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Natural search algorithms as a bridge between organisms, evolution, and ecology

Andrew M. Hein^{a,1}, Francesco Carrara^{b,c}, Douglas R. Brumley^{b,c}, Roman Stocker^{b,c}, and Simon A. Levin^a

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The ability to navigate is a hallmark of living systems, from single cells to higher animals. Searching for targets, such as food or mates in particular, is one of the fundamental navigational tasks many organisms must execute to survive and reproduce. Here, we argue that a recent surge of studies of the proximate mechanisms that underlie search behavior offers a new opportunity to integrate the biophysics and neuroscience of sensory systems with ecological and evolutionary processes, closing a feedback loop that promises exciting new avenues of scientific exploration at the frontier of systems biology.

sensing | navigation | evolutionary strategy | encounter rates | exploration–exploitation

In the summer of 1899, Harvard entomologist Alfred Mayer traveled from Massachusetts to an isolated island in the Florida Keys with a collection of *Promethia* silk moth cocoons. What interested Mayer was a curious observation: Male moths were able to navigate from great distances to the exact location of a female. Mayer wanted to know how. Through a clever series of experiments (1), he showed that males find females by tracking the pheromones females emit into the wind. Mayer and his contemporaries, including Jean-Henri Fabre (2), initiated the study of what is now one of the most heavily investigated search algorithms in nature: the olfactory search strategies of insects. Over a century later, studies of how insects and other animals find odor targets have led to major discoveries about the structure and information contained within chemical plumes (3–5) and the properties of the nervous system that allow animals to extract and respond to that information in a complex and ever-changing landscape (6–11).

The search behavior of moths and other species is inspiring a new generation of scientists to take a closer look at natural search algorithms, broadly defined as the behavioral strategies organisms use to find targets. A recent surge of studies of natural search algorithms has begun to reveal novel search behaviors in a wide range of biological systems, suggesting that the need to search successfully is a strong selective force at many levels of biological organization. We need only look within our own bodies to verify both the ubiquity

and significance of search. Immune cells use chemical signals to navigate to target tissues; when cells fail to do this, the immune system cannot mount normal responses to infections (12). Development of the vertebrate nervous system depends, in part, on chemotactic search of axonal growth cones (13), and failure of these cells to locate their targets can cause neurological disorders.

The study of natural search algorithms presents a fertile research frontier that merges ideas and techniques from neuroscience, biophysics, and ethology. Here, we argue that recent research on the mechanistic basis of animal and cellular search strategies has created a unique opportunity for a dialogue between scientists studying the biophysical and neural bases of search, and ecologists and evolutionary biologists, who study the ecological tasks and selective pressures that shape search strategies (Fig. 1). This Perspective is not intended to provide a comprehensive review of the ecology or evolution of search behavior. Rather, we focus on two questions—one evolutionary and one ecological—that have come to light as a result of recent advances in search research: (i) Do the search strategies that different kinds of organisms have evolved share a common set of features? (ii) To what extent do these search strategies affect the rates of ecological interactions that underpin the functioning of ecological systems? We provide suggestions for how merging a mechanism-based understanding of search strategies with an ecological and evolutionary perspective may

^aDepartment of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544; ^bRalph M. Parsons Laboratory, Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, MA 02139; and ^cInstitute of Environmental Engineering, Department of Civil, Environmental, and Geomatic Engineering, Eidgenössische Technische Hochschule (ETH) Zürich, 8093 Zurich, Switzerland
Author contributions: A.M.H., F.C., D.R.B., R.S., and S.A.L. wrote the paper.

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¹To whom correspondence should be addressed. Email: ahein@princeton.edu.

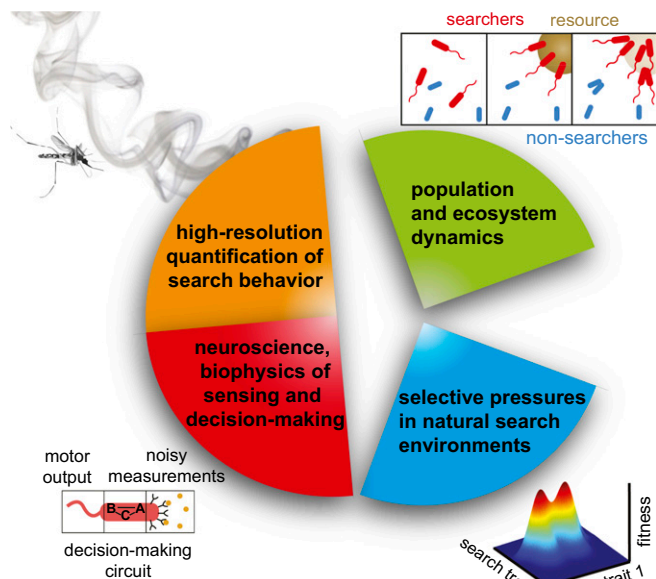


Fig. 1. The biology of natural search algorithms. Recent studies have used high-resolution/high-throughput experimental techniques to quantify search behavior, and tools from neuroscience and biophysics to dissect the mechanisms involved in sensing and decision-making during search. These more proximate approaches should be merged with ecological and evolutionary perspectives to yield a more holistic understanding of how organisms search the natural world, and how the process of search relates to ecology and evolution.

help answer these questions and lead to new discoveries at the interface of biophysics, neuroscience, evolution, and ecology.

The Evolution of Search Strategies

The fact that biological entities of many kinds must overcome what appear, at least on the surface, to be similar challenges in their search processes raises a question: Has evolution led these entities to solve their respective search problems in similar ways? Clearly the molecular and biomechanical mechanisms a bacterium uses to climb a chemical gradient are different from the neural processes a moth uses to search for a potential mate. But at a more abstract level, it is tempting to speculate that the two organisms have evolved strategies that share a set of properties that ensure effective search. This leads to our first question: Do the search strategies that different kinds of organisms have evolved share a common set of features? If the answer to this question is “yes,” many other questions follow. For example, what are the selective pressures that lead to such convergent evolution? Do common features of search strategies reflect common features of search environments? Can shared features of search strategies inform the design of engineered searchers, for example, synthetic microswimmers for use in human health applications (14) or searching robots (15)?

An example of a common feature of many search strategies is the use of spatial gradients in the strength or timing of sensory cues. In Box 1, we describe parallels between the responses of single cells to chemical gradients, and the responses of single animals and animal groups to environmental gradients. The important point is that the use of spatial gradients is a fundamental part of the search strategies of cells like neutrophils (16) and bacteria (17), solitary animals like mice and fruit flies (18, 19), and large animal groups like fish schools (20). In all cases, the searching individual

or group has a means of measuring a signal differential (e.g., difference in signal strength or the timing of signal arrival between sensors) over space, and responding to that differential by altering locomotory behavior in a way that causes the individual or group to climb the gradient (Fig. 2A).

Modern experimental techniques have been crucial for identifying the ingredients that enable these gradient-climbing behaviors. Studies of biochemical receptors in single cells (23, 24) and sensory receptor neurons in animals (11) have identified the raw input available to inform search decisions. In well-studied microorganisms, such as *Escherichia coli*, the biochemical pathways involved in decision-making are understood thoroughly enough that models of gradient-climbing can be formulated directly from the knowledge of intracellular signaling pathways that govern the gradient response (23–25). In the case of animals, the neural processes involved in integrating and making decisions using measurements of a gradient are not as well understood; however, the key features of the signal integration and decision-making process can be inferred using experiments that provide known sensory input and map this input to observed searcher motions (18, 20, 26). In this way, researchers are beginning to understand how measurements of spatial gradients lead to gradient-climbing behavior in a wide variety of model systems.

Although the biophysical and behavioral mechanisms cells, animals, and animal groups use to respond to gradients differ, these entities are all capable of readily climbing spatial gradients. Responding to gradients is, however, just one component of the set of rules organisms use to guide search behavior (Fig. 2B). Indeed, orienting using gradients alone suffers from well-known pitfalls when the environment contains many signal sources (27) or signals are highly intermittent, as is the case in turbulent chemical plumes (4). Accordingly, most species likely use gradient-climbing as one behavioral “module” (21) in a larger set of sensory-motor responses that, together, generate the long sequences of search behavior needed to locate targets in large spatial landscapes. Other modules may include exploratory behaviors that increase the likelihood that the searcher will encounter sensory cues emitted by a target—for example, the cross-wind casting of insects (21) and seabirds (28)—and memory-based mechanisms for returning to previously visited locations: for example, the path integration-based homing of the desert ant, *Cataglyphis bicolor* (22). We define the set of behavioral modules a searcher employs and the rules the searcher uses to transition between modules as a natural search algorithm (Fig. 2B). We expect natural selection to drive the evolution of algorithms that yield high search performance, while balancing fitness costs, such as exposure to predation risk (29). By developing mathematical descriptions of natural search algorithms and a more thorough understanding of the environments in which search takes place, we can begin to compare the strategies of searchers as diverse as human cells, bacteria, flies, and schooling fish in quantitative terms.

Mapping the Search Environment. What are the salient features of the search problems organisms solve in nature? What do target landscapes look like? What sensory cues do searchers have access to? These seem like straightforward questions, but even in the case of well-studied species like *E. coli*, we know surprisingly little about their answers (30–32). Without knowing more about the landscapes in which organisms search, experiments risk being arbitrary and the connection between experimental findings and search behavior in natural systems is liable to be loose. Recently, some important progress has been made toward characterizing

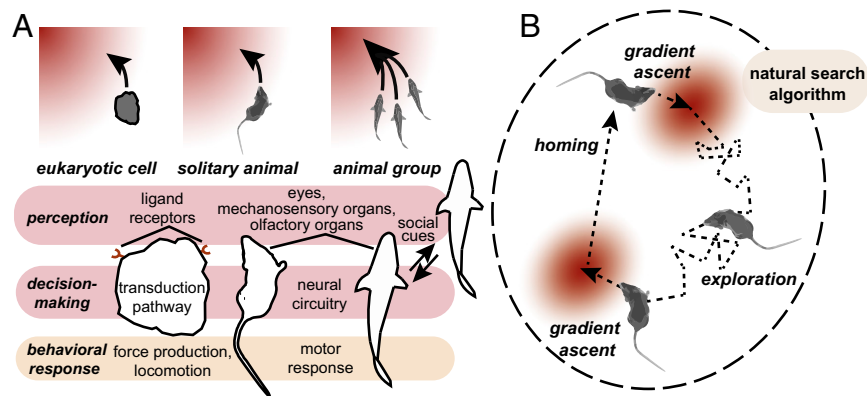


Fig. 2. Spatial gradient climbing, behavioral modules, and natural search algorithms. (A) Single cells, solitary animals, and animal groups are capable of measuring and responding to spatial gradients in the environment. These responses involve measuring a signal (e.g., chemical concentration, light), processing multiple measurements to calculate a spatial differential in signal strength or timing, and responding by altering locomotory behavior to ascend or descend the gradient. (B) At larger scales, organisms combine responses to spatial gradients with other behavioral modules [e.g., periods of exploration, memory-based homing to known locations (21, 22)] to generate flexible sequences of search behavior. We define this set of modules and the rules a searcher uses to transition between them as a natural search algorithm. By developing mathematical descriptions of natural search algorithms, search behavior can be studied using the mathematical tools applied to analyze engineered search algorithms.

the physical and chemical environment that marine microbes experience in the ocean (17), the flow environment that influences search decisions of planktonic predators (33), and the physical structure and chemical composition of the odor plumes to which moths and other olfactory searchers respond (5, 10, 11, 34, 35). These studies notwithstanding, we have little quantitative information about the structure and spatiotemporal dynamics of the environments in which most organisms search, largely because of the difficulty of quantifying spatially and temporally varying cues in natural settings.

Mapping the structure of the search environment is particularly crucial in field studies of animal search behavior (36), where the processes that generate an animal's movement trajectory are difficult or impossible to infer without some knowledge of the

sensory cues the animal has access to as it makes movement decisions (37). Combining technologies for measuring the structure and dynamics of sensory cues, such as geographical information system (GIS)-based and computational modeling of water currents or winds (28, 38), acoustic methods for quantifying the locations of prey aggregations (39), and onboard sensors that measure real-time conditions at the animal's location (40), will dramatically increase what we can learn about search strategies using animal tracking data from the field.

Cross-disciplinary collaborations could further increase the value of field data by using direct measurements or simulations to characterize sensory cues in the field, and then recreating these sensory landscapes in the laboratory. This will not only help make experiments more realistic, but may also reveal how organisms

Box 1

Shared features of search: Sensing and climbing spatial gradients. Detecting and navigating using environmental gradients is a common feature of the strategies used by a wide range of searchers, from single cells to groups of social animals (Fig. 2A). The mechanisms through which organisms measure and respond to gradients are diverse, but the outcome of these processes—ascending or descending local signal gradients—is highly conserved. Eukaryotic cells detect chemical gradients by sensing concentration differentials across their length (45), and respond through a variety of motility mechanisms. Bacteria such as *E. coli* and *Vibrio* spp. are too small to directly perceive concentration gradients, but instead detect gradients by measuring changes in concentration over time as they swim and delaying reorientations when swimming in a favorable direction (23). Searching animals, including humans, use information from paired sensory organs (eyes, ears, nares, antennae) to detect differentials in the strength of signals or the timing of signal arrival (11, 100, 101), which they use to decide which way to turn in response to a signal gradient (19, 100). Groups of animals also respond to environmental gradients and do so in a coordinated fashion. Schools of minnows are capable of collectively descending and tracking dynamic light gradients, even amid considerable noise (20). Individuals within these schools respond not only to measurements of the environment, but also to social cues from nearby group members (Fig. 2A), allowing the group to act as a spatially distributed sensor that collectively “computes” the signal gradient (63, 102).

Although single cells, solitary animals, and animal groups all use spatial gradient sensing as a component of their search strategies, a quantitative framework for exploring these similarities is lacking. In examining similarities more deeply, it will be important to consider how gradient climbing fits into the broader set of rules that constitute an organism's search strategy (Fig. 2B). For example, mice use spatial gradients in scent concentration as well as exploratory movements to locate odor targets in novel environments, but over time, rely increasingly on learned information about the location of targets to navigate more efficiently (18). Bacteria combine random search with directed gradient climbing and rescale their responses by adapting to prevailing conditions, which increases the dynamic range of their search capabilities (42, 103). Developing a common mathematical formalism that can connect gradient climbing and other components of search strategies with the structure of real search environments will facilitate more rigorous comparisons between microbes, animals, and animal groups, and help uncover shared features.

distinguish relevant environmental signals from irrelevant ones. For example, when approaching flowers from short distances, moths in the wild encounter filaments of high odor concentration that arrive at time intervals within a relatively narrow frequency range (10). In wind-tunnel experiments with moths, odors that are pulsed in this natural frequency range cause strong firing responses in central olfactory neurons, and elicit stereotyped search behavior, whereas odors outside this range elicit weak responses at both the neural and behavioral levels. At greater distances from an odor source, pulses of odor are far more intermittent, yet moths and other insects are still able to distinguish relevant olfactory cues from noise and to use these cues to navigate (5). The neural mechanisms that underpin this long-range response to odors are still poorly understood, but quantitative characterization of odor landscapes has provided crucial clues (5, 11).

Another advantage of quantitatively characterizing natural search environments is that doing so may help answer long-standing questions about the features of sensory systems. Many chemosensory organs are exquisitely sensitive to variations in chemical concentration. *Dictyostelium* cells can detect concentration gradients amounting to differences in the occupancy of only five chemoattractant receptors between the up-gradient and down-gradient sides of the cell (41). Silkworms detect and respond to as few as 170 molecules of sex pheromone by temporally integrating subthreshold activity of olfactory receptor neurons (8). Sensitivity often comes at the cost of susceptibility to noise, raising the question of what kinds of environmental conditions could have selected for such extreme sensitivity. Some species cope with the sensitivity–susceptibility trade-off by rescaling their responses to stimuli via adaptation, allowing them to respond to cues across a wide dynamic range; bacteria, for example, retain high sensitivity to chemical gradients over several orders-of-magnitude in chemical concentration (42). However, this too comes at a cost. Rescaling their response to gradients by overall chemical concentration means that bacteria respond to high- and low-concentration sources in the same way, an outcome that may or may not be desirable depending on the environmental and ecological context in which these species search (42) (see also ref. 32 for further discussion of the drawbacks of sensory adaptation). Quantitatively studying the signal and noise landscapes that searching organisms navigate (43) may help us understand why evolution has selected for sensory systems that both adapt and, in some cases, operate close to the physical limits of sensitivity (44, 45).

Convergent Evolution and Shared Features of Effective Search Strategies. One might expect to find convergent search strategies across a diverse array of biological systems if some general features distinguish good search strategies from poor ones. Several studies have proposed statistical properties that could serve this role. One hypothesis posits that searchers can achieve robust search performance by using a strategy that is “maximally informative” (46), in the sense that the searcher makes decisions that maximize the rate at which it reduces uncertainty about the location of its target (4). Maximizing the rate of information gain would appear to require fairly sophisticated neural or biochemical machinery; however, at least in simple environments, a heuristic that approximates a maximally informative search can be implemented by a decision circuit containing a surprisingly small number of components (46). Recent research efforts have begun to explore whether search strategies and behavioral circuits can be understood in more general terms by

studying how they affect information acquisition from the environment (31, 47).

A second feature that may prove to be shared among search strategies is risk-aversion. For example, the chemotactic search algorithm used by *E. coli* does not maximize the rate at which cells reach local hotspots of high chemical concentration, but instead maximizes the minimum chemical concentration the cell will experience over a wide range of possible environmental conditions (48). Similarly, it has been argued that some animal foraging strategies do not maximize the rate of resource acquisition, but instead ensure that the animal acquires a minimum required quantity of resources (often called “satisficing”) (49). Such strategies serve to minimize the risk of bad outcomes in uncertain environments, often at the cost of underperforming when the environment is favorable. Whether a strategy appears risky or risk-averse, however, may depend on how risk is measured. For example, in the ocean, male copepods search for mates by adopting a swimming pattern that makes them conspicuous to predators (50). This strategy may lower the risk of not finding a mate but it increases the risk of predation.

Determining whether different kinds of organisms use strategies that maximize the rate of information gain, minimize risk, or involve other shared properties requires formal methods of comparison. By studying search behavior through an algorithmic lens, we can begin to apply existing frameworks from the rich field of engineered search algorithms to better understand the features of search strategies in nature. Mathematical tools from reinforcement learning (51), information theory (47), and operations research (52) are commonly used to design and evaluate engineered search algorithms, but they may also provide a way of making quantitative comparisons between natural search algorithms. To take advantage of these tools, we propose a systematic approach (Fig. 3), in which field and laboratory studies of model organisms are used to identify the salient features of natural search environments and constraints on sensing and decision-making in real biological systems. These features can then be mapped onto an appropriate algorithmic framework for modeling search behavior and for comparing the search strategies of different kinds of organisms (Fig. 3).

A particularly promising mathematical tool, often used in operations research, is the multiarmed bandit framework (MAB) (53). This framework models a sequence of actions taken by a decision-maker or set of decision-makers, in this case the searchers. Each action yields a reward and the success of different decision-making strategies can be compared over time. The term “bandit” is an analogy to a slot machine, and the “arms” refer to the set of choices the decision maker has available to it. This framework is powerful because it allows one to compare search strategies to one another and to theoretical performance bounds (54, 55). MAB models are among the simplest models of decision-making that capture the essential challenges associated with making choices amid uncertainty about the state of the environment; however, a crucial feature of the MAB framework is that it can be extended to include important physical and neural constraints on the search capabilities of real organisms (e.g., limited memory, limited perception of space, and so forth). For example, this framework has recently been extended to accommodate spatial constraints on the choices an individual can make, and transition costs incurred when moving from one choice to another, key characteristics of search problems in spatial landscapes (56), where moving costs energy (57) and can expose a searcher to predation risk (29). Mapping natural search algorithms onto the MAB framework would

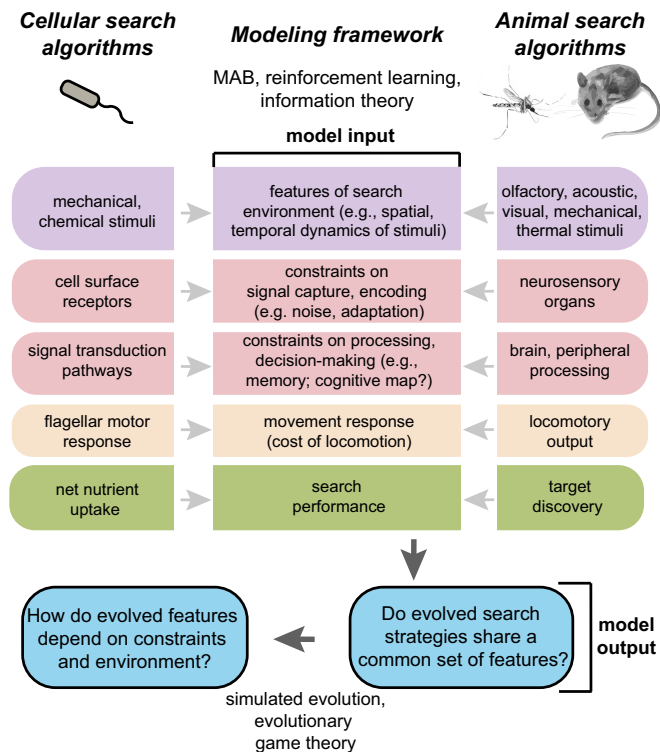


Fig. 3. Combining models and data to study shared features and evolution of natural search algorithms. Quantitative information from laboratory and field studies of model organisms can be combined to determine the essential features and constraints that are common to search problems faced by different kinds of organisms. These features are then used to select a modeling framework (e.g., MAB) and to build a model that retains the essential features of the search problem. The model can then be used to understand sensitivity to differences in biophysical, physiological and environmental constraints across systems, and to operationally define shared features. Tools from evolutionary theory can be used to identify the selective pressures that lead to convergent or divergent search strategies.

constitute a major step toward a quantitative understanding of the similarities and differences between search strategies. Recent studies of the neural and biophysical mechanisms involved in search behavior (6, 7, 9, 10, 46, 58) provide the quantitative information needed to define such models in a way that respects the constraints on search strategies in real biological systems.

To better understand how evolution shapes search strategies over the long term, modeling approaches like MAB models can be combined with tools, such as game theory (48, 52, 59–61) and simulated evolution (30, 62, 63) (Fig. 3). The most complex of such models combine behavioral simulations of entire populations of heterogeneous individuals with computational evolution of populations of searchers over time (30, 62, 63). Such models are extremely flexible and allow one to include detailed knowledge of environmental structure, biophysics and neuroscience of sensing, decision-making, and motility specific to particular model systems. This flexibility may come at the cost of generalizability, but simpler approaches from evolutionary game theory can help distill the results of detailed computational models into a form that can be more readily applied to other systems (64).

To realize the connection between experimental studies of search behavior and the theoretical tools described above,

collaborations between behaviorists, neuroscientists, and ecological and evolutionary modelers are needed. Many organisms studied in the laboratory readily execute search behaviors and research groups are already using techniques like computer vision, virtual reality, microfabricated landscapes, and optogenetics to measure and manipulate search behavior and to link sensory input to behavioral output (8, 65–67). The high-resolution data such studies generate provide the kind of information needed to build and parameterize mathematical models of search strategies. Theoreticians and experimentalists could benefit by working together to develop and test such models. In addition to revealing underlying similarities and differences among search strategies, models that are carefully linked to experimental systems could identify steps in the search process that strongly influence performance, but are poorly studied experimentally. More generally, the approach described in Fig. 3 may help reveal the broader biological relevance of search behaviors identified in individual model systems. An active feedback between mathematical models and data will be crucial if we are to understand, at a more fundamental level, how evolutionary forces structure the search strategies in the world around us.

Search Strategies and the Pace of Ecological Interactions

The fact that search behavior is ubiquitous in biological systems and that organisms appear exquisitely adapted to finding their targets leads us to our second question: To what extent do search behaviors affect the rates of ecological interactions that underpin the functioning of ecological systems? Examples of ecological interaction rates are the rate at which male and female copepods encounter one another in the turbulent sea (50), the rates at which marine bacteria find and attach to nutrient particles (68), or the rate at which foraging seabirds locate prey aggregations (28). How do the search behaviors of anchovy schools influence the rate at which these species locate and consume their prey (39)? How do the search strategies of neutrophils and T cells influence the overall rate at which the immune system can suppress infections?

The answers to these questions could change the way we model the dynamics of biological systems. This is because sensory-mediated search behavior is largely absent from population dynamic theory, the theory typically used to describe the dynamics of populations of organisms or cells. Ecologists have long appreciated that natural environments are dominated by patchiness (69), and that the way organisms respond to this patchiness can influence the pace and outcome of ecological interactions (70). However, a historical lack of quantitative information about search behavior has made it challenging to incorporate these responses into ecological models. With the increasing availability of tracking data from animals in the wild (36, 71) and from carefully designed laboratory experiments (67, 72), and growing knowledge of the search behaviors of a widening range of organisms, it may soon be possible to formulate models of ecological interaction rates in a way that incorporates active search. The challenge will be finding a tractable means of moving from individual-based descriptions of how organisms search their environments, to macroscopic descriptions of the rates of interactions among populations of organisms.

Search and Ecological Dynamics: Model Systems as a Way Forward

Several recent theoretical studies have developed models of ecological interaction rates in ways that explicitly consider how

organisms use sensory cues to modify search behavior (57, 73–75). Results of these studies demonstrate that active search behavior can both qualitatively and quantitatively change the population dynamics of consumers and resources, and affect the outcome of competition between searchers and nonsearchers. For example, Hein and McKinley (74) developed a simple model of search decision-making, which showed that when consumers search for resources using sensory cues, consumer-resource encounter rates can diverge strongly from the mass-action kinetics assumed in most models of consumer–resource interactions. This departure from mass action qualitatively alters the dynamics of consumer and resource populations. Such models provide starting points for future theoretical investigations; however, attempts to understand whether and how search behavior influences ecological dynamics will be most effective if new ecological theory can be tied to model systems in which search behavior and its effect on ecological dynamics can be measured directly. A promising model system involves marine bacteria, because of their large numbers and the relative simplicity of quantifying their search behaviors (76).

Microscopic marine autotrophs are responsible for roughly one half of Earth's primary productivity, and much of this productivity becomes available to the rest of the marine food web only after being consumed by bacteria and other microorganisms (77). Understanding the processes whereby microorganisms locate, consume, and convert primary productivity to energy and matter that fuel marine food webs is, therefore, a high priority. Like most ecological models, many oceanographic models rest on the assumption that microbes passively encounter dissolved organic matter (DOM) and that DOM is distributed homogeneously throughout the water (77). However, even at very small scales, localized DOM releases, augmented by turbulence, can create ephemeral resource hotspots that are separated by voids where resources are scarce or absent (17, 78). Many microorganisms exploit this heterogeneity by using chemotactic search to actively seek out hotspots and, in doing so, consume resources at rates that are far higher than would be expected in the absence of active search (57, 76, 79, 80). Estimates as well as measurements of the importance of chemotactic search for lysing phytoplankton cells, marine particles, and the plumes of DOM that leak from them as they sink, suggest that chemotactic behavior may enhance bacterial reproductive rates by several fold (76, 78, 81). For example, during phytoplankton blooms, bacterial species that are capable of chemotactic search can capitalize on localized nutrient pulses to generate threefold greater biomass than competing populations of bacteria that do not perform chemotaxis (76).

Patchiness in nutrient environments can also facilitate the coexistence of bacteria that use different search strategies. Two very closely related populations of *Vibrio cyclitrophicus*, specializing in particle colonization by biofilm formation and particle exploitation by chemotaxis, respectively, are able to coexist through a "competition-dispersal" trade-off (68). These and other findings (e.g., refs. 57 and 80) suggest that by incorporating active microbial search behavior into models of marine microbial ecology, we may be able to understand ecological interactions and ecosystem processes in the microbial ocean at a much deeper level. Moreover, these findings illustrate that concepts that are familiar in theoretical ecology (70), such as trade-offs between competitive dominance and the ability to locate new resources quickly, emerge in dynamic, patchy ecosystems through the interplay of environmental heterogeneity and active search behavior.

Studies of chemotactic search in marine microbial systems provide a blueprint for how search behavior might be incorporated into models of other ecological systems. Several factors have made this synthesis possible. First, researchers have begun to develop a quantitative understanding of the resource landscape in which marine microbes search (particles, plumes, lysis events), the biochemical properties of targets (DOM hotspots), and the physical processes (molecular diffusion, particle sinking, turbulence) that influence how that distribution changes over time (17, 82). Second, researchers have built upon the long history of studies of the mechanisms behind *E. coli* chemotaxis (23) by using microfluidics, video microscopy, and automated tracking tools to refine our understanding of the search behavior of *E. coli* and extend it to other microorganisms in controlled microenvironments. Direct visualization of microbial motility under highly controlled physical (e.g., presence of surfaces, fluid flows) and chemical (e.g., nutrient particles, steady gradients, diffusing resources) conditions has yielded quantitative information about microbial movement and search strategies across a broad range of environmental conditions (67, 83, 84). Third, early individual-based models have described the behavioral modules involved in bacterial chemotaxis in mathematical terms (85, 86), which has allowed researchers to estimate behavioral parameters from data and simulate search behavior of entire populations. Combining these models with high-performance computational tools (57, 87) has provided a way to connect the search behavior of individual bacteria with population dynamics. This, in turn, is leading toward the kinds of scalable mathematical models that can answer questions about how chemotactic search affects ecosystem processes at much larger scales (76, 82).

Similar synthesis may soon be possible in other systems. For example, researchers have started to develop a quantitative understanding of the sensory cues and search strategies used by insect vectors of human disease (66) and foraging marine predators (28, 38) alongside the processes that generate relevant sensory cues in the environments where these species live (34, 38, 88). Using this knowledge to develop new ecological models will likely improve our understanding of system-level phenomena, such as rates of nutrient cycling in the oceans (76, 89), disease outbreaks from environmental reservoirs (90), and the outcome of interactions between invading pathogens and our own immune systems (91), all of which involve enormous numbers of ecological interactions between searchers and their targets.

Conclusions and Prospects

We have focused on emerging connections between the biophysical and neural basis of natural search algorithms and the ecological and evolutionary processes that both shape and are shaped by them. The topics we have covered connect deeply with central questions in the study of behavior, evolution, and ecology: for example, the question of how organisms decide whether to explore or exploit their environments (92); how organisms make decisions with limited information (93, 94); how the social context in which foraging decisions are made can shape the evolution of decision-making strategies (61, 95, 96); how and why motility has evolved so often throughout evolution (97, 98); and how environmental patchiness and behavioral responses to that patchiness can affect the rates and outcome of ecological interactions (69, 70). Knowledge of the proximate mechanisms that organisms use to capture and integrate sensory information will help address these and other fundamental ecological and evolutionary

questions. The flow of ideas can and has also moved in the opposite direction; understanding the selective pressures imposed by the need to search effectively and the physical properties of search environments can help to reveal the function of neural and biophysical structures (e.g., bursting olfactory receptor neurons) (11, 58), and may also help explain the striking sensitivity of many sensory organs (8, 45, 99). Progress in these and other areas will benefit from a more formal integration of studies of sensory biology and decision-making, the physics and ecology of search environments, and the evolution of search strategies by natural selection. By combining these approaches, we may find a path

toward realizing one of the emblematic goals of systems biology: linking the molecular workings of sensory and decision-making systems to the processes that drive populations, communities, and perhaps even ecosystems.

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