Random foraging and perceived randomness

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Abstract

Research in evolutionary ecology on random foraging seems to ignore the possibility that some random foraging is an adaptation not to environmental randomness, but to what Wimsatt called "perceived randomness". This occurs when environmental features are unpredictable, whether physically random or not. Mere perceived randomness may occur, for example, due to effects of climate change or certain kinds of static landscape variation. I argue that an important mathematical model concerning random foraging does not depend on randomness, despite contrary remarks by researchers. I also use computer simulations to illustrate the idea that random foraging is an adaptation to mere perceived randomness.

1 Introduction

I argue that in an important research area in evolutionary ecology focusing on random foraging, researchers seem not to have noticed that their arguments don't depend on ran-

domness within environments, but only on what Bill Wimsatt (1980) called "perceived randomness". An organism or population experiences perceived randomness in dimensions or aspects of its environment that are unpredictable, whether those elements are physically random in the sense of being probabilistically distributed or not. The environmental variation may be entirely systematic—to take the most extreme case—but if the organisms are not sensitive to that systematicity, they experience perceived randomness. Analogously, if an environment changes too quickly for heritable biases to be modified by mutation or other natural variation and selection, perceived randomness may occur. This may occur, for example, when elevation in an area changes flora and fauna, or when climate change causes systematic changes in an environment.

Section 2 gives a quick overview of relevant history and concepts concerning research on random foraging. Section 3 argues that a mathematical model that has played a central theoretical role in random foraging research does not depend on environmental randomness. In section 4, I describe a computer simulation that illustrates the idea that random foraging can serve as an adaptation for mere perceived randomness.

2   The Lévy foraging tradition

When an animal seeks prey or other food, a mate, shelter, or an appropriate place to deposit eggs, they may by guided by perceptual information, learned information, or heritable biases due to past selection. What should an animal do if this kind of information is lacking or provides only broad constraints about where to search? One strategy might be to systematically examine every possible location for a target (food, mate, etc.). A terrestrial animal hunting for mice in a field could, theoretically, walk from one end of the field to the other, in rows whose width didn't exceed the animal's perceptual range, analogously to how lawns are mowed. This kind of foraging is inefficient, since it could take a

long time to cover the entire field, and all of the prey might be clustered at the far end of the search pattern or could have left by the time the hunter arrives. Other systematic patterns that cover the entire field—a spiral, for example–would be just as inefficient, and just as likely to take a long time to find the mice. A better strategy is to randomly choose different regions and then randomly explore within each such region. This is because arbitrarily spending a lot of time in one part of the environment risks missing out on resources that are in a another area, perhaps for systematic reasons. The mice might always be at the far end of the field, for example, because the food they prefer grows well there. So a random sampling strategy with local exploration is adaptive (cf. Dennett 1984, pp. 68, 128f).

In 1986, a pair of physicists, Michael Shlesinger and Joseph Klafter—following up on a remark by another physicist, Barry Ninham—suggested that it might be beneficial for ants to randomly sample an environment by foraging in a kind of random walk known as a truncated Lévy walk (Shlesinger and Klafter, 1986; Shlesinger, 2021). To understand this proposal, it will be helpful to begin with some terminology.

A *Lévy flight* (Mandelbrot, (1977) 2021) in the narrow sense (see below) is a random walk in which an object moves from one point to another point in a *direction* that is randomly selected according to a uniform probably distribution, and in which the *distance* or length l between the starting and stopping points is randomly chosen with a probability that is approximately proportional to $l^{-\mu}$, where μ is near 2. This means that short step lengths l have high probability, because when l is small, $\frac{1}{l^2}$ is large, so short jumps occur most often. However, much longer jump step lengths also occur regularly in a Lévy flight. An entity performing a Lévy flight in the narrow sense occasionally jumps randomly to a distant region, after which it is likely to randomly explore that region with short jumps (figure 1). In a broader sense of "Lévy flight", μ may be near 3 or near 1. When $\mu = 3$, long jumps are less probable ($\frac{1}{l^2} > \frac{1}{l^3}$ for $l > 1$), and the vast majority of step lengths are of a similar short scale. The resulting exploration of a space tends to be local. This pattern is
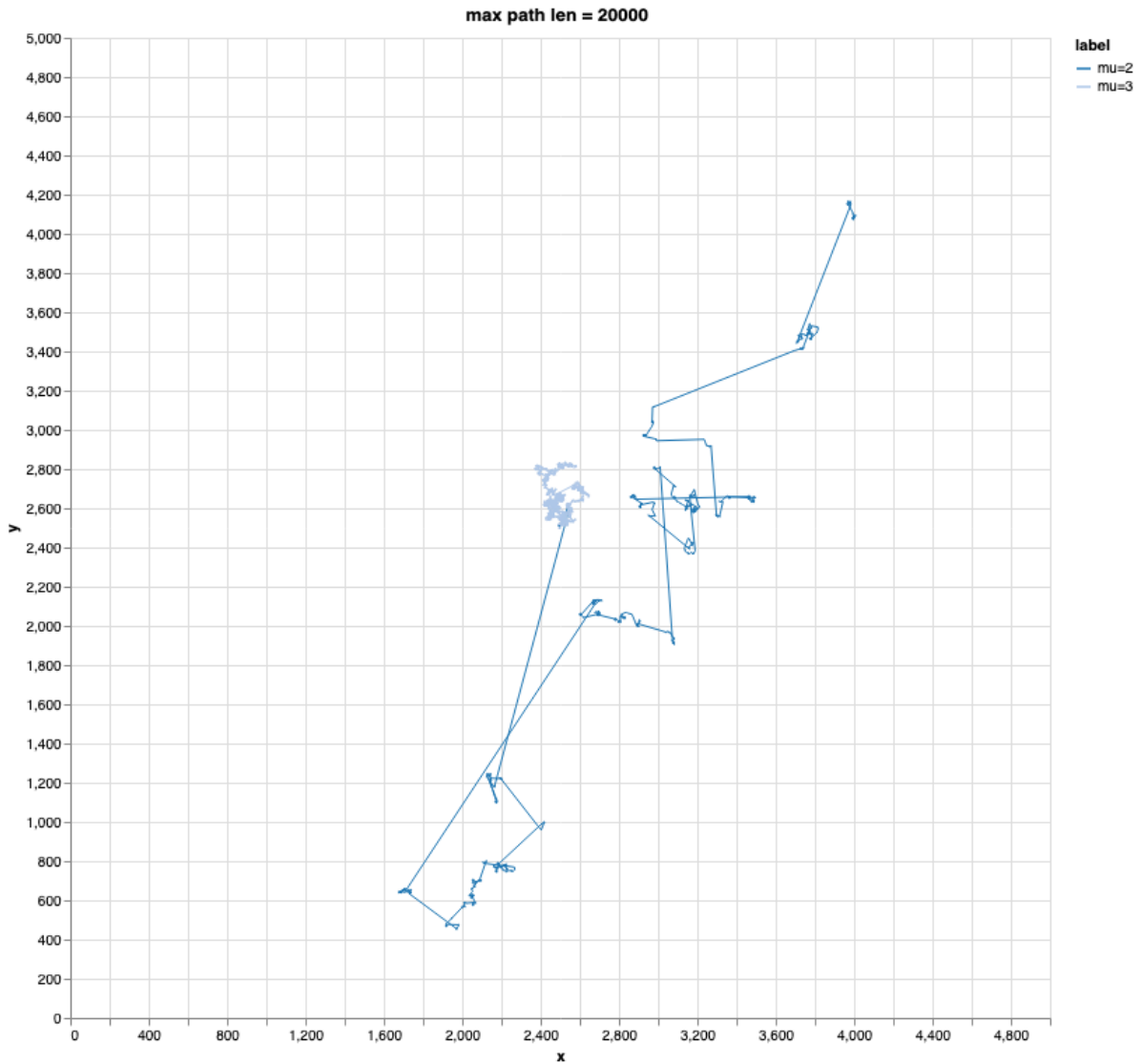
Figure 1: Lévy walks of the same length with $\mu = 3$ (fainter dense blotches confined to the center—most segments are too close to distinguish) and $\mu = 2$ (jagged path from center, to bottom, to upper right). The two paths have the same overall length.

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similar to Brownian motion, so such walks are sometimes called Brownian walks. When μ is near 1, many step lengths are long, since $\frac{1}{l}$ gives long jumps a higher probability. This known as as ballistic motion. (A ballistic walk of the same length as those in figure 1 would normally run off the page.)

A Lévy flight is a random walk in which the walker instantly jumps from one point to another. A *Lévy walk* (in a narrow sense) is based on a Lévy flight (in the narrow sense), in that distances between points at which turns may occur have probabilities proportional to $l^{-\mu}$, with μ near 2. However, in a Lévy walk, we assume that there are microsteps making up a single step connecting any two such points. That is, in a Lévy walk, the endpoints of jumps in a Lévy flight become endpoints of straight lines over which a walker travels at some fixed speed (figure 1). In both normal Lévy flights and Lévy walks, step lengths of any finite length, no matter how long, have some probability of occurring. (In fact the mean step length may be infinite.) By contrast, a *truncated* Lévy flight or Lévy walk is one in which there is a maximum value that step lengths can take. (So the mean step length is finite, but it may be large.) Both "Lévy flight" "Lévy walk", whether truncated or not, are sometimes used in a broader sense to refer to random walks characterized in terms of probabilities of distances between turns proportional to $l^{-\mu}$, for any μ in $(1, 3]$, and sometimes for even larger values.

It's the truncated Lévy walk pattern in the narrow sense, with μ near 2, that Shlesinger and Klafter (1986) proposed as an adaptive search strategy for ants. Because such a random walk mixes occasional movements to distant regions with local random exploration of new regions, and less often, moves to even more distant regions, a Lévy walk has the potential to explore an environment more thoroughly than a Brownian walk would. Further, Brownian walks tend to cross over themselves more often than Lévy walks, leading to redundant searching (Viswanathan et al., 2011). Ballistic searches may be advantageous in some circumstances (more on this below), but tend not to explore local regions very

thoroughly.

Inspired partly by Shlesinger and Klafter, a team of physicists and biologists (Viswanathan et al., 1996) studied data from recording devices attached to five wandering albatrosses in their natural environment. The researchers argued that the albatrosses' movements were similar to Lévy walks.[1] Around the same time, Cole (1995) used experimental evidence on timing of activity in *Drosophila melanogaster* to argue that these fruit flies moved according to a Lévy walk pattern. A paper by some of the authors of the albatross study (Viswanathan et al., 1999) was the first to use mathematical models and simulations to argue that particular versions of a truncated Lévy walk could provide an evolutionary advantage for animals searching for randomly and sparsely distributed resources. The hypothesis that natural selection favors Lévy walks in foraging for sparse resources became known as the *Lévy flight foraging* hypothesis (LFF). Previously, some models had focused on Brownian motion as a model of foraging, but according to arguments by Viswanathan et al. and others, Brownian foraging is at best optimal only when resources are not sparsely distributed.

In subsequent decades more than a hundred papers and at least two books have appeared that focus on Lévy walk foraging. This literature introduced a variety of mathematical and computer models, new empirical research, criticisms of statistical methods and data, arguments that some animals thought to engage in Lévy walks don't, or that animals that do, don't do so due to natural selection. There has also been research on interactions between random search and other factors such as risk of predation on foragers and learning about environmental variation. While at this point it's now well established that many animals often engage in movement patterns that can be modeled as Lévy walks,

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[1]Subsequently Viswanathan et al.'s (1996) statistical analysis was challenged by a team that included some of the same authors (Edwards et al., 2007), but a later analysis supported the original claims (Humphries et al., 2012).

there are only a few cases in which mechanisms driving Lévy walk behavior have been elucidated.[2] There is still debate about whether certain non-Lévy-walk models are better fits to some data, and some authors argue that in many cases Lévy walk behavior is driven by patterns in the environment rather than natural selection. Reviews of the literature and debates can be found in (Viswanathan et al., 2011; Wosniack et al., 2017) and in Reynold's (2015) target article and its responses in the same issue.

3 Viswanathan et al.'s 1999 model

Viswanathan et al. (1999) used a mathematical model of truncated Lévy walk foraging in one dimension (e.g. for fish foraging in a river) to argue that when resource targets are distributed randomly but sparsely, and foraging is not "destructive"—targets do not subsequently become unavailable—more targets per distance traveled will be found if step lengths are nearly proportional to l^{-2} (i.e. $\mu \cong 2$).[3] (Such nondestructive foraging can occur, for example, when the targets are schools of fish or patches of foliage that are not depleted after a visit by a forager, or when targets are potential mates (Viswanathan et al., 2000).) The authors argue that similar conclusions should apply in two or three dimensions, and support this point with computer simulations of foraging in one and two dimensions.[4] For destructive foraging, in which targets are removed when found (perhaps being eaten), Viswanathan et al. argue that a ballistic search (with μ near 1) will be opti-

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[2]One of the most interesting mechanisms for Lévy walk behavior was revealed in (Sims et al., 2019), which shows that larvae of *Drosophila melanogaster* fruit flies perform a truncated Lévy walk when there is no sensory information to guide them to food. The researchers showed that this behavior is generated by a relatively small neural circuit in the body of each larva; it can operate independently of the brain.

[3]Other helpful presentations of this model can be found in (Viswanathan et al., 2000, 2008, 2011; Zaburdaev et al., 2015).

[4]It's apparently quite difficult to develop similar analytical models for more than one dimension.

mal. However, simulations in some later studies (e.g. Wosniack et al. 2017) have shown that Lévy walks with μ near 2 can be more efficient than ballistic searches even with destructive foraging.

In presenting their mathematical model, Viswanathan et al. "assume that target sites are distributed randomly" (Viswanathan et al., 1999, p. 910), i.e. according to a uniform probability distribution. However, I'll argue that randomness of targets plays no role in the mathematics of Viswanathan et al.'s model. Rather, the model depends on average values that are functions of the distribution of targets. It is, of course, essential to the justification of the model that the animal has no better way of discovering resources than by random exploration of its environment. However, this need only be due perceived randomness; the environment need not be physically random.

More specifically, Viswanathan et al.'s (1999) model of random foraging in one dimension defines an abstract component of fitness, the *search efficiency* η, as the number of resources, or targets found per distance traveled while foraging for them. The authors approximate this quantity as the reciprocal of the average number N of straight segments before a target is found, times the average segment length $\langle l \rangle$ or $\mathsf{E}(l)$:

$$\eta = \frac{\text{targets found}}{\text{total distance traveled}} = \frac{1}{\dfrac{\text{total distance traveled}}{\text{targets found}}}$$

$$= \frac{1}{\text{average distance traveled per target}} \cong \frac{1}{\mathsf{E}(lN)} = \frac{1}{\mathsf{E}(l)N}$$

Without walking through all of the details of Viswanathan et al.'s derivation of their approximation for η, a few points about it are worth noticing.

I'll begin with some simple observations about the first step in deriving an approximation for $\mathsf{E}(l)$:

$$\mathsf{E}(l) \cong \frac{\int_{r_v}^{\lambda} l^{1-\mu}\, dl + \lambda \int_{\lambda}^{\infty} l^{-\mu}\, dl}{\int_{r_v}^{\infty} l^{1-\mu}\, dl} \tag{1}$$

In this equation, r_v is the perceptual distance—the radius around a target resource within which the animal will perceive it. λ is the mean free path, i.e. the reciprocal of the number of targets that a straight path by a forager would see on average. It's an estimate of the upper bound on step lengths (**?**). Recall that the probability of a straight segment of length l is proportional to $l^{-\mu}$. The point to notice is that this equation depends on only averages and constants:

- The perceptual radius r_v is assumed to be constant.

- λ is the number of targets within the perceptual radius of an animal averaged over the entire search space. That is, it is the average number of targets within the perceptual range of an animal located at a random point in the environment. (In a two-dimensional environment, λ would be equal to $1/(2r_v\rho)$, where ρ is the average density of targets.)

So the efficiency η depends only a constant and the average value λ, as well as N, the average number of straight segments per search. Further steps in the evaluation of equation (1) don't assume randomness, either.

Viswanathan et al. (2000) also give two approximations of the average number N of steps in a Lévy foraging walk, one for destructive searches in one dimension,

$$N_d \cong \left(\frac{\lambda}{r_v}\right)^{\mu-1} \tag{2}$$

and the other for nondestructive searches in one dimension,

$$N_n \cong \left(\frac{\lambda}{r_v}\right)^{(\mu-1)/2}. \tag{3}$$

The most rigorous argument for these approximations occurs in another set of works (Viswanathan et al., 2000; Buldyrev et al., 2001a). In (Viswanathan et al., 2000) the preceding approximations are derived from the following general formula for the average

number of steps before a resource is located (p. 7, eq. 4):

$$N = C \left(\frac{x(L-x)}{r_v^2} \right)^{(\mu-1)/2} \tag{4}$$

This equation is proved in (Buldyrev et al., 2001a).[5] Here $[0, L]$ is full the extent of the "environment" which is used to model the one-dimensional region between two targets at 0 and L. L is thus assumed to be an average distance between targets. x is a forager's initial starting location, and C is a constant that is independent of x and L. Viswanathan et al. (2000) say a bit further on that:

> This situation corresponds in terms of [equation (4)] to the case when the walker starts from the previously destroyed site that is about the same distance λ away from the two remaining target sites, so that $x = L - x = \lambda$. Hence, the mean number of flights N_d in case of destructive foraging is given by [equation (2)]. (Viswanathan et al., 2000, p7)

Note that the phrase "about the same distance λ away"—where λ is a function of the number of targets seen on average—again refers to an average, which need not depend on random distribution of resources. The proof extends over several pages, but it keeps

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[5]For the proof of (4), (Viswanathan et al., 2000) cited a paper only identified only as "S.V. Buldyrev et al., preprint". However, a later work (Viswanathan et al., 2011), references (Buldyrev et al., 2001a,b) as the source of an equivalent formula. Here is the version of my equation (4) [equation (4) in (Viswanathan et al., 2000)] that's proved in (Buldyrev et al., 2001a) as equation (36):

$$n_\alpha(x_0) = \frac{\sin(\pi\alpha/2)}{\pi\alpha/2} \left[\frac{(L-x_0)x_0}{l_0^2} \right]^{\alpha/2}$$

To see the equivalence with my (4), let $N = n_\alpha(x_0)$, $\mu - 1 = \alpha$, $r_v = l_0$, $x = x_0$, and $C = \frac{\sin(\pi\alpha/2)}{\pi\alpha/2}$. The exponent of the probability distribution over step lengths in a Lévy walk is often represented as $\alpha + 1$ rather than μ, and l_0 is the minimum step length, which (Viswanathan et al. 2011, p. 136) model as equal to the perceptual distance r_v. Abbreviated Versions of this proof are given in (Buldyrev et al. 2001b eq. 24) and (Viswanathan et al. 2011, eq. B.14, appendix B).

fixed the distance L between targets, and integrates over probabilities of possible steps that might lead from an initial location x in $[0, L]$ to one end of the interval or the other.[6]

So though it may be a reasonable assumption in many contexts to assume that resources with locations unknown to an animal are randomly—probabilistically—distributed, the 1999 model does not in fact require that it is random distribution of resources that helps to select for tuning of the μ parameter in random foraging. What is needed, in addition to ignorance by the forager, is just that the resources be sparsely distributed so that the averages have certain values. But this sparsity could just as well be due to a non-random, systematic distribution, as long the forager is unaware of it.

There are other factors that may be relevant to selection for Lévy foraging, but they don't require random distribution of targets either. First, note that non-truncated mathematical Lévy walks with μ in the neighborhood of 2 are are *scale-free*. This means, roughly, that very long steps will be followed, now and then, by long but shorter steps, which in turn will often be followed by even shorter steps, each of which is likely to be followed by very short steps. The same general pattern would be true of a real-world truncated Lévy walk—more or less—within the range of possible step lengths. Now, Wosniack et al. (2017) responded to arguments that in some situations natural selection might favor some specific types of random walk behavior *other than* a Lévy walk. Wosniack et al. argued that when resources occur in clumps or patches that are far apart, perhaps with small patches

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[6](Viswanathan et al., 1999) and (Viswanathan et al., 2008) each gives a different informal, back-of-the-envelope style mathematical argument for equations (2) and (3). Neither of these arguments depends on assuming random distribution of targets as far as I can see, but the more rigorous argument I discuss in the text makes these informal arguments irrelevant to my claims regardless. (cf. Viswanathan et al.'s (2011) remark on page 139 after equation (B.14), which reduces to equation (1) here: "Note that this result is in agreement with Equations (10.4) [my (2)] and (10.5) [(3)], ...which were derived in Chapter 10 using scaling arguments." The scaling argument is not spelled out in this book, but the text seems to allude to the arguments in the 1999 and 2008 papers.)

within the larger ones, and smaller patches within those—i.e. when resource distribution is itself scale-free—then a scale free foraging pattern can be better suited for exploring such an environment than other foraging strategies. The general idea is that a scale-free foraging pattern such as a Lévy walk is one that's able to travel between distant patches, then explore smaller patches, and also find patches within those. For similar reasons, Wosniack et al. argued that a Lévy walk might be better adapted to changing environments in which the average spacing of resources changes. Since a Lévy walk is relatively scale free—it exhibits jump lengths of many different sizes—it might be adapted to resources that are spread out to different degrees at different times. However, again, none of this depends on any sort of randomness. The simulation below illustrates the first kind of scale-free distribution of resources in a non-probabilistic context.[7]

4   Simulating random foraging with perceived randomness

A wide variety of simulations has been used to investigate Lévy foraging. All of the ones I've seen so far model environments by randomly distributing targets within simulated environments. For example, (Wosniack et al., 2017) performed simulations of Lévy walks with uniformly distributed resources, resources distributed as by a Lévy flight, resources distributed in patches with a variety of internal distribution of resources in patches, and with a variety of kinds of distribution of patches.

Given that Viswanathan et al.'s seminal mathematical model doesn't depend on random distribution of resources, and given the wide variety of resource distributions that authors such as Wosniack et al. have examined in simulations, it's reasonable to expect that Lévy foraging would be adaptive when resources are distributed sparsely but nonran-

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[7]Self-similarity of patterns at different scales is characteristic of both probabilistic and non-probabilistic fractals (Mandelbrot, (1977) 2021; Falconer, 2014).

domly. On the other hand, Viswanathan's mathematical model is for a one-dimensional environment. Even if it seems obvious that Lévy walk foraging should be adaptive for cases of sparsely distributed resources that are merely nonrandom but perceived-random, models sometimes show that the obvious was incorrect. So I'll report preliminary work on simulations intended to explore the idea that random foraging can be an adaptation for mere perceived randomness. My aim is to show that in at least some situations in which it's clear that resources are distributed nonrandomly, certain kinds of random foraging are beneficial to a forager. To that end, I've invented an entirely fictitious scenario which, though of questionable realism, should suffice to make my theoretical point.

Suppose that plants in a vast centuries-old garden are arranged in a form like that shown in figure 2, with the pattern continuing beyond the boundaries of the image.[8] There are five largest diamond patterns, each containing five smaller diamonds, each of which in turn contains five diamonds, each composed of five plants. (The dots representing the plants—which may or may not be distinguishable depending on resolution—are 500 times larger than the perceptual range of the insects mentioned below. Otherwise the dots would be not be visible in the image.) The central plant is missing. In this garden, the centers of the largest diamonds are 50,000 units apart. The distances between the largest surrounding diamonds from this center is 0.15 times this distance, and the diamonds around the resulting centers are again 0.15 times their distance, with the distance between plants in the smallest diamonds again 0.15 times the previous distance, so that plants are 506.25 units apart. This geometry, inspired by Mandelbrot's ((1977) 2021) discussion of Fournier d'Albe's model of the universe, is designed to produce an environment that is entirely regular, but that has a range of scales of the kind that Lévy walks are supposed to favor.

Now we suppose that a certain crawling insect has evolved to eat these plants, and

[8]The simulations use what is known as a "toroidal" world or "periodic boundary conditions": when an animal moves past a nominal boundary, it continues from the other side of the environment.
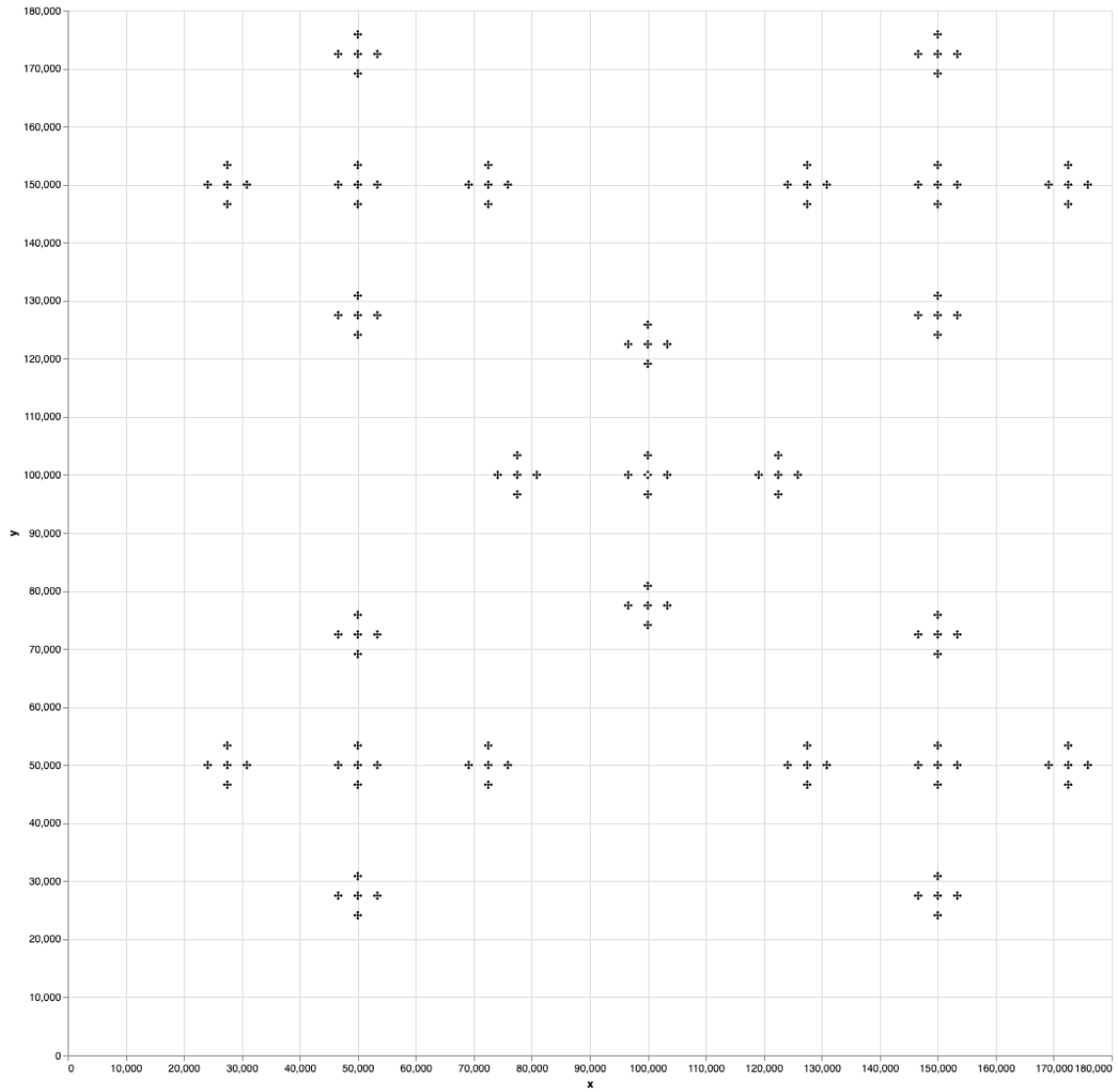
Figure 2: Clusters of plants in a large, sparse garden.

only these plants. The insect has a very simple foraging strategy. Its body incorporates a magnetosome sensitive to the Earth's magnetic field, which allows insects to forage by simply traveling in a single straight path either precisely north, south, east, or west. Since for centuries, the plants have been placed in the same orientations, this strategy usually works. Natural selection has pruned and continues to prune all heritable influences that might cause an insect to move in some other direction. In some directions, an insect must travel very far to reach one of the plants, but except on the edge of the garden, it eventually reaches one of the plants.

However, a new gardener decides that while the traditional orientations of plants to each other should be maintained, it's desirable to rotate the plants—literally: every year the gardener will rotate the orientation of the garden as a whole by a small but precise number of degrees. After many years, the entire garden will return to its original orientation. If the rotation occurs slowly enough, mutations or other small heritable variation that affects the insects' direction of travel might allow natural selection to spread traits for foraging behaviors coordinated with the orientation of the garden. However, if the rotations are not so small, the insects will find at some point that there are no plants in directions in which they move, and the population will go extinct. Though there will be new orientations of the garden that would allow insects to find distant plants that happen to be due north, south, east, or west, before then the garden will have many orientations such that insects will not find a plant, even after traveling for a long distance. The problem is not that the skewed orientations of the garden prevent many of the insects from eating. It's that it prevents *all* of them from eating. In simulations I allowed the insects to travel for 500,000 units before expiring from lack of energy. There were very few orientations for which insects could find food.

Notice that there is absolutely nothing that is random about this setup. There is a fixed, symmetrical, geometric set of relationships between plants that never changes. The envi-

ronmental change is entirely regimented and predictable. The insects don't die because randomness in the environment makes it unpredictable. They die because they don't have the ability to respond, either via perception or evolution, to systematic change in a systematic environment.

Insects of another species, who forage randomly to find the same plants, don't have this problem. Many of them don't end up finding food, but at least some do, and they reproduce. Since the direction of each step is random, the fact that the orientation of the garden is changing doesn't matter. When insects move in straight lines for long distances, and then begin foraging randomly in a local area, that allows them to (sometimes) find distant diamonds within diamonds where there are plants that might be found.

In simulations, I generated 1000 Lévy walks for each of the first values of μ listed below, and 500 Lévy walks for the fourth. (The program was very slow and required a great deal of memory with $\mu = 3$.)

- $\mu = 1.001$ ("ballistic": many long, straight steps, and few short steps).

- $\mu = 1.5$ (a mixture of long and short steps)

- $\mu = 2$ ("Lévy walk" proper: mostly short steps, quite a few long steps)

- $\mu = 3$ ("Brownian": mostly short steps)

Plants and insects are represented as points in the model. A plant is perceived the insect is within one unit of length of the point. Each walk ended when either a plant was found or the walk grew to 500,000 units of length. As a stand-in for Viswanathan's efficiency measure η, I divided the number of plants found with walks using a given value of μ by the average walk length:

μ	plants found	average length	efficiency
1.001	16	495374	0.0000323
1.5	15	496058	0.0000302
2	31	487763	0.0000635
3	134	414136	0.0003235

The Lévy walks with $\mu = 2$ clearly do a better job of finding food than walks using the lower μ values. However, contrary to what I expected, the Brownian walk with $\mu = 3$ did much better than any of the other walks. Brownian walks over-explore regions near where the foraging begins; I believe this strategy was successful in my environment because the starting points of all walks, in the middle of the garden, was surrounded by a diamond (of diamonds of diamonds) of plants that are relatively nearby.[9] Nevertheless, the simulations show that random foraging can succeed as a way of addressing ignorance, by sampling the environment in a way that is appropriate for it, even though there is nothing random about the environment.

5   Conclusion

I've argued that a central model in the Lévy foraging tradition, one often thought to show that natural selection will tend to favor kinds of random foraging as a response to randomness in the environment, does not in fact depend on randomness in the environment. Instead, it depends on more abstract characteristics of environments along with limitations of foragers. In simulations I illustrated the idea that that random foraging can be beneficial where environmental change makes selected biases detrimental, where animals or populations have insufficient ability to respond to changes in the environment.

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[9]Subsequent simulations, which I'll report elsewhere, have confirmed this suggestion.

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