to produce a heavy tailed step-size distribution.

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

6. $\phi_{[1]}, \dots, \phi_{[S]} < 0$, indicating a negative relationship between encounters and step-size over some range of time lags.

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, ℓ , 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, ℓ , 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

The simulation models suggest that adaptive search outperforms Lévy search by increasing foraging returns. If prey are patchy in distribution, information-based measures should behave this way (see also Benhamou and Collet, 2015)—better information generally allows for better predictive inference.

In the case of non-destructive foraging, adaptive search sharply outperforms 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 and consequently encounters decrease to zero, the Lévy and adaptive search strategies can converge to identical behavior. However, as prey become more dense within their patches and encounters provide information to the forager, gains to adaptive search increase. Moreover, not only is adaptive search more efficient on average, our risk sensitive foraging analysis shows that it also minimizes the chances of resource shortfalls.

Our findings here echo previous theoretical (Bartumeus et al., 2002; Benhamou and Collet, 2015) and empirical (Humphries et al., 2010) results demonstrating that a forager's search behavior is expected to change as a function of environmental conditions. 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 are abundant (Bartumeus et al., 2002), with foragers altering their search tactics as the environment shifts. Our model provides a formal, biologically-rooted explanation for these findings, as it explicitly accounts for the feedbacks between environmental conditions and predator movement through the use of encounters as a metric of local environmental richness. It advances theoretical understanding of search behavior by considering how both heading and step-size changes between time-steps should be related to environmental conditions. We expect to see as much structured variation in heading change conditional on encounters in empirical data as we observe for step-size, and we provide a statistical framework along with model code that might help to test for such variation.

3.2. Adaptive search heuristics and the marginal value theorem

The adaptive search model leads to forager behavior similar to that predicted by the marginal value theorem (MVT) (Charnov, 1976), but generalizes the MVT model to continuous environments with spatially auto-correlated yields, rather than discrete patches, which are frequently difficult to define in empiri-

cal contexts. This result arises from the fact that once in a high-density region of prey, the forager adaptively decreases step-size and increases heading angle change to thoroughly search the local environment (intra-patch behavior). However, as the prey in the local environment become sufficiently depleted, encounters become less likely and the forager adaptively increases step-size and decreases heading angle change in order to return to a locomotion style that elevates search efficiency between high density clusters (inter-patch behavior).

Thus, “giving up time,” a classic metric from the marginal value theorem literature (Krebs et al., 1974; Oaten, 1977; Wildhaber et al., 1994) used to measure patch leaving, has a simple analog 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 marginal value theorem and our model of search to future work.

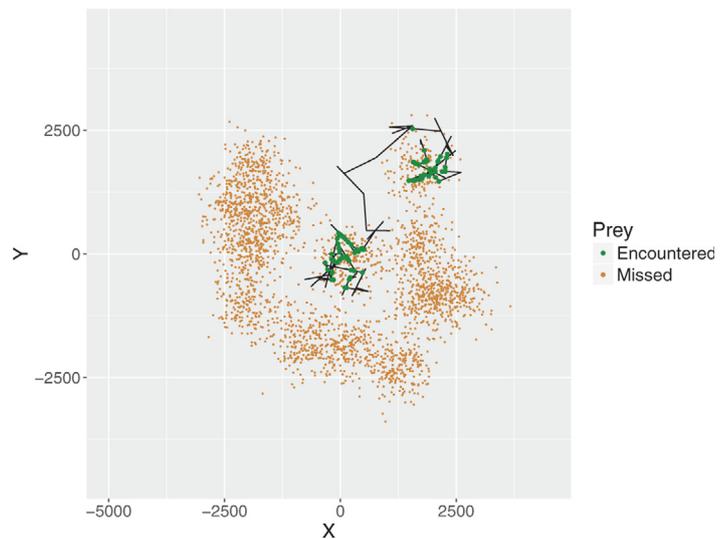
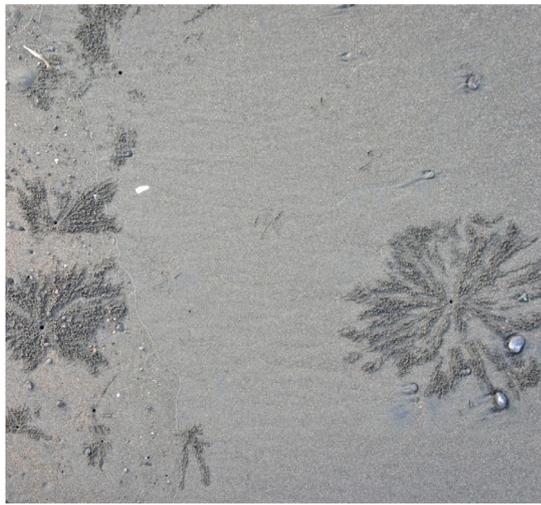
3.3. Modeling optimal search, beyond Brownian and Lévy movement

Although Brownian and Lévy movement are well studied, many animals forage in ways that are not easily described by either of these models. For example, the movement behavior of sand-bubbler crabs (e.g., *Scopimera* and *Dotilla*) normally consists of a series of radially distributed linear paths to and from burrow holes (Gherardi and Russo, 2001), see Fig. 7. This style of foraging, like Brownian and Lévy movement, can also be described by a special case of our model. Specifically, these paths correspond closely to our simulation results under contexts with a very low value of ν —note here that small values of $\nu < 1$ force turning angles to primarily take values very close to 0 or 180°; i.e., the forager predominantly moves directly away from or directly back to the origin.

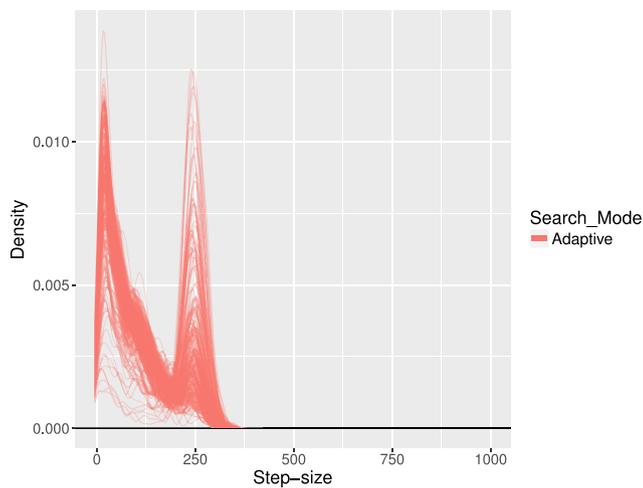
The search problem of these deposit feeders differs from that of large predatory fish, birds, and mammals normally modeled as using Lévy or Brownian search. Here the challenge is not one of encountering hard to find prey items, since the crabs feed on a roughly uniform substrate of tidally deposited detritus and plankton (Gherardi and Russo, 2001; Maitland, 1986); rather, the search problem consists of minimizing the risk of being attacked by a predator while foraging in a completely open environment. Absent other cues, the difficulty of calculating the optimal heading direction to minimize travel distance back to one's primary shelter (e.g., the burrow for a sand-bubbler crab) will depend on the complexity and length of the foraging sequence since departure. The greater the range of possible turning angles taken at each step, for example, the greater the difficulty in calculating the shortest path to home. For a fixed value of $\mu_{[t]}$, the complexity of the path can be reduced by minimizing ν as much as possible—i.e., only ever taking steps directly away from, or directly towards one's shelter. This, in turn, reduces the time required to reach shelter if a predator is spotted.

While our model was not developed to examine the search patterns of sand-bubbler crabs, its generality allows a theoretically based exploration of many forms of movement that do not correspond to the standard Brownian and Lévy modes of search. For the same reason, by incorporating many standard search modes as special cases, our model allows wider-scale investigations of the relationship between environmental context and the parameter values of a single generative model of search. For example, according to Gherardi and Russo (2001); Gherardi et al. (2002), sand-bubbler crabs sometimes engage in wandering behavior while foraging, rather than foraging around the primary burrow. Wandering typically yields access to higher quality food deposits, and quicker nutrient acquisition, but increases predation

- (a) Deposits left by sand-bubbler crabs foraging during low tide. Photograph by author (CTR). (b) Simulated path of a forager with $\nu = 0.1$. This parameter value produces a movement form with predominate ‘out-and-back’ behavior.



- (c) Kernel density distribution of step-size under each simulation of a forager with $\nu = 0.1$.



- (d) Circular density plot of heading angle of a forager with $\nu = 0.1$. Note high density on values near zero and $-1.0/1$, where zero represents no change in heading and a value of 1 or -1 represents a 180° change. There is very low density on other heading angles. This leads to a form of search where the forager generally moves either directly out from, or directly back towards, a given location.

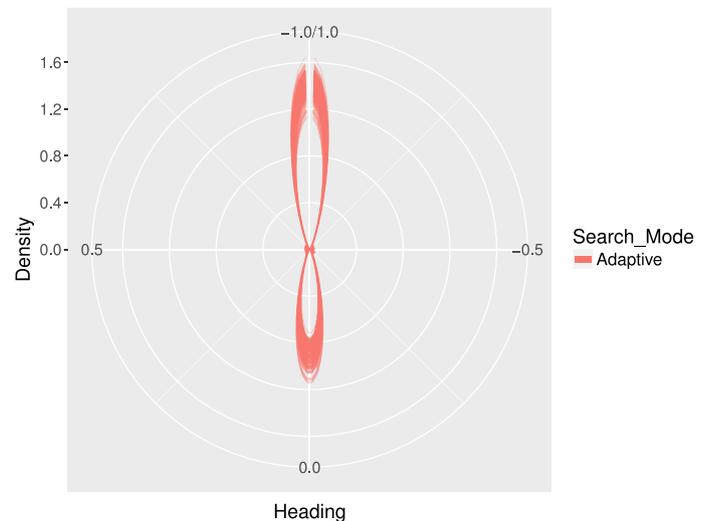


Fig. 7. Empirical and theoretical foraging movement by sand-bubbler crabs.

risk (Gherardi and Russo, 2001; Gherardi et al., 2002). Our model predicts that wandering behavior (high ν) would be favored in contexts where predation risk is relatively low, whereas the standard foraging behavior would be favored when it is high. Although ν was not modeled as a function of predictor variables in the current draft, such an extension of our model could be implemented to address such a question.

3.4. Conclusions

In environments with patchy prey distributions, adaptive encounter-conditional heuristics can improve search efficiency relative to Lévy flights. In our simulations, adaptive encounter-conditional heuristics outperformed Lévy flights under both non-

destructive and destructive foraging tasks, but the relative difference in performance was greater in cases of non-destructive foraging—and/or when patches have high density.

Nevertheless, nothing about our model demonstrates that heavy-tailed step-size distributions are inefficient when combined with encounter conditional heuristics. In fact, as argued by Kölzsch et al. (2015) it is theoretically possible for animals to have innate adaptations for both adaptive encounter-conditional modulation of search parameters and adaptations for search using a heavy-tailed step-size distribution. Validation of such predictions about search tactics and their possible dependence on encounters, however, will require estimates of the parameters of a generative model that explicitly accounts for both possibilities. Our approach provides the conceptual basis and code (Supplemental Materials)

needed to fit such a model using empirical movement data collected from human and non-human foragers.

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Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jtbi.2018.07.031.

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