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Optimal search behavior and classic foraging theory

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Abstract

Random walk methods and diffusion theory pervaded ecological sciences as methods to analyze and describe animal movement. Consequently, statistical physics was mostly seen as a toolbox rather than as a conceptual framework that could contribute to theory on evolutionary biology and ecology. However, the existence of mechanistic relationships and feedbacks between behavioral processes and statistical patterns of movement suggests that, beyond movement quantification, statistical physics may prove to be an adequate framework to understand animal behavior across scales from an ecological and evolutionary perspective. Recently developed random search theory has served to critically re-evaluate classic ecological questions on animal foraging. For instance, during the last few years, there has been a growing debate on whether search behavior can include traits that improve success by optimizing random (stochastic) searches. Here, we stress the need to bring together the general encounter problem within foraging theory, as a mean for making progress in the biological understanding of random searching. By sketching the assumptions of optimal foraging theory (OFT) and by summarizing recent results on random search strategies, we pinpoint ways to extend classic OFT, and integrate the study of search strategies and its main results into the more general theory of optimal foraging.

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Introduction

Random walks and diffusion theory initially penetrated into ecology as methods to analyze and describe animal movement (e.g., [1, 2]). Statistical physics was mostly seen as a toolbox rather than as a conceptual framework that could contribute to evolutionary biology and ecology. In this way, the possibility that certain statistical features of movement patterns could emerge from behavioral rules aimed to increase search efficiency was not an *a priori* assumption.

However, during the last few years, there has been an on-going debate on whether organism's behavior can include traits that aim to improve the foraging success based on rules of optimal random (stochastic) searches (for a review, see [3]).

Evolutionary functionalism seeks for understanding morphological, physiological and behavioral traits in terms of how they increase an organism's fitness. Implicitly, it assumes that organisms conform to some optimization principles in their physical performances, which may conduct to understanding why organisms are, what they are, and do what they do. Population genetics demonstrates that the idea that evolution maximizes fitness is only an approximation, which is particularly clear in maladaptations occurring because of inbreeding and genetic drift in small populations [4]. Beyond purely genetic limits, there are several ecological and evolutionary aspects that limit or prevent full optimization of particular traits in organisms. First, selection pressure on some traits decreases as soon as suboptimal solutions sufficiently contribute to fitness and other selective pressures become more critical for the final outcome. Second, individual traits only cover a part of the whole process contributing to fitness, optimization of some traits may be irrelevant compared to the relevance of others, or even there may exist trade-offs between traits, so the final maximization of fitness can, in fact, appear from different combinations of partial trait optimizations. Finally, organisms interact with the environment and other organisms as well; thus behavioral optimization goes beyond an individual's isolated decisions, and it also depends on the decisions of the rest of the population, as well as on the nature and evolutionary responses of the interacting species. The understanding of this interdependence of individual strategies' payoffs may demand using evolutionary game theory [5–8] instead of classic optimization theory [9].

Natural selection has an astonishing capacity to create complex adaptations, and all in all, it causes the appearance of conceivably optimal design. Nevertheless, careful inspection provides evidence of vestigial structures, functional relicts, largely suboptimal traits, which denotes the contingent trial and error process inherent to natural selection as an evolutionary agent. These general concerns about optimization have caused skepticism about the so-called adaptationist program [10–13] and the actual implications of any theoretical analysis based on an optimality rationale [14, 15]. However, optimization analyses become extremely useful in evolutionary biology when they are not exclusively seen as hypothesis to test in the Popperian sense but as archetypical options to confront with real animal behavior [16–18].

Defining the biological context of the optimization process is crucial to figure out its evolutionary implications [19]. A search process, for example, acquires evolutionary sense when considering the purpose (context) of that search, for instance, foraging or reproduction. Yet, considering the physics of the searching alone can provide a greater level of generality to the problem, leading to a better understanding of animal search strategies than that obtained from specific species case studies. In fact, statistical physics and random walk theory allow us to mathematically define and test search optimization models in a very broad context. But of course, only through empirical evidence can we evaluate how feasible these models are in nature. For example, several theoretical studies have shown that power-law or scale-invariant displacements (i.e. Lévy walks) may be efficient strategies under specific (though general enough) search conditions [20], but so far, the empirical evidence of Lévy walks as search strategies is not strong enough. First, power-law or scale-invariant behavior (Lévy type of statistics) is always difficult to assess from short-length empirical data sets such as those usually available in ecological studies [21–25]. Second, the power-laws are expected to be truncated at some scale; therefore, when upscaling these patterns we might lose the original statistical signals. Third, it may happen that these statistical patterns had nothing to do with behavioral rules for efficient stochastic searching and come from other sorts of behavioral

rules or from environmental forcing as discussed in [26–28]. All these aspects have recently been debated in the scientific literature, e.g., [22, 23, 29, 30–32].

Our aim here is to show that in order to progress in accepting (or rejecting) the relevance of random search optimization in a biological and thus evolutionary context, the framework of analysis has to be enlarged considering the ultimate biological function of the search, either food acquisition or mating. In particular, we will consider how emerging views of random search as adaptive traits can be considered within foraging theory and analyzed from an optimization perspective. Furthermore, we discuss how statistical physics contributions to foraging can, in certain instances, show under which circumstances random search optimization may (or may not) be relevant for survival.

First we make a brief introduction to the traditional optimal foraging theory, essentially the patch model and its main assumptions. Next we discuss the role of the search component in this conceptual framework including inter-patch and within patch search, and random and systematic searching. Then, we introduce the key issue of behavioral intermittence and we describe general stochastic search rules that can help us to comprehend how animals may adjust random search strategies to increase the search efficiency. Finally, we comment on some aspects that appear crucial for fruitfully merging optimal search theory and bring new interesting ideas and hypothesis to the fields of animal behavior and movement ecology [33] in general.

A brevia on classic optimal foraging theory

Optimal foraging theory (OFT) is one of the most extensively developed biological optimization theories, e.g., [34–37]. Suppose a predator (consumer) that hunts (feeds) on patchily distributed prey or resources (e.g. a patch meaning a high resource area compared to the average environment). It spends its foraging time traveling between patches or searching and handling food within patches. Moreover, while it is searching it gradually depletes the food within a patch. Therefore, the benefit of staying in the patch gradually diminishes with time [38]. In their review of OFT, Pyke *et al* [39] listed four problems a forager might face: (1) what prey to take (optimal diet choice), (2) what patch type to search (optimal patch choice), (3) when to leave a patch (optimal giving up or departure times from patches) and (4) how to move between patches (optimal movements). The optimality approach to foraging assumes that animals should make decisions, according to optimal decision rules, so as to maximize their foraging efficiency. Therefore, mathematical models of a particular foraging problem seek for solutions that usually maximize energy intake per unit time spent foraging, although other efficiency functions might be adequate as well [34].

The nugget of the OFT has been the marginal value theorem [40] illustrated in figure 1. It states that if the predator aim is to maximize the net energy gain while foraging in a patchy environment, it should leave any particular patch when the expected net gain from staying drops to the expected net gain from traveling to and starting to search in the next patch. In other words, the marginal value theorem [40] specifies the best leaving rule for a deterministic model in which the net energy gained after searching for unit of time S in a patch is a continuous function, $G(S)$, with a negative second derivative. The forager should leave a patch when $\frac{dG(S)}{dS}\Big|_{S=S^*} = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t G(\tau) d\tau$, for G already averaged over possible different types of patches and S^* denoting the departure time from a patch. As stated by Green [41], one of the attractions of the marginal value theorem is that it simultaneously illustrates the relationships among several variables (see figure 1): (1) G itself is a function of S . (2) The rate of finding a prey at any time, S , is a derivative, G' , which is shown as the slope of G at S . (3) The long-term rate of finding a prey achieved by a forager leaving each patch at time S , namely

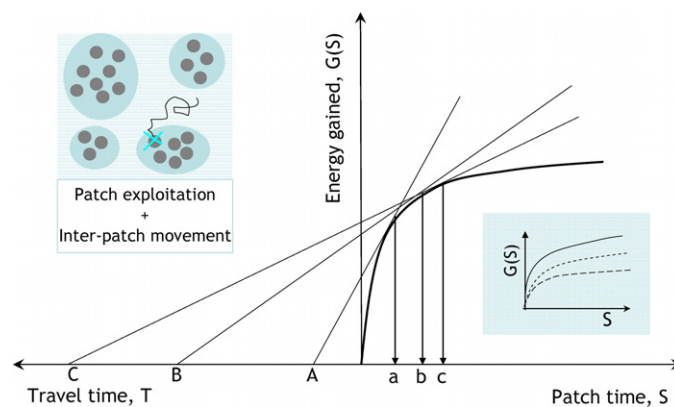


Figure 1. The x -axis on the right of the y -axis represents patch exploitation time, and to the left of the y -axis represents travel time increasing toward the left. At each expected travel time A , B and C there is a corresponding and distinct tangent point that determines the optimal patch time for each patch (a , b and c), and therefore also the different marginal values. As long as the expected travel time increases, the marginal value (here the slope of the straight lines) for the patch decreases. The left inset shows a schematic illustration of the ecological setup assumed in classic optimal foraging theory and its two major components: patch exploitation and inter-patch movement. The right inset shows different patch exploitation curves. The search component (random or systematic) can impinge either in the inter-patch travel times or in the patch exploitation curves. (Redrawn from [42]).

(This figure is in colour only in the electronic version)

$R = G(S)/(S + T)$, is the slope of the secant line from $(-T, 0)$ to $(S, G(S))$, where T is the travel time between patches.

The patch model of foraging has three components. One, the animal decision: whether to continue exploiting the patch or abandon it to search for another. Two, the currency or efficiency function: the long-term net rate of energy intake. And three, the assumptions on predator and prey behavior. The model assumes that the predator has all the information necessary for a rational decision: it can recognize a patch instantaneously, it knows the average travel time between patches in the habitat and the expected quality of the patches [42]. Even if some of the assumptions do not look very realistic, the model predictions match qualitatively with some empirical data (e.g., [43]). Further, there are more realistic models which relax the assumption that the forager has full knowledge on the habitat, either by considering that animals must expend some effort in sampling patches previously to exploitation [44, 45] or by accounting for stochasticity in the patch exploitation process [46]. Clearly, the optimal rules that govern the behavior of an animal that does not know everything about its foraging ground are quite different from those of an animal that already has all the available information. In the former case, optimal motility strategy and sensorial capacity are of much relevance.

The search component in classic optimal foraging theory

Foraging can be divided into different sequences of events depending on the trophic level or the peculiarities of the species considered [47]. Classic OFT distinguishes decision (e.g., diet choice, patch departure condition) and energy costly activities (e.g., patch exploitation, movements between patches). The latter have been subdivided in different ways. For example, MacArthur and Pianka [48] considered search and pursuit (including capture

and eating) as the basic costs of a foraging process, Shoener [49] distinguished search, pursuit and handling/eating costs, and Collier and Rovee-Collier [47] distinguished search, identification, pursuit, handling, as well as consumption (ingestion), and utilization (e.g. digestion, absorption) costs. Importantly, most feeding sequences involve two main categories of events: pre-encounter (the search) and post-encounter events (e.g. the pursuit, handling, digestion), the latter occurring after the target has been detected. The relative importance of the search component among other components of the foraging chain is scale dependent. In other words, the search can come into play differently at distinct scales. At least two main scales should be distinguished based on the notion of a ‘patch’: the large scale related to travel between patches and the small scale related to prey search within a patch. Can a given search strategy optimize between and within patch scales at the same time? How much information do animals use and how do they get this information outside and inside patches? These are difficult questions to answer but, as pointed out in [50], these questions lie at the core of understanding the decisions made by foraging animals, and in particular, the search strategies employed. In fact, ambiguities exist, e.g., as how to exactly define a patch for a given animal [51], and how much information animals use in making their decisions. These are very difficult issues to settle [39]. However, reasonable answers can be obtained from independent experiments designed to explore the memory or perceptual capabilities of the animals within and without patches [39, 52].

Although inter-patch movements have been considered, e.g., [39, 53], in general, optimal foraging models tend to oversimplify the large-scale search problem (i.e. patch detection) and focus the attention on the role of search strategies as a patch depletion/exploitation mechanism. Most models of OFT typically assume that animals have information about the location of the patches so that the time spent between patches does not come out from a search process, instead from the average distance between the patches. Hence, the average travel time between patches is assumed to be an attribute of the landscape (i.e. patch distribution and dynamics) and not of the animal search behavior. As information on patch locations is assumed to be known, the foraging process is commonly idealized as a ‘traveling salesman’ type of the optimization problem [55] rather than as a search optimization problem. In classic OFT, the search component only contributes to determine how prey are depleted within patches: the diminishing slope of the curve $G(S)$ is assumed to represent the gradual resource depletion due to searching and feeding *within* a patch. Coherently, early stochastic versions of Charnov’s model associated simple stochastic movement patterns (i.e. Brownian motion, normal diffusion) with patch depletion dynamics [54, 56, 57]. However, there is no general argument to sustain that random searching might always involve simple statistical properties or that it only occurs within patches. For example, if the environment is new (e.g. natal or juvenile dispersal, relocation experiments), highly dynamic (e.g., environmental forcing, many competing individuals), or simply unachievable as a whole to perception/cognitive abilities, foraging animals may need to search for patches as well as for targets within them. In the end, all may depend on our definition of what a patch or a target is, which, in turn, depends on what we believe the main animal sensorial capabilities are. From this perspective, classic OFT fails to recognize a wide range of foraging scenarios where the search and its stochastic component may play a strong role. Foraging uncertainty should be recognized as a complex scale and species-dependent phenomenon that includes much beyond the absence of environmental cues within patches.

Classic OFT will become closer to the real biological situation by adequately integrating the search component at different scales of the foraging process, and considering different scenarios regarding the amount of information available and the perceptual capabilities of the searcher at those different scales (e.g. outside and inside patches). The relationships between

the exploration and the perceptual scales [52, 58], and the consideration of a continuum of possibilities between highly informed (e.g., learning, cognitive maps) and poorly informed foragers (e.g., disorientation, sensorial failures) are thus important elements of foraging theory that need to be revised.

Systematic and random searches

Early stochastic versions of Charnov's model studying the problem of when a forager should leave a patch already distinguished between systematic and random search within patches, e.g. [54, 56, 57]. In systematic searching, it was assumed that the forager does not retrace its steps and hence the prey capture rate is assumed to be constant with time in the patch. By random search it was usually meant that a spot within a patch is equally likely to be searched whether or not it has been searched before. Thus, mathematically random search results in a rate of finding a prey that decreases exponentially with time in the patch, e.g., [41, 59]. According to Baum [59] an organism that moves about randomly in space fails to discriminate one location from any other, while if it moves about systematically then it does discriminate. Discrimination usually saves time and energy because then no attempts to situations that previously have been unsuccessful are repeated. Therefore, according to Baum [59], to be systematic means to be efficient.

As a first approximation these are acceptable assumptions; however, it is clear that a more elaborate reasoning is necessary to incorporate all the evolutionary potential of search strategies (either random or systematic) in foraging processes. First of all, systematic search strategies can only be efficient when some *a priori* relevant (although partial) information about target characteristics or patch locations is available [60]. The application of systematic searching based on misleading or meaningless information may lead to persistent errors and biases. Second, it is not a straightforward consequence that systematic searches would lead to constant prey capture rates. Even if a systematic search is simplistically defined as a search where the forager does not retrace its steps or where the locations are visited in a certain order (e.g. trapline foraging), capture rates depend, among other things, on the prey distribution: if the distribution is not uniform, the capture rates do not necessarily need to be constant in time. Last but not least, random searches are not totally unstructured searches, and hence, some amount of discrimination exists, even if stochastic. For example, random searching does not necessarily involve that all the spots within a patch are equally likely to be visited [54]. Different random searches cover the space differently and show different probabilities of revisiting certain areas [60, 61]. Random searching may also decrease competitive exploitation and interference in high-quality spots allowing much higher or less variable capture rates than systematic searching. Also, in the cases where the learning capacity of the prey cannot be discarded one must take into account the fact that the more systematic the predator's search, the easier for the prey to develop efficient escaping strategies.

There is a good deal of empirical evidence of systematic behavior in foraging movements (both between and within patches) but animal search displacements with no evident pattern are also common. For example, Pyke *et al* [50] summarize evidence that bumblebees tend to begin foraging in an inflorescence at the lowest flowers and move regularly upward when shifting to a new flower. Hummingbirds, in contrast, show little evidence of regularity when exploiting an inflorescence. Baum [59] observed systematic foraging within patches in his laboratory study of pigeons. Exceptions to the general prevalence of pigeons systematic foraging arose from unusual performances in the initial trials after a change of conditions. Thus, continued experience with the conditions appeared to change the pigeons' performance to one better described by systematic foraging. Similar examples of transitions from random to

systematic strategies (e.g. trapline foraging) can be found in hummingbirds and bumblebees, based on experiments designed to increase the predictability of nectar-refilling patterns in artificial flowers [62, 63]. However, the same authors recognize that the extension to what learned systematic search mechanisms might work in more complex situations still remains uncertain [62, 63]. Indeed, as the information on the location of the targets is degraded or it turns unreliable, forager efficiency may switch from a systematic to a random search strategy. For example, when animals have to return back to their homes (i.e. homing behavior) knowing that they are close by but without precise clues of where their home is, they can try a systematic search strategy (e.g. Archimedean spiral, foray search). If their home (e.g., nest, burrow) is not found, the animals may resolve to use a mixture of systematic (i.e., returns to the starting point) and random (i.e., meandering) search [64, 65]. In summary, empirical evidence points to two important facts: (i) the type of search strategy employed by animals (whether systematic or random) strongly depends on the amount of information that is involved in the search process, and (ii) random searching is a possible strategy when information is lacking, confusing, difficult to gather or even when it is important to minimize prey learning capacities.

The unavoidable evidence of non-systematic foraging in nature suggests that random search is a potential competitive strategy worth considering in OFT and not just a simple mathematical convenience [59]. As available information regarding positional, kinetic or behavioral characteristics of targets decreases, systematic searches become less effective. In these situations, animals must attempt to increase their chances of locating resources by heterogeneously sampling the space and by adjusting the balance between local and global exploration [60]. Future theoretical models should explore those situations where random searches might be more efficient than systematic searches, and identify what natural conditions need to be fulfilled. In general, random (stochastic) processes are well known in biology [1, 2, 66], although biologists might differ in their estimation of the relative importance of these processes. The study of random search strategies, using the common approaches of statistical physics, could help us to adequately square the role of stochastic processes in the context of optimal foraging.

The intermittent nature of the search

Ideally, the rules of searching included in OFT should link as much as possible with true biological mechanisms. Search models can be constructed either with the simple aim of phenomenologically matching the observed patterns in nature or can be based on true biological first principles. In the latter case, we should wonder about which are the mechanisms that allow animals to perform efficient stochastic searches in a foraging process. To answer this question it is essential to consider animal behavior, and in particular, animal locomotion as intermittent phenomena [67, 68]. Here, by behavioral intermittence we mean movements, which are intrinsically discrete, in which the whole concept of ‘discrete walking’ may have real biological significance. Animals can behaviorally discretize their movement in a series of move lengths (displacements), pauses and turns (reorientations) as a response to certain cues of the environment [58, 69]. A consequence of behavioral intermittence is the possibility of breaking the previous directional persistence of a walk with strong reorientations [58, 69, 70]. When the environmental or resource information is confusing or very much reduced, animals could adjust their reorientation behavior in order to generate Lévy-type search strategies, e.g. [20, 61, 70–74]. Some empirical evidence consistent with Lévy-like movement patterns exists, e.g. ([75, 76], but see [3] for a thorough review). Given the difficulty to get good enough statistics from movement patterns, perhaps more relevant is the empirical evidence of specific

reorientation mechanisms capable of changing the statistical properties of movement across a wide range of species from bacteria to birds [77–82].

Scanning for prey cues or food is costly activity that can hardly be continuously maintained at high performance. Physical constraints on sensorial activities at high speeds can also deprive animals from continuous scanning. Hence, scanning behavior is often intermittent as well [78, 83–85]. O'Brien *et al* [78] identify saltatory searches as searches where animals scan only during pauses whereas displacement phases serve only to rapidly relocate the animal into previously unscanned areas. In some animals, the opposite occurs: perceptual abilities are increased and even optimized while moving, whereas they are literally ‘blind’ during pauses, e.g. [86]. Another strategy to improve random search efficiency might involve controlling the proportion of time spent in relocation and scan phases [83–85]. Saltatory scanning combined with Lévy reorientation behavior can produce a variety of efficient random search strategies, e.g. [85, 87]. Adaptive behavioral plasticity may exist to accommodate both reorientation and scanning patterns to particular environmental conditions. For example, different species of grassland birds showed continuous or saltatory search depending on whether the grass was low or high, respectively. If the grass is low, ground walk, continuous scanning is not costly and improves encounter probabilities with the prey. If the grass is too high, it becomes more efficient to combine ground-walk local scanning with relocation flights [88].

Optimal search strategies: merging evolutionary and mechanistic approaches to the encounter problem

Animal searches can be viewed as decision-making processes that result in a series of displacements and orientations. The former are energy dependent, whereas the latter are mainly shaped by information fluxes. Of note, the absence of information might be valuable information in itself, capable of triggering certain types of stochastic search strategies. The capacity to obtain, store and use both assets to deal with environmental uncertainties differs from organism to organism. Provided that optimal search strategies may be critical in determining prey (food) encounter rates, there is a need to integrate (both empirically and theoretically) the study of search strategies and its main results (e.g. current special issue) into the more general framework of optimal foraging theory.

From a biological perspective, an efficient search mode would not only involve the existence of specific search strategies that can be effective in particular situations but also, more generally, the flexibility to deal efficiently with a changing environment [73]. Hence, it may be of great value to acknowledge from the very beginning that (i) animals may show plasticity and change strategies depending on the circumstances as part of their natural evolutionary inheritance, (ii) even though we can develop theoretical optimal strategies for each separate component of the foraging activity, evolutionary trade-offs between foraging components might prevent a universal solution, and (iii) both prey and competitors tend to optimize, thus, the coevolutionary game is the rule not the exception.

Which particular foraging component is more important or which one is first optimized may respond to random attempts (mutations); however, this initial selection may condition the degree of optimality that can be achieved in other components. In any case, evolutionary trade-offs among different components of the foraging activity may canalize potential searching repertoires into more limited collections of search skills that can, thus, be studied. Progress in the development of foraging theory has to include an analysis of the hierarchy of trade-offs between the different foraging components. In that way, we should be able to define to what extent search strategies, and in particular, random search strategies, may be relevant to the

foraging efficiency of a particular animal species. Under the evolutionary view of optimal foraging theory, prey can be considered as simple passive victims; however, this is rarely the case. In the evolutionary game, prey responses may include from deterrent substances to avoidance behavior. Developments of search theory have to include at some stage how to deal with these responses and how these affect the foraging behavior itself [5].

Even though optimal search solutions show strong sensitivity to the initial and the boundary conditions related to the search problem (e.g., the location of the searcher relative to the targets, the perceptual scales of the searcher compared to the exploration scales, the average distance between targets, the initial amount of information about targets), recent theoretical studies on random search strategies illustrate the fact that some of the search rules are general and simple enough to eventually become behavioral traits susceptible to natural selection. Among candidate drivers of efficient stochastic searching are biological mechanisms accounting for ballistic motions, e.g. [48], adjusting the timing of reorientations when continuously scanning, e.g. [65], generating adequate proportions of relocation and scanning times, e.g. [78, 79], or a combination of the last two, e.g. [80, 83]. The potential real adaptiveness of a random search strategy should be evaluated based on: (i) how common in nature the initial and the boundary conditions assumed in the model are, (ii) how robust is the strategy to relaxation of these conditions and (iii) how plausible is the mechanism generating the stochastic properties of the strategy from a biological point of view.

Definitively, a more mechanistic approach to the search/encounter problem within the framework of foraging theory will set the right scene to explore the direct connections between animal behavior and stochastic properties of motion, and give further light to the open debate on whether adaptive stochastic mechanisms exist and play a role in animal foraging.

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