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### **Optimal Foraging Theory: An Introduction**

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#### Abstract

Optimal Foraging Theory (OFT) uses techniques of mathematical optimization to make predictions about foraging behavior which is a fundamental aspect of animal behavior. As it has just turned 50, it is timely to review its foundations, what it has achieved and where it is headed.

As an introduction to OFT, I discuss the classic model of patch exploitation, developed by Eric Charnov in 1973, which considers how long a forager should spend exploiting a patch before it moves to a fresh one. A graphical and mathematical approach to this problem led to predictions that were supported by early empirical studies, thus fueling enthusiasm for the optimality approach to understanding animal foraging behavior. OFT, from the outset, also considered foraging decisions regarding patch choice, diet and movements.

OFT views foraging behavior as the outcomes of a set of decisions, made continuously, assumes fundamentally that animal foraging decision-making has evolved to the point that biological fitness (i.e., ability to contribute to the next generation) of an individual forager has been maximized, and seeks to understand such decision-making by matching predicted and observed behavior as closely as possible. OFT must therefore be based on models that mathematically describe the foraging processes involved.

Because biological fitness is difficult to measure directly, it is generally necessary to adopt a surrogate 'currency' and to find the behavior that maximizes it. Examples include the net rate of energy intake and the likelihood of meeting total energy requirements during available foraging time.

The classic OFT models have been expanded and extended in many ways. Expansions have included allowing for lack of perfect information, the risk of becoming someone else's meal, and for decisions to vary with changes in an animal's state. Extensions have occurred where OFT models have been incorporated into studies of related biological phenomena that involve foraging, such as population dynamics, food webs, and co-evolutionary relationships between nectar-feeding animals and the plants they visit.

OFT has also been applied to areas outside the realm of animal feeding behavior and acted as inspiration for solving various optimization problems in human technology.

Through all of this OFT has grown enormously and been successful in terms of qualitative predictions, but less so quantitatively. It has demonstrated its usefulness and emerged as a strong theory of behavior and ecology

#### Keywords

Diet; Expansion; Extension; Game theory; Movements; Optimal foraging theory; Patch choice; Patch departure

#### Introduction

Optimal Foraging Theory (OFT) is an approach to the study of foraging behavior that uses the techniques of mathematical optimization to make predictions about this critical aspect of animal behavior (Pyke, 2010). Foraging, which is the process by which animals obtain food, is a fundamental activity for animals, as they require food to sustain their metabolism, provide energy for a wide range of activities, and support reproduction. In some situations, foraging occupies a high proportion of available time, and since animals often cannot do two things at once, increasing the time spent on foraging may reduce the time available for other activities such as mating, resource defense, and predator avoidance.

OFT began with consideration of four aspects of foraging: diet, patch choice, patch exploitation, and movement (Pyke *et al.*, 1977; Pyke, 1984; Stephens and Krebs, 1986). It was early recognized that a foraging animal will generally encounter different kinds of food items and must decide whether to consume each encountered item or continue on to the next (Emlen, 1966; MacArthur and Pianka, 1966). It was also recognized that food is generally distributed in patches, rather than uniformly, which means that a forager must decide which food patches to visit (MacArthur and Pianka, 1966) and when to leave its present food patch and move to another (Krebs *et al.*, 1974; Charnov, 1976). It was similarly recognized that when a foraging animal decides to move on from its present location, it must decide on direction, speed and possibly target destination, thus resulting in different patterns of movement while foraging (Siniff and Jessen, 1969; Cody, 1971).

As OFT has just turned 50 years of age, it is timely to review its foundations, what it has achieved, and where it is headed. This approach to understanding the foraging behavior of animals began in 1966 with the above-mentioned published articles by Mac-Arthur and Pianka (1966) and Emlen (1966), and has therefore had considerable time to grow and develop. As foraging often mirrors other kinds of search behavior, there is much scope for comparable development of approaches across different kinds of

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search behavior. As foraging is integral to interactions between animal populations and their resources and to interactions between different species, a theoretical approach to animal foraging behavior such as OFT may also contribute to other areas of biology such as co-evolution, population dynamics and community structure.

As an introduction to Optimal Foraging Theory, I shall begin with a discussion of what is now considered the classic model of patch exploitation.

#### **Optimal Foraging: The Classic Model of Patch Exploitation**

One of the classical problems of foraging theory is how long a forager should spend exploiting a patch before it moves to a fresh one, a foraging situation presented and modelled by Charnov in 1973 (Krebs *et al.*, 1974; Charnov, 1976). Consider, for example, a hummingbird drinking nectar from flowers. When our hummingbird arrives at a fresh flower it obtains nectar quickly, but as it spends more time the nectar becomes harder to obtain because the hummingbird has depleted the supply. Most food patches work this way; fresh patches provide food quickly, but the rate of intake declines as the forager depletes the patch. This simple observation presents a foraging problem, because it takes time and energy to move to a fresh patch. However, the rate of food gain will eventually decline to the point that it is better for the forager to seek a new patch than remain where it is. How a forager decides when it has reached this threshold point is the fundamental issue in this foraging problem.

A simple graphical approach illustrates this foraging problem and how it may be solved (see also Charnov, 1976). Fig. 1 shows the idea of patch depletion such that the amount of energy e extracted from the patch increases with the time t an animal spends in the patch (i.e., e=e[t]), but the instantaneous rate of energy gain (given by the slope of this function) declines steadily; so this *gain function* e[t] increases but bends down. Now, it takes *T* units of time for the animal to travel from one patch to another, which is indicated by a distance of -T along the x-axis (which is the time axis). Then the overall rate of energy gain for the forager would simply be the energy gained per patch divided by total time per patch, which is the sum of time spent at each patch and time taken to move to the next patch. In other words, this rate is e[t]/(T+t), which is the slope of the line that connects the point -*T* on the *x*-axis to the point (*t*, e[t]) on the gain function.

The classic patch model finds the optimal patch time, *t*, which gives the highest rate of energy intake. Of course, this approach assumes that rates of energy expenditure are no different for times spent at a patch and moving between patches, as then the net rate of energy gain, which may be more important to a forager than its gross rate of gain, is simply the gross rate of gain (i.e., gain function in Fig. 1) minus a constant. However, the good news is that relaxing this assumption does not affect the general qualitative conclusions that arise from the model and are explained below.

From the simple graphical approach illustrated in Fig. 1, it can be seen that there is an 'optimal patch time', such that the rate [t]/(T+t) is maximized, when the above-mentioned line (between -T on the x-axis and the point (t, e[t]) on the gain function) is tangent to this function. If you imagine increasing t along the x-axis in Fig. 1, such that the point (t, e[t]) moves along the gain function, the slope of this line, which is the rate e[t]/(T+t), will increase up to maximum when the line is tangent to the gain function, and then decline.

One prediction that arises from this graphical model is that foragers should stay longer within patches when it takes longer to travel to fresh patches. Compare, for example, topt1 and topt2, which correspond to short (*T*) and long (4*T*) travel times respectively in Fig. 1. As seen in this figure, topt1 is less than topt2, which indicates generally that topt will increase as T increases, all else remaining constant.



Fig. 1 Graphical representation of optimal departure rule.

Another prediction from the model is that, with increasing overall habitat quality, as measured by greater average patch quality (i.e., steeper gain function e[t]), foragers should spend less time per patch. To see this, just imagine counter-clockwise rotation, about the origin, of the gain function in Fig. 1. The tangent to this curve will likewise rotate such that the optimum time per patch decreases but the forager achieves a higher rate of energy gain.

Early empirical studies supported these predictions both qualitatively and quantitatively, thus fueling enthusiasm for the optimality approach to understanding animal foraging behavior (Pyke *et al.*, 1977). For example, researchers working together at Oxford University observed the foraging behavior of birds in aviaries set up with artificial food patches (Krebs *et al.*, 1974; Cowie, 1977). They found that time spent per patch decreased as habitat quality increased (Krebs *et al.*, 1974) and increased with increasing travel time between patches (Cowie, 1977), in both cases providing qualitative agreement with expectations. In addition, observed average times per patch agreed well with predicted times when allowance was made for different rates of energy expenditure for foraging at patches and moving between patches, and net rather than gross rate of energy intake was considered (Cowie, 1977).

The theoretical and empirical results of patch exploitation are further reviewed elsewhere in this encyclopedia.

The classic model of patch exploitation outlined above illustrates the following general issues in relation to animal foraging and the optimality approach to understanding its many facets.

#### **Optimal Foraging Theory: The Basic Foundations**

We can view foraging behavior as the outcomes of a set of decisions, made continuously. As described earlier, an animal can decide whether to stay in a patch or leave it. Foraging animals make many other types of decisions, of course. For example, they decide what types of food to eat, where and when to search for food, and how to move between locations. Such decisions are made continuously, as a foraging animal can always stop what it is doing and do something else. These decisions result in the foraging behavior that we observe.

OFT seeks to understand such decision-making by foraging animals by matching predicted and observed behavior as closely as possible, ideally in quantitative rather than qualitative terms (Sih and Christensen, 2001). We might, for example, assume that an animal can determine its average energy yields and its handling times associated with consuming various potential food types when encountered, as well as the average time it spends between successive food items (Pulliam, 1974; Carrillo *et al.*, 2007). Then, based on our own measurements of these variables, we could predict which food types a forager should include in its diet (Pulliam, 1980; Carrillo *et al.*, 2007). This would amount to a quantitative prediction that could be compared with the observed diet (Pulliam, 1980; Carrillo *et al.*, 2007). On the other hand, we might settle for a qualitative prediction, such as that a forager's diet should expand with decreasing overall food abundance. In general, the extent to which our observations match our predictions would indicate how well we understand the forager's dietary decisions.

OFT assumes fundamentally that animal foraging decision-making has evolved to the point that the biological fitness (i.e., ability to contribute to the next generation) of an individual forager associated with its foraging behavior has been maximized. In this sense, foraging behavior may be considered to have been optimized, and it is appropriate to describe such behavior as being 'optimal'. Of course, it is always possible that evolution has been proceeding in the direction of increasing biological fitness but maximal fitness has not yet been reached, an issue that I shall return to later. For now, however, let us assume that time has been sufficient for biological fitness to be maximized, and then we can use the mathematical machinery of optimization to critically formulate our predictions about foraging behavior.

To apply this logic, OFT must be based on foraging models that mathematically describe the foraging processes involved. In the patch model described earlier, for example, we explicitly imagined a foraging animal moving from one food patch to another and spending time collecting food within each patch. At the same time, we implicitly assumed that food patches are recognizably distinct from one another and that a forager does not re-cross its path as it moves between patches. We could then express the outcome of the foraging process as a simple mathematical function of its ingredients, namely the energy gain function, time spent per patch and travel time between patches, with differences between activities in energetic costs being easily incorporated as well. As I shall discuss below, it is possible to modify the assumptions of this model.

It is also necessary, as part of the foraging model, to assume that certain behavioral variables are subject to choice and decision on the part of a foraging animal, as these variables will determine the foraging outcomes. In the case of patch exploitation, described earlier, the forager is assumed able to choose its patch residence time, upon which will depend the rate (net or gross) of energy intake.

The next step in the process is to determine, or assume, how variation in foraging outcome affects biological or evolutionary fitness. Ideally, in our patch exploitation example, we would find the fitness, measured in terms of offspring production, associated with a given rate of energy intake and hence be able to relate the fitness of an individual forager directly to its patch residence time. Determining the patch residence time that maximized fitness would then be a straightforward exercise.

However, it is generally difficult in practice to measure the relationship between the biological fitness of an individual forager and either the outcomes of its foraging or the underlying behavioral variable that affects foraging outcomes. It is hard, for example, to imagine or implement an experiment in which patch residence time is artificially varied and fitness consequences determined. On the other hand, it may sometimes be possible to vary an animal's diet and see how this affects its survival, growth, development and reproduction (Wacker and Baur, 2004; Cook *et al.*, 2012; Videla *et al.*, 2012), all components of its biological fitness.

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It is therefore necessary, in general, to adopt a surrogate 'currency' as a proxy for biological fitness and to find the behavior that maximizes this currency. We did this, in the example of patch exploitation, by assuming (implicitly at the time!) that the appropriate currency is net rate of energy intake. The adoption of such a currency simplifies things considerably and allows one to estimate the optimal, and hence predicted, foraging behavior.

Net rate of energy intake has been frequently adopted as currency for fitness of a foraging animal (Pyke, 2010), but it makes reasonable sense in some situations and probably little or no sense in others. It would seem quite reasonable for nectar-feeding animals that are foraging for floral nectar, which is essentially just an energy source, while doing little or nothing else at the same time and not subject to other factors such as becoming someone else's meal. However, it would be much less reasonable for animals that forage on foods that differ in nutritional content, and may even contain toxins, or that are subject to varying levels of predation, depending on where, when and how they forage. Some researchers have therefore adopted nutrient combinations as foraging currencies (Schaefer *et al.*, 2003; Jensen *et al.*, 2012) or included predation risk in the currency (Kotler *et al.*, 2016).

It is also possible that the important thing to a foraging animal is not the rate of intake of energy or some other nutrient, but rather the amount collected in available time, in which case the forager might benefit by minimizing the probability of suffering a shortfall in this amount. It is possible, for example, that an individual forager's fitness might hinge simply on whether or not it survives a period, such as night or winter, when it is unable to forage, and hence it should seek to ensure that it obtains sufficient food to survive this period (Carmel and Ben-Haim, 2005; Nolet *et al.*, 2006). A model that incorporates minimization of the likelihood of starvation may lead to different predictions from one based on rate maximization (Carmel and Ben-Haim, 2005; Nolet *et al.*, 2006).

#### **Beyond the Classic Foraging Models**

Optimal foraging models can and do take many forms, but the classic models are important as starting points. Models can differ in the behavioral decision they consider (e.g., patch use, prey choice, movement), and they differ in how they model the environment (e.g., sequential encounter with resources vs. simultaneous encounter) and in which currency they maximize (e.g., rate of net energy intake vs. probability of survival). Notwithstanding this diversity, we recognize a classic set of foraging models, as illustrated by the patch exploitation model discussed in some detail above, that are important because they serve as starting points for further development.

Investigators have expanded and improved the classical models in many ways. For example, a fairly large family of models considers tradeoffs between foraging and other aspects of behavior. The best location for foraging might, for example, be the worst location in terms of the risk of predation. Tradeoffs between foraging and predation risk have been the focus of many recent theoretical and empirical studies (Brown and Kotler, 2007). Also, some studies have considered situations where foraging animals encounter potential food items simultaneously, rather than sequentially (Lima *et al.*, 2003), as was assumed in early models of optimum diet.

The classical models also assume that the forager's behavior is tuned to environmental conditions as if it has perfect information about the properties of the environment such as patch quality, prey quality or encounter rates. Realistically, however, variables like these will often change, and a forager will need to adjust its behavior in response to these changes. Several models have considered the problems of 'incompletely informed foragers' (Klaassen *et al.*, 2006; Berger-Tal and Avgar, 2012). Commonly, these models make assumptions about how the environment varies, and consider how experience and information acquisition should influence foraging decisions (Klaassen *et al.*, 2006; Berger-Tal and Avgar, 2012). This approach, therefore, provides an important bridge to other aspects of animal behavior such as learning, cognition, and decision making.

Another important trend is the development of so-called dynamic foraging models. In the classical models, we imagine that the animal adopts, for example, a fixed patch residence time that represents the single best choice. Dynamic optimization models suppose, instead, that the best patch residence might change as the animal's state (e.g., it's hunger or recent experience) changes (Ydenberg and Houston, 1986; Visser *et al.*, 1992). Instead of predicting a single optimal choice, dynamic models predict an optimal decision trajectory that predicts how decisions might change over the course of a day or some other period, and how this change covaries with a state-variable like hunger (Ydenberg and Houston, 1986).

Optimal foraging models have also been extended through incorporation into models of related biological phenomena that involve foraging. Population dynamics, for example, generally depends on the foraging success, or otherwise, of the individuals that make up a population. Interactions between species likewise depend on the foraging behavior of individuals as, for example, when individuals compete for access to the same food resource or members of one species consume those of another species. Models of population dynamics and species interactions should therefore include models of foraging by individuals (Genkai-Kato, 2007; Mougi and Nishimura, 2007).

Optimal foraging models can also help us to understand co-evolutionary relationships between species, such as those between nectar-feeding animals and the plants they visit, where the foraging behavior of an individual of one species affects both its own fitness and the fitness of individuals of another species. Such co-evolution is clearly indicated by 'pollination syndromes', where a trait for various nectar-feeding animal species, such as proboscis length, is correlated with a trait, such as corolla-length, associated with flowers on the plant species visited by each animal species. In this example, the foraging behavior of an animal affects both its fitness through foraging outcomes as well as the fitness of the plants through the process of transferring pollen between flowers. It

should therefore be possible to consider both optimal foraging and optimal plant traits, but surprisingly few studies have so far been carried out along these lines (Pyke, 2016).

Another fascinating development is the application of the optimal foraging approach to phenomena that involve searching but are outside the realm of animal feeding behavior. Engineers, economists, computer scientists, sociologists, anthropologists, archaeologists, psychologists, and many others have all adapted foraging models for their purposes, and assumed that search processes are, in some sense, 'optimal' (Rode *et al.*, 1999; Hanning *et al.*, 2010; Wells, 2012). Investigators have, for example, adapted foraging models to consider criminal behavior (e.g., areas with relatively high incidence of burglaries; bird poaching) (Johnson and Bowers, 2004; Pires and Clarke, 2011), military search strategies (Andrews *et al.*, 2007), and how human computer users distribute their time while searching within and among various web sites (e.g., online dating?) (Held *et al.*, 2012).

Optimal foraging models can also act as inspiration for solving human optimization processes. For example, imagining how social animals, such as ants, communicate information about foraging conditions and thus adjust their collective foraging behavior, has inspired the concept of 'swarm intelligence' which has been used in engineering and other applications (Saber, 2012; Tapkan *et al.*, 2012).

It is therefore hardly surprising that the classic set of foraging models has been replaced with a large and growing array of modified and extended models of animal foraging, and that such models have been used or acted as inspiration in a variety of other contexts. Such extensions, applications and inspirations of OFT are discussed in other articles in this encyclopedia.

#### **How Successful has OFT Been?**

OFT has clearly been reasonably successful in terms of qualitative predictions, but less so when observations have been compared with quantitative expectations. Many studies have, for example, supported the qualitative predictions arising from the above patch exploitation model that time spent per patch should increase with increasing travel time between patches and decrease with increasing average patch quality (Stephens and Krebs, 1986). However, quantitative comparisons between observed and expected residence times per patch have often found significant differences between them, with animal foragers typically spending more time in patches than predicted by the model (Nonacs, 2001).

The most common response to such quantitative failure of OFT has been to seek explanations in terms, for example, of model assumptions warranting revision. A foraging animal might, for example, optimally spend extra time in each patch if its risk of suffering predation were greater while moving between patches than while foraging within a patch (Nonacs, 2001). The original patch exploitation model could be modified to allow for this differential predation risk, leading to revised predictions and tests of them (Nonacs, 2001). This would be standard scientific practice.

Another response would be to consider any model modification as unacceptable post hoc rationalization, warranting abandonment of the optimal foraging approach (Pierce and Ollason, 1987). However, this conclusion would fail to acknowledge the overall qualitative success of OFT and the fact that marked improvement in agreement between observations and predictions has generally followed reasonable model revision. It would thus be unscientific.

#### **Growth and Prognosis**

The optimal foraging approach has grown enormously in terms of numbers of publications and continues to grow (see Fig. 2). Beginning in the mid-1960s, the annual number of publications considering foraging theory grew exponentially, especially during the late 1970s, and has continued to grow ever since. Unlike many other areas of research, OFT has not yet begun to show a decline in publication rate.

Optimal foraging theory has survived a number of criticisms and passed all the reasonable tests that one could apply to any theoretical approach. Some have criticized it for being on overly simplistic and unrealistic; but most significant conceptual paradigms develop iteratively, improving assumptions and refining models as new data comes to light. Some critics argue natural selection has not had enough time to optimize foraging behavior (discussed in Pyke, 2010). For others, the premise of optimization is valuable and justified, because behavior can evolve relatively rapidly, and because it has manifestly improved our understanding of animal foraging behavior. Other critics, as mentioned above, point to quantitative disagreements between expectations and observations and pronounce the theory dead or a 'waste of time' (Pierce and Ollason, 1987). In contrast, proponents point to consistent qualitative agreement and reasonable (but more modest) quantitative agreements with the theory. Investigators have used ideas from optimal foraging theory in several other areas of biology. Ecologists have, for example, used the theory to predict (1) how food density affects consumer behavior (via the so-called functional response) (Abrams, 1992), (2) population dynamics of foraging animals (Svanback and Bolnick, 2005; Mougi and Nishimura, 2007), and (3) species coexistence (Gleeson and Wilson, 1986; Krivan and Diehl, 2005). It has also had a major impact on the area of psychology through its involvement with issues such as learning, memory, and decision-making (Epstein, 1985; Hamblin and Giraldeau, 2009).

Optimal foraging theory has therefore demonstrated its usefulness and emerged as a strong theory of behavior and ecology (Marquet *et al.*, 2014).

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Fig. 2 Number of scientific articles relating to Optimal Foraging Theory published per year vs Year period.

See also: Cognition: Rational Choice Behavior: Definitions and Evidence. Evolution: The Importance of Animal Behavior for Charles Darwin and Other 19th Century Theorists.

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